Forest Bird Communities of the Hawaiian Islands: Their Dynamics, Ecology, and Conservation

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Studies in Avian Biology No. 9

A PUBLICATION OF THE COOPER ORNITHOLOGICAL SOCIETY

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Drawings of native birds by H. DOUGLAS PRATT

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Cover Photograph: **Iiwi (*Vestiaria coccinea*) perched on kolii (*Trematolobelia kauaiensis*) on Kauai, by David Boynton.**

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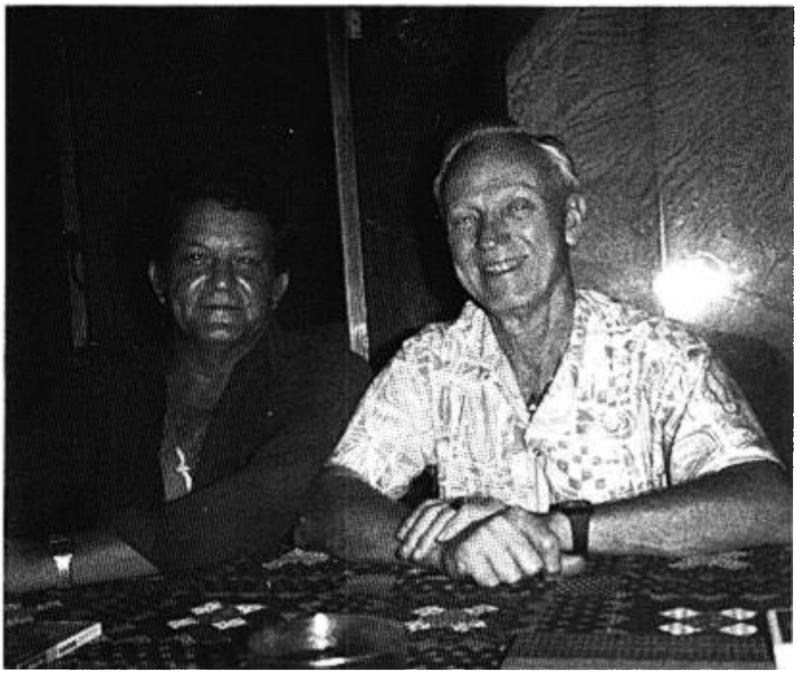

DEDICATION

We dedicate this book to all those who participated in the arduous and hazardous field work for these studies. A special debt is owed to Eugene Kridler (right), first U.S. Fish and Wildlife Service biologist stationed in the islands, who often went out on an administrative "limb" to support and encourage us, and to John L. Sincock (left), who spent many rain-drenched nights alone in the forest pioneering field techniques. Without the help, encouragement, and example of these two, the Hawaii Forest Bird Survey would still be a dream.

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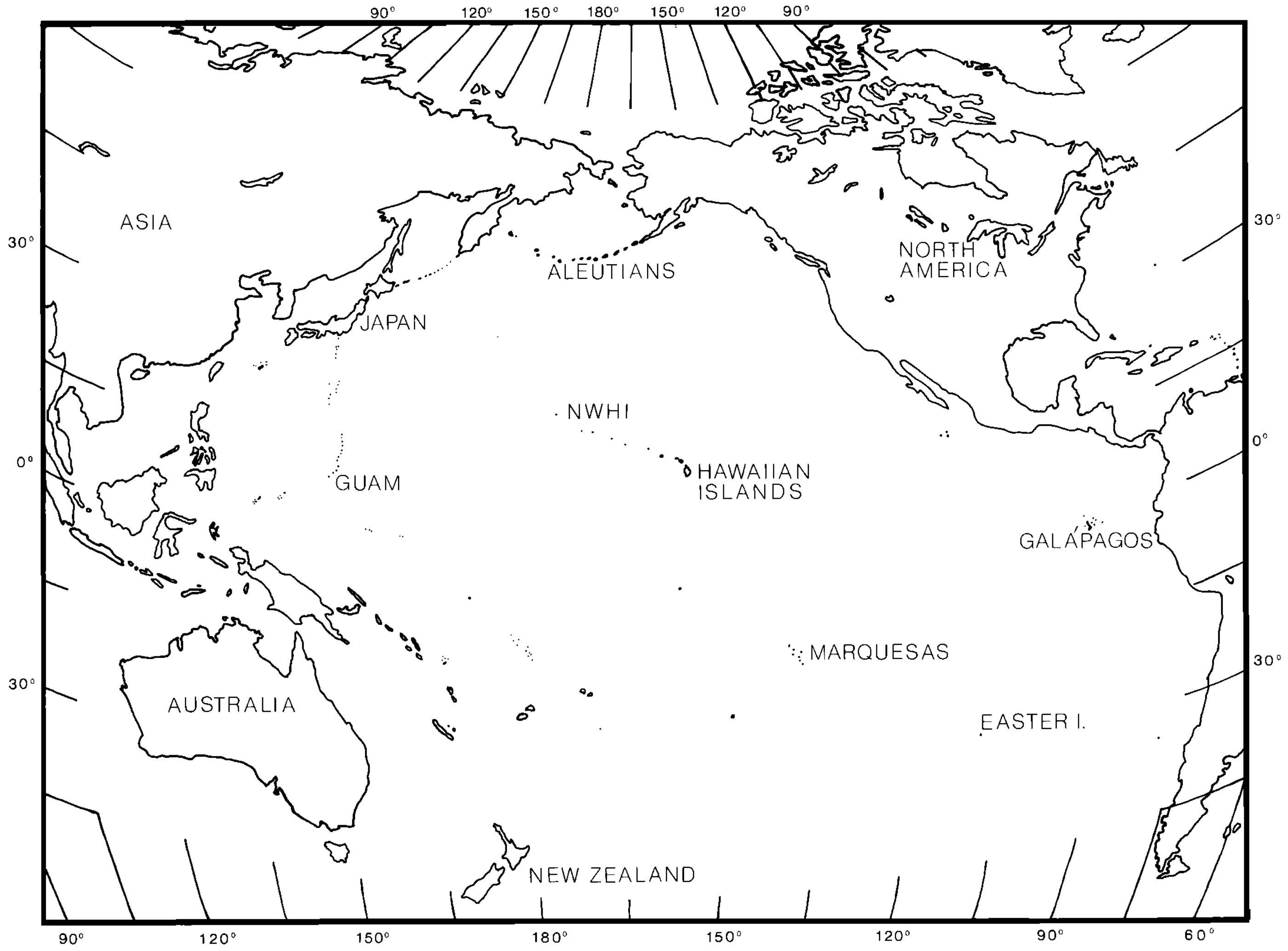


FIGURE 1. Map of the Hawaiian Archipelago showing nearest continents and high islands. (NWHI = Northwestern Hawaiian Islands)

INTRODUCTION

The Hawaiian Archipelago, located more than 4000 km from the nearest continent and 3000 km north of the Marquesas, the nearest high islands, is the world's most isolated group of islands (Fig. 1). As a result, the Hawaiian flora and fauna, derived from a relatively small number of colonists, have a high degree of endemism and are rather vulnerable to disturbance. Many groups, notably Hawaiian honeycreepers (Drepanidinae), lobeliads (Lobeliaceae), pomace flies (Drosophilidae), and land snails (Achatinellidae, Amastridae, and others), offer outstanding examples of adaptive radiation.

The stimulating evolutionary insights provided by Hawaiian plants and animals are tempered by the bleak prospects for their continued survival. The ecological consequences of their remarkable adaptation to the isolated Hawaiian environment have been severe. Native plants and animals have been ravaged by anthropogenic activity since Polynesians arrived ca. 400 A.D. (Kirch 1982). Recent fossil finds (Olson and James 1982a, 1982b) indicate that over 40 species of birds became extinct between Polynesian contact and the landing of Captain Cook in 1778, including an entire group of large, flightless geese, at least eight rails, and a constellation of lowland dry habitat passerines. In the 200 years since Western contact, an additional 20 species and subspecies of birds appear to have been extirpated, and 31 taxa have become endangered or threatened (Table 1; U.S. Fish and Wildlife Service 1983). The greatest concentration of endangered birds in the world occurs in the Hawaiian Islands; they represent 7% of the taxa on the International Council for Bird Preservation list (King 1978).

The reasons for these losses are numerous. With the Polynesians came the Polynesian rat (*Rattus exulans*), the pig (*Sus scrofa*), and the dog (*Canis familiaris*). Early Hawaiians probably hunted a large number of flightless birds to extinction and essentially eliminated lowland forests and woodlands by burning and clearing for agriculture (Barrau 1961, Kirch 1982). Subfossil bird bones interred with the charred shells of extinct land snails are the last remnants of these vanished ecosystems (Olson and James 1982b). The extinction rate drastically increased in many taxa following Western contact due to further habitat degradation by man and introduced ungulates (Perkins 1903, Berger 1981), disease (Warner 1968, van Riper et al. 1982), hunting (Munro 1944), competition from introduced birds and insects for food (Banko and Banko 1976, Berger 1981, Mountainspring and Scott 1985), predation by introduced mammals, particularly the cat (*Felis catus*), black and Norway rats (*Rattus rattus* and *R. norvegicus*), and the mongoose (*Herpestes auropunctatus*) (Perkins 1903, Atkinson 1977), and perhaps gene pool impoverishment due to reduced populations (Zimmerman 1948, Sincock et al. 1984). Inimical factors continue to threaten the endemic biota, and today entire communities are threatened with extinction. An air of urgency thus surrounds studies of the Hawaiian avifauna.

The study of the Hawaiian avifauna has spanned three phases. The first was a descriptive and exploratory phase that began with the Hawaiians who named the species they encountered. This phase intensified with the arrival of Cook in 1778. Eleven taxa of birds were described from specimens collected during Cook's visit to Hawaii and Kauai (Medway 1981). Collection and description of new species continued with the work of Bloxam, Townsend, and Deppe during the early 19th century (Wilson and Evans 1890–1899). Many new species were collected by Pickering and Peale (Peale 1848) during the Wilkes Expedition of 1838–1842. The first reliable listings of the birds of the Hawaiian Islands were by Dole (1869, 1879).

Ornithological interest in the islands increased dramatically in the second phase, beginning with the last two decades of the 19th century, when most taxa were described. The turn-of-the-century era significantly increased our understanding of the Hawaiian avifauna at a time when birds were apparently declining rapidly in numbers. Wilson made extensive collections during 1887–1888 and described the avifauna in his classic tome *Aves Hawaiienses: The Birds of the Sandwich Islands* (Wilson and Evans 1890–1899). Wilson's efforts were followed by the major collecting expeditions of Palmer in 1890–1892 and Perkins in 1892–1894 and 1895–1897. Relying on Palmer's collections, Baron Rothschild (1893–1900) produced three lavishly illustrated volumes entitled *The Avifauna of Laysan and the Neighbouring Islands* that covered the entire Hawaiian archipelago. Important studies and collections by Perkins on the systematics and natural history of the native land birds, insects, and molluscs culminated in the great *Fauna Hawaiiensis* (Sharp 1899–1913, Perkins 1903). During the early part of the 20th century, Henshaw (1902) and W. A. Bryan (1905, 1908; Bryan and Seale 1901) recorded many important observations on the natural history and distribution of Hawaiian forest birds. Following this productive era, a long period of relative dormancy en-

TABLE 1
STATUS AND DISTRIBUTION OF ENDEMIC HAWAIIAN BIRDS[a]

Taxa	Hawaii	Maui	Molokai	Lanai	Oahu	Kauai	NWHI
Dark-rumped Petrel (Uau)							
Pterodroma phaeopygia sandwichensis	EN	EN	EN	EN	EX	EN	...
Townsend's (Newell's) Shearwater (Ao)							
Puffinus auricularis newelli	TH	TH	TH	...	?	TH	...
Band-rumped Storm-petrel (Oeoe)							
Oceanodroma castro cryptoleuca	...	?	...	...	...	NE	...
Hawaiian Goose (Nene)							
Nesochen sandvicensis	EN	EN	...	...	...	...	...
Hawaiian Duck (Koloa)							
Anas wyvilliana	EN	EX	EX	...	EN	EN	...
Laysan Duck							
Anas laysanensis	...	...	...	...	...	...	EN
Hawaiian Hawk (Io)							
Buteo solitarius	EN	...	...	...	...	...	...
Hawaiian Rail (Moho)							
Porzana sandwichensis	EX	...	??	...	...	...	...
Laysan Rail							
Porzana palmeri	...	...	...	...	...	...	EX
Common Moorhen (Alae-ula)							
Gallinula chloropus sandvicensis	EX	EX	EN	...	EN	EN	...
American Coot (Alae-keokeo)							
Fulica americana alai	EN	EN	EN	...	EN	EN	...
Black-necked Stilt (Aeo)							
Himantopus mexicanus knudseni	EN	EN	EN	...	EN	EN	...
Short-eared Owl (Pueo)							
Asio flammeus sandwichensis	NE	NE	NE	NE	NE	NE	...
Hawaiian Crow (Alala)							
Corvus hawaiiensis	EN	...	...	...	...	...	...
Millerbird							
Acrocephalus familiaris familiaris	...	...	...	...	...	...	EN
Acrocephalus familiaris kingi	...	...	...	...	...	...	EN
Elepaio							
Chasiempis sandwichensis sandwichensis	NE	...	...	...	...	...	...
Chasiempis sandwichensis ridgwayi	NE	...	...	...	...	...	...
Chasiempis sandwichensis bryani	NE	...	...	...	...	...	...
Chasiempis sandwichensis gayi	...	...	...	...	NE	...	...
Chasiempis sandwichensis sclateri	...	...	...	...	...	NE	...
Kamao							
Myadestes myadestinus	...	...	...	...	...	EN	...
Amaui							
Myadestes oahensis	...	...	...	...	EX	...	...
Olomao							
Myadestes lanaiensis	...	EX	EN	EX	...	...	...
Omao							
Myadestes obscurus	NE	...	...	...	...	...	...
Puaiohi (Small Kauai Thrush)							
Myadestes palmeri	...	...	...	...	...	EN	...
Kauai Oo (Ooaa)							
Moho braccatus	...	...	...	...	...	EN	...
Oahu Oo							
Moho apicalis	...	...	...	...	EX	...	...
Bishop's Oo							
Moho bishopi	...	?	EX	...	...	...	...
Hawaii Oo							
Moho nobilis	EX	...	...	...	...	...	...
Kioea							
Chaetoptila angustipluma	EX	...	...	...	...	...	...
Laysan Finch							
Telespyza cantans	...	...	...	...	...	...	EN
Nihoa Finch							
Telespyza ultima	...	...	...	...	...	...	EN

TABLE 1
CONTINUED

Taxa	Hawaii	Maui	Molokai	Lanai	Oahu	Kauai	NWHI
Ou							
Psittirostra psittacea	EN	EX	EX	EX	EX	EN	···
Palila							
Loxioides bailleui	EN	···	···	···	···	···	···
Lesser Koa-Finch							
Rhodacanthis flaviceps	EX	···	···	···	···	···	···
Greater Koa-Finch							
Rhodacanthis palmeri	EX	···	···	···	···	···	···
Kona Grosbeak							
Chloridops kona	EX	···	···	···	···	···	···
Maui Parrotbill							
Pseudonestor xanthophrys	···	EN	···	···	···	···	···
Common Amakihi							
Hemignathus virens virens	NE	···	···	···	···	···	···
Hemignathus virens wilsoni	···	NE	NE	EX?	···	···	···
Hemignathus virens chloris	···	···	···	···	NE	···	···
Hemignathus virens stejnegeri	···	···	···	···	···	NE	···
Anianiau							
Hemignathus parvus	···	···	···	···	···	NE	···
Greater Amakihi							
Hemignathus sagittirostris	EX	···	···	···	···	···	···
Hawaiian Akialoa							
Hemignathus obscurus obscurus	EX	···	···	···	···	···	···
Hemignathus obscurus lanaiensis	···	···	···	EX	···	···	···
Hemignathus obscurus ellisianus	···	···	···	···	EX	···	···
Kauai Akialoa							
Hemignathus procerus	···	···	···	···	···	EN	···
Nukupuu							
Hemignathus lucidus affinis	···	EN	···	···	···	···	···
Hemignathus lucidus lucidus	···	···	···	···	EX	···	···
Hemignathus lucidus hanapepe	···	···	···	···	···	EN	···
Akiapolaau							
Hemignathus munroi	EN	···	···	···	···	···	···
Kauai Creeper							
Oreomystis bairdi	···	···	···	···	···	NE	···
Hawaii Creeper							
Oreomystis mana	EN	···	···	···	···	···	···
Maui Creeper							
Paroreomyza montana newtoni	···	NE	···	···	···	···	···
Paroreomyza montana montana	···	···	···	EX	···	···	···
Molokai Creeper							
Paroreomyza flammea	···	···	EN	···	···	···	···
Oahu Creeper							
Paroreomyza maculata	···	···	···	···	EN	···	···
Akepa							
Loxops coccineus coccineus	EN	···	···	···	···	···	···
Loxops coccineus ochraceus	···	EN	···	···	···	···	···
Loxops coccineus rufus	···	···	···	···	EX?	···	···
Loxops coccineus caeruleirostris	···	···	···	···	···	NE	···
Ula-ai-hawane							
Ciridops anna	EX	···	···	···	···	···	···
Iiwi							
Vestiaria coccinea	NE	NE	NE	EX	NE	NE	···
Hawaii Mamo							
Drepanis pacifica	EX	···	···	···	···	···	···
Black Mamo							
Drepanis funerea	···	···	EX	···	···	···	···
Crested Honeycreeper (Akohekohe)							
Palmeria dolei	···	EN	EX	···	···	···	···

TABLE 1
CONTINUED

Taxa	Hawaii	Maui	Molokai	Lanai	Oahu	Kauai	NWHI
Apapane							
Himatione sanguinea sanguinea	NE	NE	NE	NE	NE	NE	···
Himatione sanguinea freethii	···	···	···	···	···	···	EX
Poo-uli							
Melamprosops phaeosoma	···	EN	···	···	···	···	···
Totals							
Extinct	11	3	5	6	7	0	3
Endangered or threatened	13	10	7	2	5	12	4
Not endangered	8	5	4	2	5	8	0

[a] Nomenclature follows the 1983 A.O.U. Check-list and 35th Supplement. NE = nonendangered; TH = threatened; EN = endangered; EX = extinct; ? = present status uncertain; ?? = presently absent, status uncertain at Western contact (1778); ··· = believed to be absent at Western contact.

sued until after World War II, relieved only by the noteworthy forest bird surveys of Munro (1944).

The third phase, the modern era, was heralded by the early studies of Baldwin (1944, 1945a, 1945b, 1947a, 1947b) and Schwartz and Schwartz (1949). World interest in the Hawaiian avifauna was greatly stimulated by the systematic studies of Amadon (1950) and ecological studies of Baldwin (1953). Warner (1968) demonstrated the potential role of disease in decimating Hawaiian birds. A. J. Berger and his students at the University of Hawaii began in-depth studies of breeding biology of the Hawaiian avifauna (Berger 1969a, 1969b, 1969c, 1970; Berger et al. 1969; Conant 1977; Eddinger 1969, 1970, 1972; van Riper 1972, 1973b, 1978c, 1980, 1982, 1984). A complete review of the Hawaiian avifauna was written by Berger (1972) and revised in 1981. H. D. Pratt (1979) provided the latest major taxonomic revision of Hawaiian land birds. During the 1970s, the International Biological Program focused research efforts on the mid-elevation east slope of Mauna Loa; these results were reviewed in Mueller-Dombois et al. (1981).

Interest in the Hawaiian avifauna intensified during the 1960s with major efforts by U.S. Fish and Wildlife Service biologists on literature review (Banko 1980–1984, Banko and Banko 1976), the birds of the Northwestern Hawaiian Islands (J. L. Sincock and E. Kridler, unpub. data) and the birds of Kauai (Richardson and Bowles 1964, Sincock et al. 1984). The Smithsonian Institution launched a major investigation of Pacific seabirds that added tremendously to our knowledge of the Northwestern Hawaiian Islands (Kepler 1967, 1969; Clapp and Woodward 1968; Amerson 1971; Clapp 1972; Woodward 1972; Ely and Clapp 1973; Amerson et al. 1974; Fleet 1974; Clapp and Wirtz 1975; Clapp and Kridler 1977; Clapp et al. 1977). From 1976 to 1982, the U.S. Forest Service funded a major research program by C. J. Ralph to study the behavior of native birds. This study focused on a limited number of sites and obtained a perspective on seasonal and year-to-year variation lacking in our study. A manuscript describing these results is in preparation.

Olson and James (1982a, 1982b) have unearthed dozens of new fossil birds species that prompted a reassessment of the impacts of Polynesians on the Hawaiian avifauna. Laboratory investigations have also contributed to our understanding of the relations of the evolution, ecology, morphology, and physiology of native birds (Richards and Bock 1973; MacMillen 1974, 1981; Raikow 1975, 1976, 1977; Weathers and van Riper 1982).

Despite earlier studies, in 1976 we knew little about the current status of most native Hawaiian forest birds, because vast areas of the islands were still ornithologically unexplored (Berger 1972). As recently as 1973, a new genus of honeycreeper was discovered on the island of Maui (Casey and Jacobi 1974), and even by 1980 the nests, eggs, and young had been described for only 11 of 37 extant passerine taxa (Scott et al. 1980). In 1976, recovery plan drafts for Hawaiian forest birds were largely statements of the need for information on the basic biology of endangered forest birds.

The primary reason for this lack of information on Hawaiian forest birds was the difficulty of working in most forested areas of the State. Hawaiian rainforests have been described as having some of the most inhospitable terrain in the world for conducting field research (Seale 1900). The difficult conditions include rainfall of 10–20 m/year, continual cold drizzle for days or weeks on end, frequent dense fog, steep slopes, sheer cliffs, 10–15 deep gulches per kilometer along contours in many areas, nearly impenetrable vegetation, treacherous earth cracks and lava tubes, and remote areas far from road access.

FIGURE 2. Field crew for the Kau forest bird survey of 1976. (Photograph by Miles Nakahara)

THE SURVEY AND ITS OBJECTIVES

By the mid 1970s it was generally acknowledged that any hope for preserving the unique Hawaiian avifauna and associated biota would require obtaining basic information on distribution, abundance, habitat response, and limiting factors. In order to meet these needs, Eugene Kridler, John L. Sincock, and J. Michael Scott conceived the idea of a state-wide forest bird survey in 1975, because such an approach was needed to identify areas requiring protection, research priorities, and management strategies. The Hawaiian Forest Bird Survey (hereafter HFBS), the results of which are detailed herein, began in 1976 (Fig. 2) on the southeast slopes of Mauna Loa, Hawaii, and ended in 1983 in the subalpine woodland of Mauna Kea, Hawaii. About one-third of the area covered by the HFBS had never been explored by ornithologists.

The principal objectives of the Hawaiian Forest Bird Survey were to determine for each bird species in the forests we studied: (1) distribution; (2) population size; (3) density (birds/km^2) by vegetation type and elevation; (4) habitat response; and (5) geographical areas where more detailed studies were needed to clarify distributional anomalies and to identify limiting factors of various species. Subsidiary objectives were to (1) develop, improve, and continually evaluate forest bird survey techniques and their statistical analysis; (2) determine the distribution of native habitat types; and (3) compare land-use patterns and habitat stability in forested areas.

The areas surveyed included all native forests above 1000 m elevation on the islands of Hawaii, Maui, Molokai, and Lanai, and the known distributional area for endangered forest birds on Kauai. We were able to stratify our sampling effort on Kauai because of the pioneering work of John Sincock (unpub. data, Sincock et al. 1984). The islands of Kahoolawe and Niihau were not surveyed because they lack native forest birds. We did not survey Oahu because of the low densities of native birds and the completion of a forest bird survey on military lands (Shallenberger and Vaughn 1978). Sampling efforts 10 times greater than we undertook on the island of Hawaii would have been necessary to make meaningful statements about some nonendangered native birds on Oahu, and it was decided that the money and manpower required would be better spent at that time on other needs.

THE NATURAL ENVIRONMENT

Because the study areas cover a great diversity of habitats and are distributed over a broad area, we include a general account of the major geological, climatic, and vegetation patterns. More

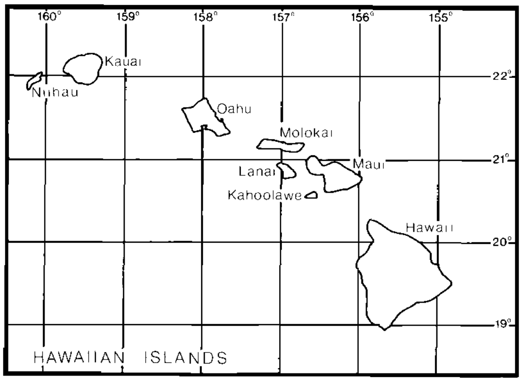


FIGURE 3. The main Hawaiian Islands.

detailed accounts of Hawaiian ecosystems may be found in Rock (1913), Carlquist (1970), Kay (1972), and Mueller-Dombois et al. (1981).

In this monograph we use "Hawaii" to refer only to the big island of Hawaii and "Hawaiian Islands" to refer to all the islands collectively. Names of places, plants, and birds are spelled without the glottal stops and macrons often used in transliterating the Hawaiian language. Scientific names for birds are given in the species account section.

GEOLOGY

The Hawaiian Islands extend for 2650 km across the north Pacific Ocean (Figs. 1, 3). The chain is volcanic in origin, and was formed as the Pacific plate moved over a fixed area of vulcanism currently located under the island of Hawaii (Macdonald et al. 1983). More than 80 shield volcanoes, progressing in age from southeast to northwest, extend northward from the main islands (age 0–6 million years [my] by potassium-argon dating) through the low leeward islands (7–27 my) to the submerged Emperor Seamounts (37–70 my), where additional older volcanoes probably existed to the north but have been subducted into the Kurile-Aleutian trench (Macdonald et al. 1983).

Hawaii, the youngest island, was formed from five independent volcanic systems: Kilauea, Mauna Loa, Hualalai, Mauna Kea, and Kohala. Kilauea on the southeast side of the island is currently active and has erupted over 40 times in the last century (Macdonald et al. 1983). Mauna Loa, the largest mountain on earth, forms the south half of Hawaii, rises to 4169 m, and has erupted 19 times in the last century, most recently in 1975 and 1984. Hualalai, a steep dome studded with cinder cones, forms a portion of west Hawaii, rises to 2522 m, and last erupted in 1800 or 1801. Mauna Kea, the highest insular mountain on earth, forms most of the north half of Hawaii, reaches 4205 m, and has not erupted for at least 2000 years (Macdonald et al. 1983). Kohala Mountain forms the north end of the island and is aged at approximately 300,000 years (Macdonald et al. 1983).

Maui, Molokai, Lanai, and Kahoolawe are part of a huge massif formed by six volcanic systems. During Pleistocene sea level depressions, these islands were at times joined together as one island called Maui Nui (Stearns 1966); during sea level rises, East and West Maui became separate islands. Haleakala volcano on East Maui, 3055 m elevation, is 800,000 years old and last erupted about 1790; the other volcanic systems of Maui Nui date to 1.3–1.8 my and have not erupted for thousands of years (Macdonald et al. 1983).

Kauai, the oldest main island, has been dated to 5.6 my and has a heavily eroded landscape. The Alakai Swamp occupies the floor of the ancient Olokele caldera (Stearns 1966).

CLIMATE

Interaction between high mountains and prevailing trade winds affects rainfall and produces much of the vegetational zonation in native Hawaiian ecosystems. Prevailing moisture-laden northeast trade winds blow about 90% of the time in summer and 50% in winter (Blumenstock and Price 1967). When these trades encounter highlands, the wind is channelled up and then around or over the upland area, depending on the height. Because of adiabatic cooling, the rising air becomes saturated with water, clouds form, and precipitation occurs. Montane windward slopes of Hawaii, Maui, Molokai, Oahu, and Kauai receive 700–1000 cm of rain annually by this process. At 2000–2300 m elevation, a regional temperature inversion marks the upward limit of the flow of moist air; above this inversion lies a fairly stable mass of dry air (Blumenstock and Price 1967). After passing the crest, shoulder, or ridge of the highland area, the trade air descends, adiabatically warms, and absorbs moisture from substrates. This creates an arid rainshadow on leeward areas exposed to trade flow, where annual precipitation averages 50 cm and may drop below 20 cm (Blumenstock and Price 1967).

Where the trade wind is blocked from areas on the lee side of large mountain masses, convection cells tend to develop in the relatively stationary air, such as along the Kona coast of Hawaii. Strong diurnal sea breezes create an upland precipitation zone similar to that on the windward side, but the lowland areas in a convection cell are arid.

VEGETATION

The indigenous Hawaiian flora, with 1200–1300 species (Wagner et al. 1985), has the highest proportion of endemic species (95%, St. John 1973) of any major flora on earth. The dominant native tree species in a vast breadth of communities is ohia, or ohia-lehua, *Metrosideros polymorpha.* Occurring from sea level to over 2500 m elevation in dry, mesic, wet, and bog habitats, ohia reaches best development in montane rainforests and on recent lava flows and ash deposits. Ohia blooms profusely, and many birds are attracted to its bright red (less frequently yellow or salmon) flowers. Trees on the same landscape show tremendous variation in flowering periods due to differences in elevation, local weather, substrate, tree age, physiological condition, and genotype (Perkins 1903, Baldwin 1953, Porter 1973); ohia forest canopies thus frequently resemble a tapestry of green sprinkled with flowering red patches of many sizes. Particularly in wet areas, ohia exhibits a cohort senescence phenomenon characterized by widespread death or defoliation of canopy trees (Mueller-Dombois and Krajina 1968; Petteys et al. 1975; Mueller-Dombois 1980, 1982, 1983a, 1983b; Jacobi 1983).

Another major tree species is koa, *Acacia koa.* Its range broadly overlaps that of ohia, but it has a narrower elevational range, is absent from very wet rainforests and recent lava flows, and reaches best development on upland mesic sites. It bears small flowers with modest amounts of nectar, produces hard seeds on which several extinct honeycreepers fed, and supports a more diverse and abundant insect fauna than ohia (Swezey 1954). Mamane, *Sophora chrysophylla,* is dominant in dry woodlands at mid to high elevation, but also occurs at low elevations. Its yellow flowers attract several nectarivorous birds, and the Palila is specialized to feed on its seed pods. Naio, *Myoporum sandwicense,* frequently occurs with mamane and may form mixed forests with it and koa. Naio berries provide food for the Palila and several introduced bird species.

The Hawaiian lobeliads (Lobeliaceae) are small understory trees and shrubs that were important nectar and fruit sources for native birds, particularly the Hawaiian Akialoa, Iiwi, Hawaii Mamo, and Black Mamo (Perkins 1903). The seven native genera (*Brighamia, Clermontia, Cyanea, Delissea, Lobelia, Rollandia,* and *Trematolobelia*) have distinctive growth forms and provide a fascinating example of adaptive radiation (Rock 1919; Carlquist 1970, 1974); most species are in *Clermontia* and *Cyanea.* Many species are now extinct or quite rare, and most populations are greatly reduced in numbers due to habitat degradation and feral ungulate activity.

Tree ferns (*Cibotium* spp.) are especially characteristic of wet areas on Hawaii, and have monopodial stipes up to 5 m high. Matted ferns, also called uluhe or false staghorn ferns (*Dicranopteris* spp., *Hicriopteris pinnata,* and *Sticherus owhyensis*), are coarse woody-stemmed ferns that often form nearly impenetrable mats 2–3 m thick under open tree canopies, particularly in areas of ohia dieback. The most prominent native vine, ieie (*Freycinetia arborea*), is a stout climber that bears fleshy inflorescence bracts and fruit eaten by the Hawaiian Crow and Ou (Perkins 1903). Typical native ground covers in relatively undisturbed montane areas include the bunchgrass *Deschampsia australis* in dry areas, several sedges (*Carex alligata, Uncinia uncinata,* and *Machaerina angustifolia*), several species of *Peperomia,* ground ferns, club mosses, mosses, liverworts, and lichens. Few native ground cover species are not severely impacted by pig activity, and in many rainforest areas the epiphytic flora gives the only indication of the original ground synusium.

Vegetation zonation generally follows precipitation and elevation patterns (Figs. 4–8). Wet forests develop on windward slopes and at the upper portions of convection cells; mesic forests at the margins of wet forest; and dry forests above the inversion layer, on leeward rainshadow slopes, and at the bottom of convection cells.

The vegetation on dry, mesic, and wet montane sites differs strikingly in floristic composition and physiognomy (Table 2). Dry montane areas typically support open woodlands of ohia, mamane, or naio, with substantial cover by small trees and shrubs of *Dodonaea, Styphelia,* and *Vaccinium.* Mesic areas tend to have taller, denser forests with ohia, koa, *Coprosma, Myrsine,* and a native raspberry (*Rubus hawaiiensis*) frequent. Wet habitats are similar in structure to mesic ones, but have dense epiphytic growth, and subcanopies dominated by small trees of ohia, olapa (*Cheirodendron* spp.), *Broussaisia, Coprosma, Ilex, Myrsine, Pelea, Psychotria,* and by tree ferns, matted ferns, and vines.

In sharp contrast to dry montane woodlands on recent substrates are the mature dry and mesic forests below 1300 m elevation having a very rich flora (Table 2). These forests are now very localized and most are badly degraded, but they give a glimpse into what was probably an important habitat for many native birds known only from fossils (Olson and James 1982b). Dominant trees in mature dry and mesic woodlands and forests include lama (*Diospyros ferrea*), ohia, kolea (*Myrsine* spp.), sandalwood or iliahi (*Santalum* spp.), olopua (*Osmanthus sandwicensis*),

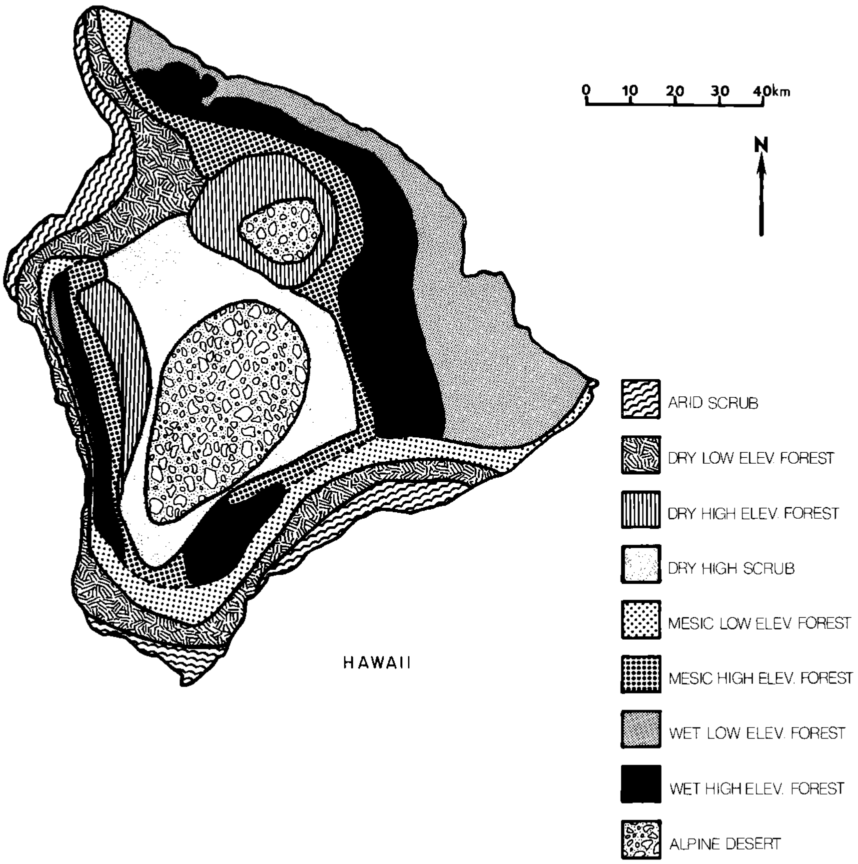


FIGURE 4. Vegetation zones of Hawaii, after Ripperton and Hosaka (1942).

manele (*Sapindus saponaria*), and halapepe (*Dracaena aurea*) above 500 m elevation, lama, wiliwili (*Erythrina sandwicensis*), ohe (*Reynoldsia sandwicensis*), and alahee (*Canthium odoratum*) below 500 m. Many dry forest species bear flowers or fruits that were probably extensively utilized by birds before Polynesian disturbance.

Substrate and disturbance are major modifiers of vegetation structure and composition. Recent lava flows, for example, have highly porous immature substrates that support early seral vegetation. Because of poor soil development, the vegetation is more xerophytic than on adjacent older substrates. Anthropogenic disturbance encompasses ranching, forestry, agriculture, and urban development. The communities most drastically modified by disturbance include dry lowland (below 700 m elevation) habitats, most mid-elevation dry forests, most lowland wet forests, and virtually all mesic forests and grasslands. Showing less disturbance are montane rainforests, early seral communities, dry subalpine woodland, alpine scrubland, and mid to high elevation barrens. Feral ungulate disturbance (goats and sheep in dry areas, pigs and deer in wet and mesic areas, cattle formerly in all) is pervasive and quite severe over large areas. Adverse modification of native communities by introduced plants has often accompanied human disturbance, but is less frequent in undisturbed areas.

Introduced plant species dominate disturbed communities and are nearly ubiquitous in occurrence. Strawberry guava (*Psidium cattleianum*) and lemon guava (*P. guajava*) are the most frequently encountered trees and often occur with Christmas-berry (*Schinus terebinthifolius*) in drier areas below 1300 m elevation. Plantations of conifers (especially *Pinus radiata, Cryptomeria japonica,* and *Araucaria* spp.) and eucalyptus (*Eucalyptus* spp.) are fairly frequent. Haole koa (*Leucaena leucocephala*) and mesquite or kiawe (*Prosopis pallida*) are common in dry to mesic lowlands. Silky oak (*Grevillea robusta*) occurs on some dry lower elevation sites. Fire tree (*Myrica faya*) is locally common on windward Hawaii on

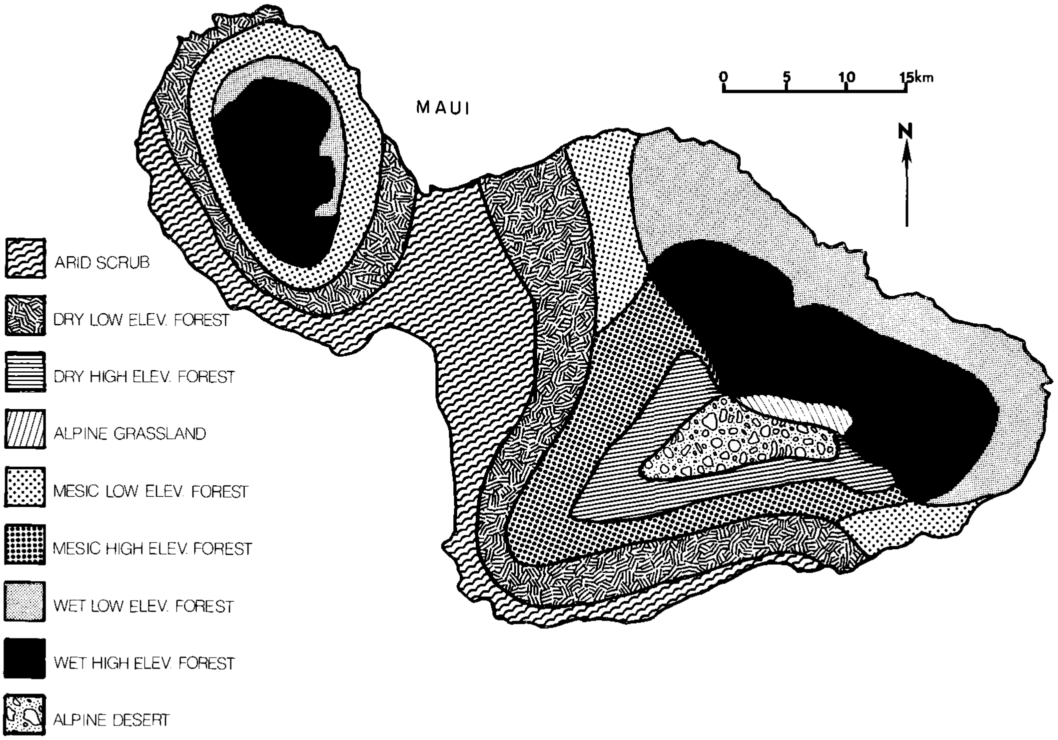


FIGURE 5. Vegetation zones of Maui, after Ripperton and Hosaka (1942).

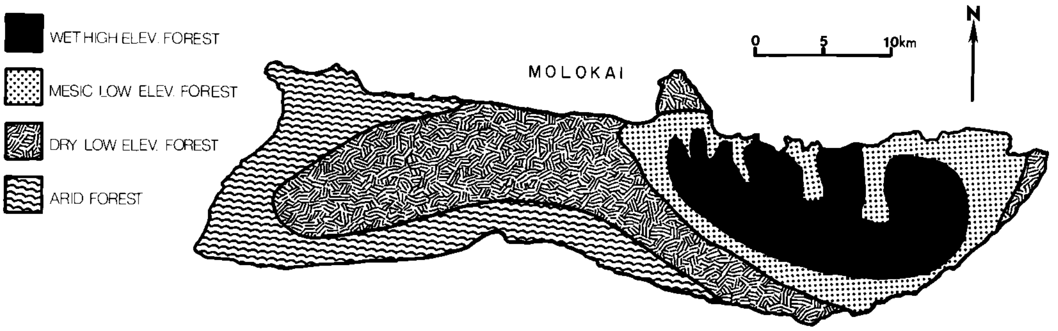


FIGURE 6. Vegetation zones of Molokai, after Ripperton and Hosaka (1942).

dry to wet sites at 500–1300 m elevation. *Passiflora* species (referred to generically in this work as "passiflora"), especially banana poka (*P. mollissima*), have rich nectar and fruit resources that attract many birds. Banana poka is aggressive, forms tree-strangling curtains that extend to the canopy, and inhibits seedling growth in the understory (Warshauer et al. 1983, La Rosa 1984). Other introduced understory plants that invade and disrupt native ecosystems include blackberries (*Rubus* spp., especially *R. penetrans*), gingers (*Hedychium* spp., especially kahili ginger, *H. gardnerianum*), lantana (*Lantana camara*), Koster's curse (*Clidemia hirta*), and several aggressive grasses: bush beard grass (*Andropogon glomeratus*), broomsedge (*A. virginicus*), velvet grass (*Holcus lanatus*), molasses grass (*Melinis minutiflora*), meadow ricegrass (*Microlaena stipoides*), kikuyu grass (*Pennisetum clandestinum*), fountain grass (*P. setaceum*), and palm grass (*Setaria palmaefolia*).

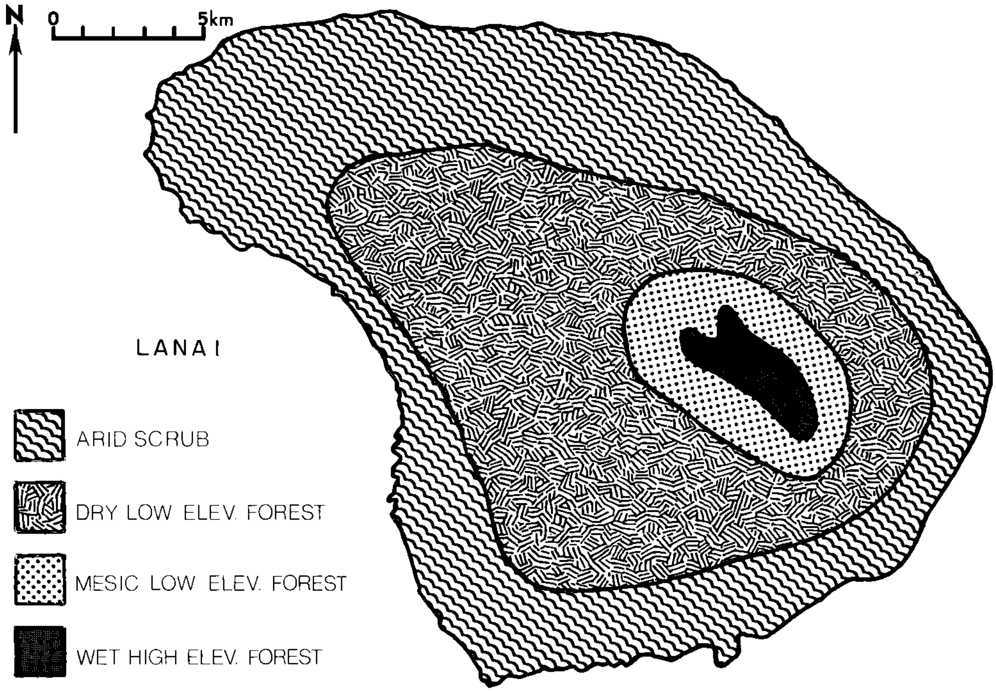


FIGURE 7. Vegetation zones of Lanai, after Ripperton and Hosaka (1942).

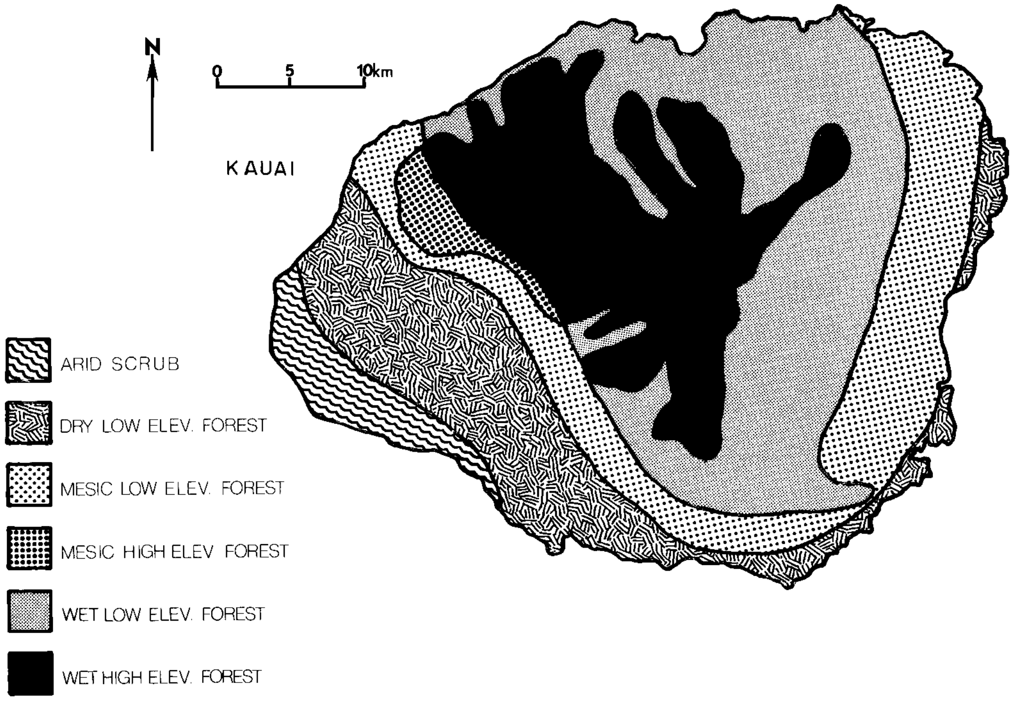


FIGURE 8. Vegetation zones of Kauai, after Ripperton and Hosaka (1942).

TABLE 2
NATIVE TREE AND SHRUB GENERA ON KONA, EAST MAUI, AND MATURE DRY FOREST SITES

	Kona[a]			East Maui[a]			Remnant mature dry forests[b,c]						
	Dry	Mesic	Wet	Dry	Mesic	Wet	H1	H2	H3	MA	MO	LA	OA
Feature													
Precipitation (cm/y)													
Mean minimum	50	75	125	90	100	200	125	125	50	75	75	30	165
Mean maximum	125	150	250	125	200	350	150	150	75	100	125	35	190
Elevation (100 m)													
Minimum	12	6	6	17	14	7	12	5	6	8	8	5	3
Maximum	24	18	15	26	20	20	13	8	9	11	9	5	5
Genus[d]													
Pteridophyta													
Blechnaceae													
Sadleria	...	1 (06)	2 (04)	1 (06)	15 (100)	1 (45)	C	C	...	...	C	...	...
Dicksoniaceae													
Cibotium	...	3 (44)	51 (100)	...	1 (33)	6 (70)	C	C	R	...	R	...	C
Gleicheniaceae													
Dicranopteris	...	6 (09)	14 (33)	...	...	18 (45)	...	R	...	...	C	...	...
Monocotyledoneae													
Liliaceae													
Dracaena	...	...	...	...	...	...	...	C	C	A	C	R	A
Palmae													
Pritchardia	...	...	...	...	...	+ (09)	...	R	...	...	...	...	R
Pandanaceae													
Freycinetia	...	...	12 (54)	...	...	1 (45)	...	C	...	R	...	...	...
Dicotyledoneae													
Amaranthaceae													
Charpentiera	...	...	+ (08)	...	...	...	C	C	R	C	...	...	C
Nototrichium	...	...	...	...	...	...	...	R	C	R	C	X	C
Anacardiaceae													
Rhus	...	...	...	...	...	...	...	...	...	R	...	...	...
Apocynaceae													
Ochrosia	...	...	...	...	...	...	R	...	R	C	...	...	C
Pteralyxia	...	...	...	...	...	...	...	...	...	...	...	...	C
Rauvolfia	...	...	...	...	...	...	...	...	...	...	...	R	C
Aquifoliaceae													
Ilex	...	2 (31)	6 (83)	...	+ (33)	1 (70)	...	...	...	...	...	...	...

TABLE 2
CONTINUED

	Kona[a]			East Maui[a]			Remnant mature dry forests[b,c]						
	Dry	Mesic	Wet	Dry	Mesic	Wet	H1	H2	H3	MA	MO	LA	OA
Araliaceae													
Cheirodendron	...	1 (34)	6 (58)	...	10 (100)	24 (100)	R	R	R	C	...	...	...
Reynoldsia	...	...	...	...	...	...	...	R	C	C	...	R	A
Tetraplasandra	...	+ (06)	+ (04)	...	...	1 (33)	...	C	R	C	...	...	C
Celastraceae													
Perrottetia	...	+ (03)	4 (50)	...	...	2 (39)	R	R	...	...	...	...	...
Chenopodiaceae													
Chenopodium	...	...	...	...	...	...	...	...	R	C	C	...	C
Compositae													
Dubautia	1 (22)	+ (06)	...	1 (24)	3 (67)	1 (36)	C	R	R	R	C	...	...
Ebenaceae													
Diospyros	...	+ (06)	...	...	...	...	...	A	A	C	C	A	A
Epacridaceae													
Styphelia	15 (73)	5 (41)	...	28 (94)	9 (100)	2 (55)	C	C	C	C	C	R	C
Ericaceae													
Vaccinium	3 (40)	1 (38)	1 (38)	13 (88)	9 (100)	5 (85)	R	R	...	...	R	...	...
Euphorbiaceae													
Antidesma	...	+ (06)	2 (21)	...	...	+ (06)	...	C	R	...	C	X	R
Claoxylon	...	...	...	...	...	...	...	...	R	R	...	...	R
Drypetes	...	...	...	...	...	...	...	R	...	R	...	...	R
Euphorbia	+ (02)	+ (06)	...	...	...	...	...	R	R	C	R	X	C
Flacourtiaceae													
Xylosma	+ (08)	...	...	...	...	...	R	R	C	C	...	R	C
Geraniaceae													
Geranium	+ (11)	+ (03)	...	1 (24)	...	...	...	...	...	...	...	...	...
Goodeniaceae													
Scaevola	...	...	...	...	...	1 (33)	...	...	...	...	...	...	...
Hydrangeaceae													
Broussaisia	...	+ (03)	9 (67)	...	+ (33)	9 (85)	...	...	...	...	...	...	...
Lauraceae													
Cryptocarya	...	...	...	...	...	...	...	...	...	...	...	...	R
Leguminosae													
Acacia	2 (14)	16 (72)	8 (33)	2 (06)	10 (33)	5 (21)	A	...	C	...	...	...	...
Cassia	...	...	...	...	...	...	...	...	R	...	...	X	C
Erythrina	...	...	...	...	...	...	...	R	C	C	C	R	A
Mezoneuron	...	...	...	...	...	...	...	...	R	X	...	...	R
Sophora	10 (48)	1 (19)	...	14 (47)	+ (33)	...	C	R	C	C	R	R	...

TABLE 2
CONTINUED

	Kona[a]			East Maui[a]			Remnant mature dry forests[b,c]						
	Dry	Mesic	Wet	Dry	Mesic	Wet	H1	H2	H3	MA	MO	LA	OA
Lobeliaceae													
Clermontia	...	1 (28)	2 (50)	...	+ (33)	1 (73)	X	...	...	...	...	...	...
Cyanea	...	...	...	...	...	+ (21)	...	...	...	X	...	...	...
Delissea	...	...	...	...	...	...	...	...	X	...	...	...	...
Lobelia	...	...	...	...	...	+ (09)	...	...	...	...	...	...	...
Trematolobelia	...	...	...	...	...	+ (09)	...	...	...	...	...	...	...
Malvaceae													
Hibiscadelphus	...	...	...	...	...	...	R	...	R	X	...	...	...
Hibiscus	...	...	...	...	...	...	...	...	...	...	...	X	C
Kokia	...	...	...	...	...	...	...	...	R	...	...	X	...
Moraceae													
Streblus	...	+ (03)	...	...	...	...	...	R	R	C	R	...	R
Myoporaceae													
Myoporum	8 (48)	3 (47)	+ (04)	...	...	...	C	C	C	C	C	C	C
Myrsinaceae													
Myrsine	2 (22)	6 (56)	6 (62)	+ (06)	...	3 (70)	C	C	C	C	C	C	C
Myrtaceae													
Eugenia	...	...	...	...	...	...	...	...	...	...	...	...	C
Metrosideros	18 (65)	54 (91)	60 (100)	3 (35)	35 (100)	47 (100)	A	A	A	C	A	...	C
Nyctaginaceae													
Pisonia	...	+ (03)	+ (04)	...	...	...	C	C	R	C	...	...	C
Oleaceae													
Osmanthus	...	+ (06)	...	...	...	...	C	C	C	A	A	A	A
Pittosporaceae													
Pittosporum	...	+ (12)	1 (58)	...	...	+ (39)	R	C	R	R	...	X	C
Rhamnaceae													
Alphitonia	...	...	...	...	...	...	...	R	R	C	...	...	...
Colubrina	...	...	...	...	...	...	...	R	C	...	...	...	C
Rosaceae													
Osteomeles	1 (27)	+ (03)	...	+ (18)	...	...	...	C	R	C	C	R	C
Rubus	+ (06)	5 (47)	3 (42)	1 (06)	9 (100)	5 (67)	C	...	...	...	R	...	...
Rubiaceae													
Bobea	...	...	...	...	...	...	...	...	...	R	...	C	C
Canthium	...	+ (06)	...	...	...	...	...	C	C	...	C	C	A
Coprosma	2 (43)	3 (66)	4 (63)	6 (82)	10 (100)	5 (82)	C	C	R	C	C	...	...
Gardenia	...	...	...	...	...	+ (03)	...	...	R	...	...	R	...
Gouldia	...	+ (09)	1 (38)	...	...	2 (85)	R	C	R	...	C	...	...
Morinda	...	...	...	...	...	+ (03)	...	...	...	...	...	...	R
Psychotria	...	+ (09)	10 (88)	...	...	1 (58)	C	C	R	R	C	...	C

TABLE 2
CONTINUED

	Kona[a]			East Maui[a]			Remnant mature dry forests[b,c]						
	Dry	Mesic	Wet	Dry	Mesic	Wet	H1	H2	H3	MA	MO	LA	OA
Rutaceae													
Pelea	···	1 (25)	1 (29)	···	3 (33)	4 (97)	R	R	R	C	···	···	C
Platydesma	···	···	···	···	···	+ (09)	···	···	···	···	···	···	···
Zanthoxylum	···	···	···	···	···	···	R	···	R	R	R	···	···
Santalaceae													
Exocarpus	+ (02)	···	···	···	···	···	···	···	R	X	R	···	···
Santalum	3 (37)	+ (06)	···	+ (12)	···	···	C	R	C	C	C	R	C
Sapindaceae													
Alectryon	···	···	···	···	···	···	···	···	···	R	R	···	C
Dodonaea	12 (75)	2 (22)	+ (04)	10 (47)	···	···	C	C	R	C	C	R	C
Sapindus	···	···	···	···	···	···	A	···	R	···	···	···	A
Sapotaceae													
Nesoluma	···	···	···	···	···	···	···	···	R	···	···	R	R
Sideroxylon	···	···	···	···	···	···	···	R	C	C	C	R	C
Solanaceae													
Nothocestrum	···	···	+ (04)	···	+ (33)	+ (09)	X	C	R	C	···	R	···
Thymelaceae													
Wikstroemia	+ (06)	···	+ (04)	···	···	+ (15)	X	C	R	C	C	···	C
Tiliaceae													
Elaeocarpus	···	···	···	···	···	···	···	···	···	···	···	···	C
Urticaeae													
Neraudia	···	···	···	···	···	···	···	···	R	X	···	···	C
Pipturus	···	+ (09)	3 (42)	···	···	1 (27)	C	C	R	C	R	···	C
Urera	···	···	1 (21)	···	···	+ (09)	X	R	R	R	···	···	C
Violaceae													
Viola	···	···	···	···	···	···	···	···	···	···	R	···	C

[a] The first entry for each genus is the average cover in percent, the second entry (in parentheses) is the frequency as percent occurrence on the sites; + indicates mean cover <0.5%.

[b] Forest locations: H1 = Kipuka Puaulu, Hawaii; H2 = Kapua Tract, Hawaii; H3 = Puu Waawaa, Hawaii; MA = Auwahi Tract, Maui; MO = central East Molokai; LA = Kanepuu, Lanai; OA = Mokuleia, Oahu.

[c] Sources: Rock 1913 (all areas); Hatheway 1952 (Mokuleia); Mueller-Dombois and Lamoureux 1967 (Kipuka Puaulu); Spence and Kobayashi 1971 (Puu Waawaa); Spence and Montgomery 1976 (Kanepuu); Medeiros et al. 1984 (Auwahi); Hodel 1985 (Kapua); HFBS data (Hawaii and Molokai sites).

[d] A = abundant in area; C = common to moderately uncommon; R = very uncommon to quite rare; X = extirpated; ··· = not known to have occurred historically.

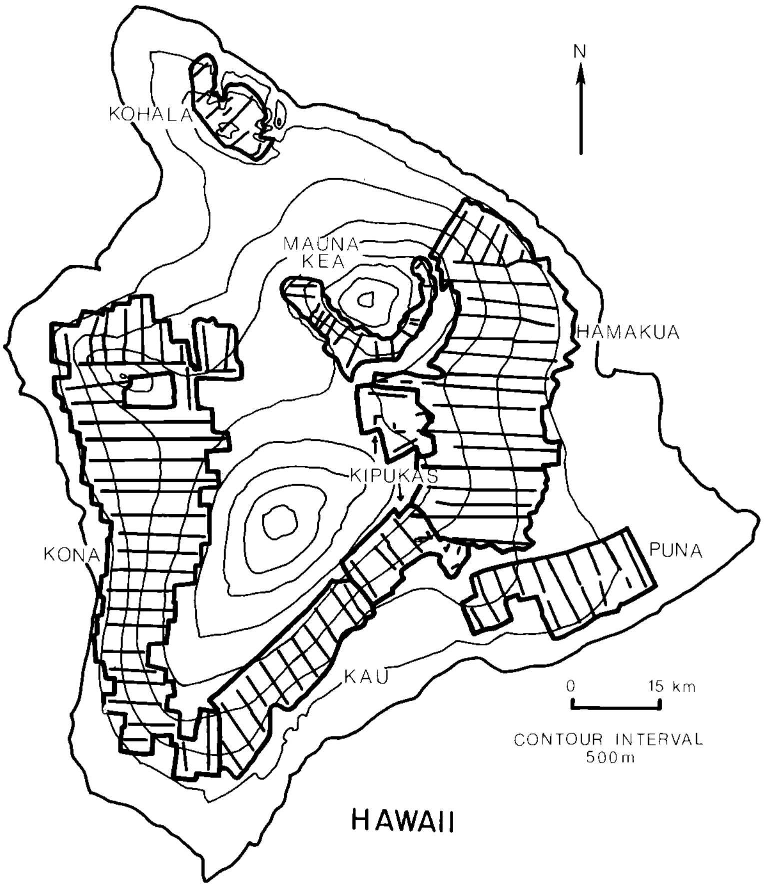


FIGURE 9. Study areas on the island of Hawaii

STUDY AREAS

We established seven study areas on Hawaii (Fig. 9): Kau, an isolated montane rainforest of ohia and koa on the southeast slopes of Mauna Loa; Hamakua, the windward montane rainforest of ohia and koa on Mauna Kea and Mauna Loa; Puna, the low elevation ohia rainforest on Kilauea; Kipukas, a high elevation dry scrub area on the windward side with scattered pockets of mesic forest; Kona, the diverse leeward montane area on Mauna Loa and Hualalai; Mauna Kea, the subalpine mamane-naio woodland on Mauna Kea; and Kohala, an isolated lower elevation ohia rainforest on the northern end of the island.

We established two study areas on Maui, and one each on Molokai, Lanai, and Kauai (Figs. 10–11). These areas are mostly in montane ohia rainforests, although other habitat types were also sampled. Place names referred to in text are shown in Figures 12–15.

KAU

The Kau study area is situated on the southeast slopes of Mauna Loa, covers 329 km², extends from 640 to 2225 m elevation, and is fairly isolated from other forests (Figs. 9 and 16). Most rainfall is derived from a large horizontal vortex wind pattern, but rainfall distribution resembles the convection cell pattern of precipitation. The top boundary of the study area lies near the inversion layer in dry alpine scrub. Below this is well-developed wet native forest (Fig. 17). Areas devoted to sugar cane, macadamia nuts, and cattle border the study area below and laterally.

The Kau study area is relatively undisturbed by human activity, as reflected in the closed canopy cover (Fig. 18). Decreasing canopy cover at higher elevations marks the transition to subalpine scrublands. No station had more than 20% cover of introduced trees, introduced shrubs, or passiflora. Koa-ohia forest is the dominant habitat in the northeast half of the study area, and ohia forest elsewhere. Mamane and naio are absent as dominants, and matted ferns are common in only one area. A vegetation map of the study area has been published (Jacobi 1978).

HAMAKUA

The Hamakua study area is situated on the eastern slopes of Mauna Kea and northeastern slopes of Mauna

FIGURE 10. Study areas on Maui, Molokai, and Lanai.

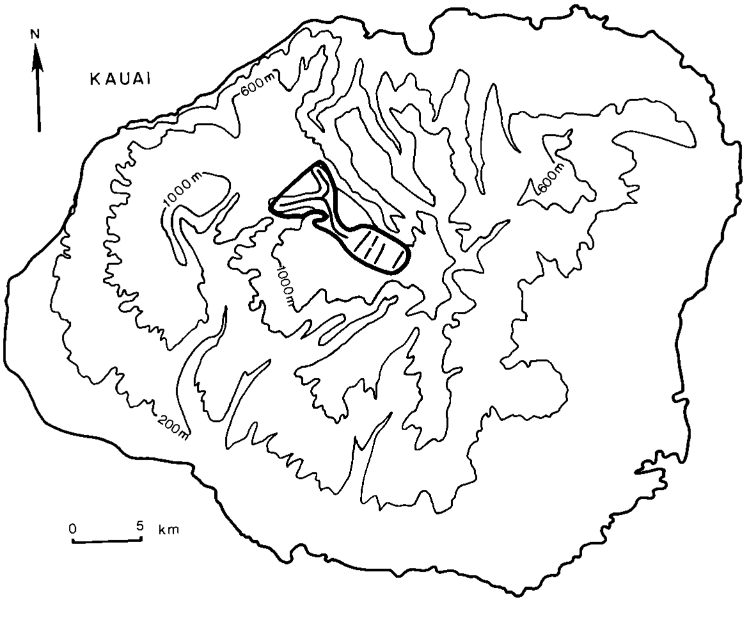


FIGURE 11. Study area on Kauai.

Loa (Figs. 9 and 19), and constitutes transects 12 to 32 of windward Hawaii. The study area covers 1112 km^2 and extends from approximately 300 to 2300 m elevation. The upper boundary lies near the inversion layer in dry, disturbed pastures and grasslands. Below this area are well-developed native forests, with introduced plants common at lower elevations (Fig. 20). Trade wind precipitation predominates, with a median annual rainfall of 700 cm (highest on the island) on the lower slopes of Mauna Kea (Blumenstock and Price 1967). Below the lower forest boundary, sugar cane plantations and cattle ranches extend as high as 1200 m elevation. Several recent lava flows (1852, 1855, 1880, 1899, 1935, 1942, 1984) from Mauna Loa

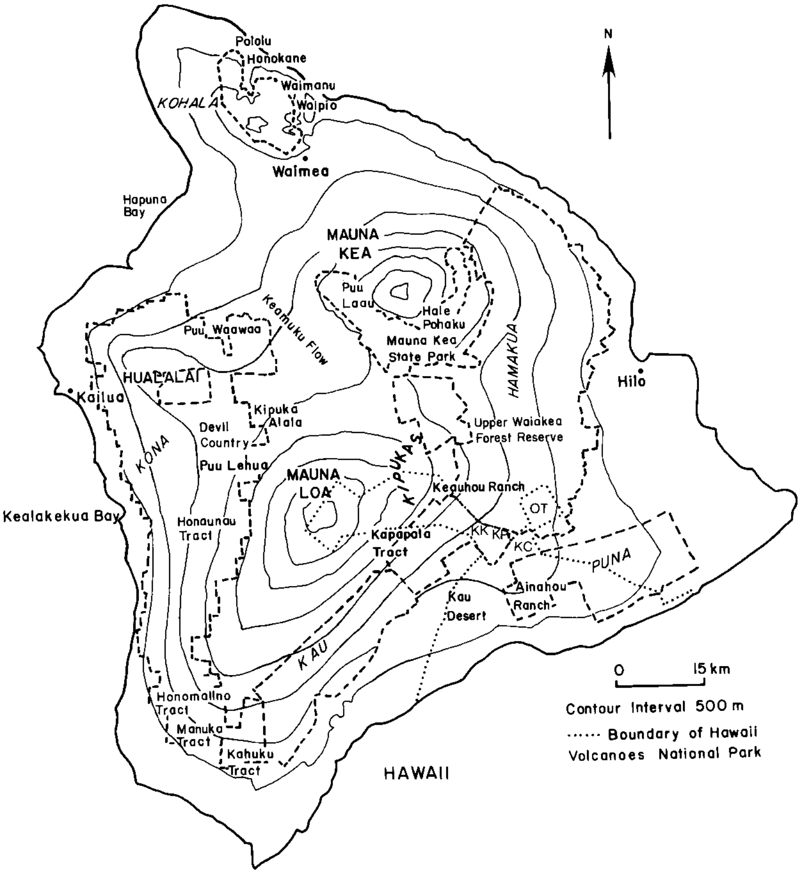


FIGURE 12. Place names on Hawaii. (KC = Kilauea Crater, KK = Kipuka Ki, KP = Kipuka Puaulu, OT = Olaa Tract).

(Stearns 1966) punctuate the mature forest and are marked by swaths of pioneer, successional vegetation that average 1 km in width.

The canopy cover varies extensively in the study area (Fig. 21). Large areas of reduced canopy cover at middle elevations reflect ohia dieback. Open canopies at upper elevations resulted from land clearing and grazing.

Koa occurs in mesic habitat, in pasture areas, and in a 5–7 km strip along the lower edge of the study area on Mauna Kea. Naio is not a dominant at any station. The small areas dominated by mamane at high elevation represent the lower degraded edges of the Mauna Kea mamane woodland. Matted ferns dominate large areas at low to mid-elevations in wet forest interiors, particularly ohia dieback areas. Tree ferns are common in most ungrazed wet forests. A large banana poka infestation occurs in undisturbed forest at 1500–2000 m elevation on the northeast slope of Mauna Kea. Introduced grasses reach their greatest cover in the park-like pasturelands below the Mauna Kea mamane woodland.

The Hamakua study area includes the last known localities for the Greater Amakihi and the Hawaii Mamo (Berger 1981).

PUNA

The Puna study area (Figs. 9 and 19) is located south and east of Kilauea Volcano on Pleistocene and Recent lavas from the Kilauea system (Stearns 1966). The study area covers 270 km^2 and extends from 300 to 1300 m elevation. Dry coastal scrub borders the area at lower elevations, and rural residential subdivisions border the north sides. Southwest of the study area (Fig. 20), a strong rainshadow effect from the Kilauea shield created the Kau Desert where ohia, *Vaccinium,* and *Dodonaea* are dominant. The time elapsed since the last lava flow in an area is an important determinant of vegetation type at the south and west margins of the study area.

The canopy cover in this area varies considerably (Fig. 21). Treeless areas reflect recent volcanic activity. Koa and naio are not dominant elements at any station. Guava and Christmas-berry occur towards the lower boundary of the study area (Fig. 20), whereas the introduced fire tree, *Myrica faya,* is fairly widespread in

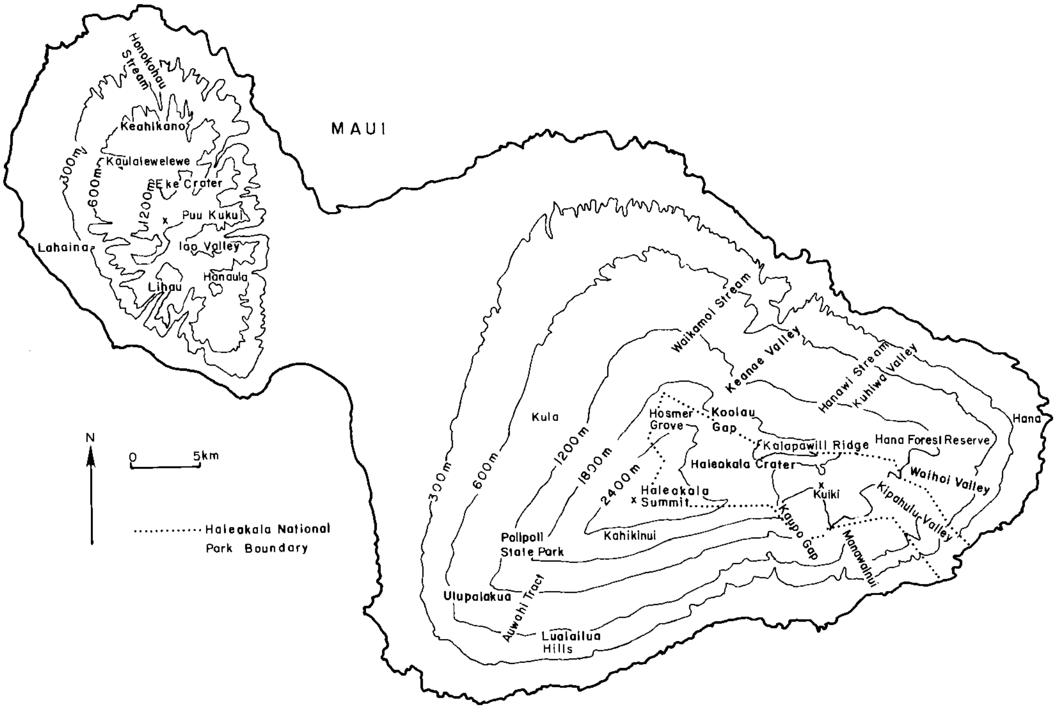


FIGURE 13. Place names on Maui.

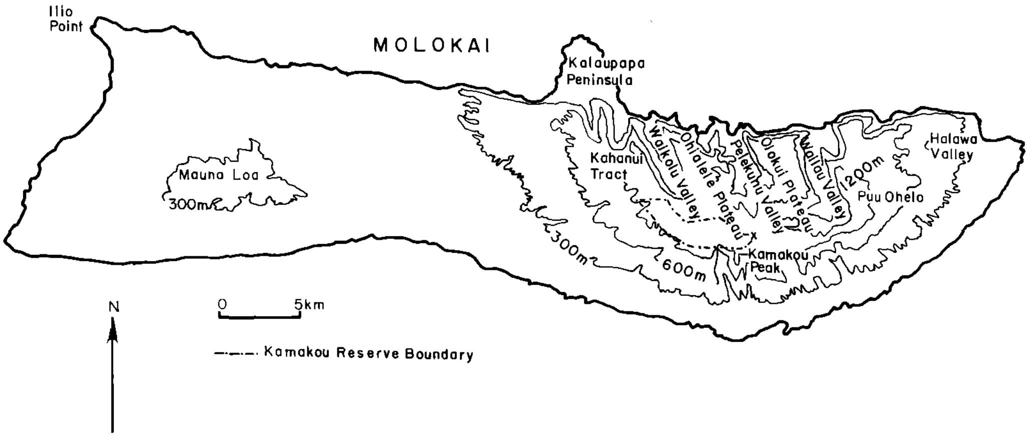


FIGURE 14. Place names on Molokai.

drier sections of the west side. Tree ferns, matted ferns, and scattered ieie occur in most wet areas. Passiflora is not found in the study area. Introduced graminoids have infiltrated most forested areas.

KIPUKAS

The Kipukas study area is situated west and southwest of the Hamakua study area (Figs. 9 and 19). This area covers 295 km², extends from 1100 to 2400 m elevation, is relatively high and arid, and lies mostly above the thermal inversion or in the Kilauea and Mauna Loa rainshadows. Kipukas, "island-like areas of older land ranging in size from a few square [meters] to several square [kilometers] surrounded by later lava flows" (Stearns 1966:58), are numerous and have more mature soils supporting a more mesic, more developed vegetation than the surrounding dry scrub habitat. Forests dominated by koa and other trees are best developed in these mesic areas. We recorded no introduced trees, passiflora, or ieie; matted ferns were found only

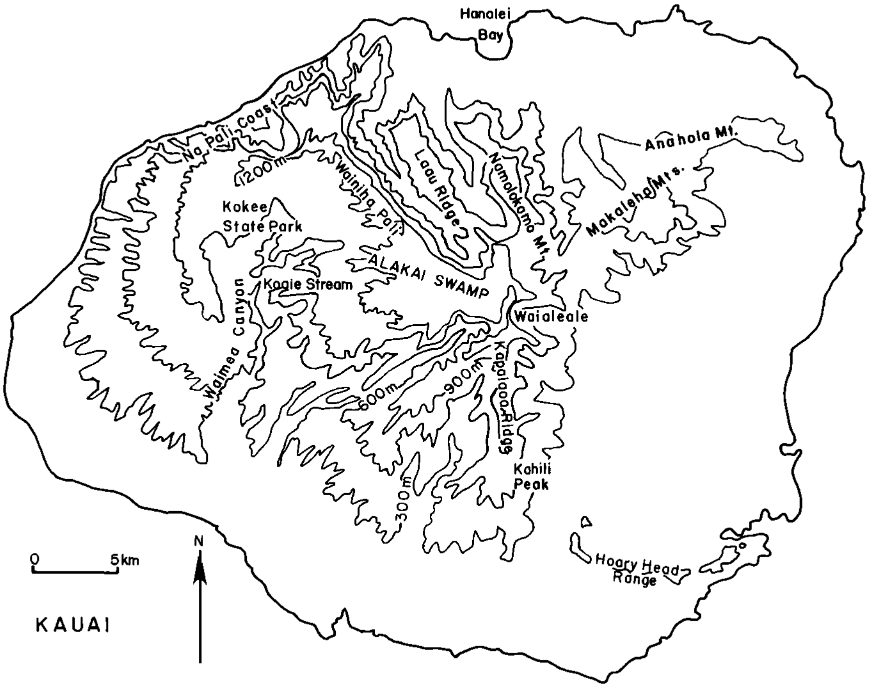


FIGURE 15. Place names on Kauai.

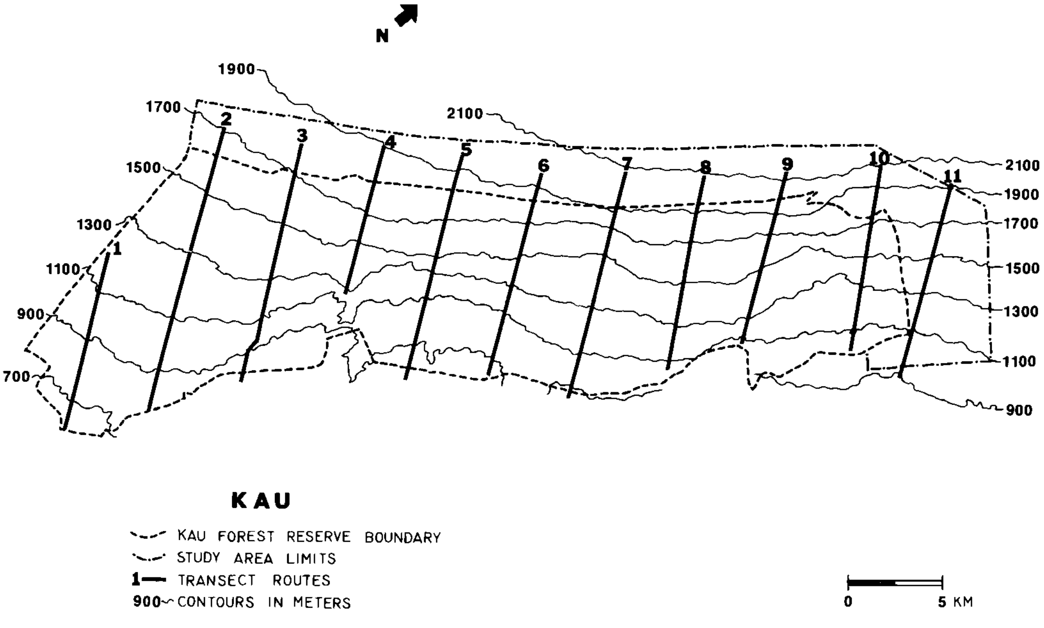


FIGURE 16. Transect locations in the Kau study area.

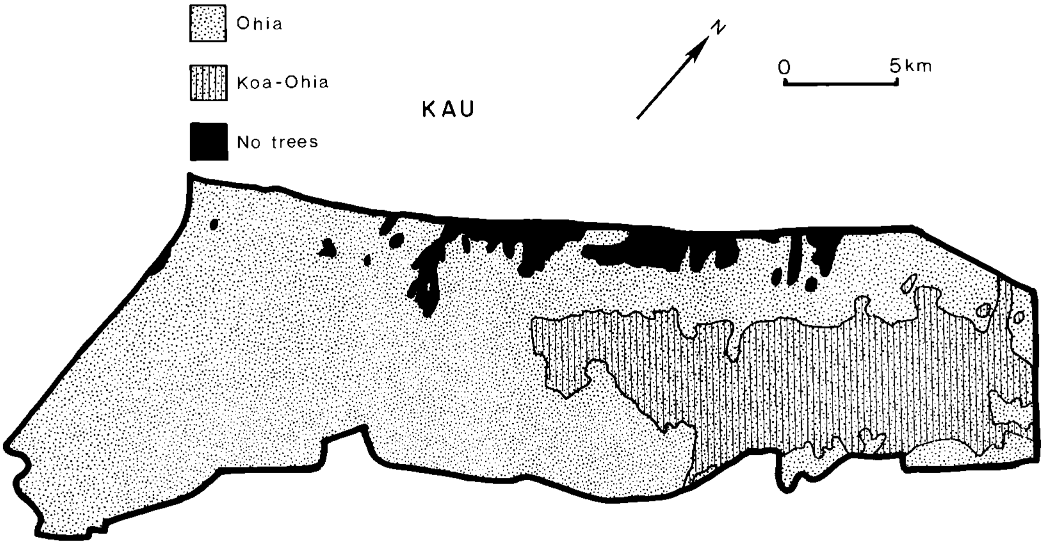


FIGURE 17. Habitat types in the Kau study area.

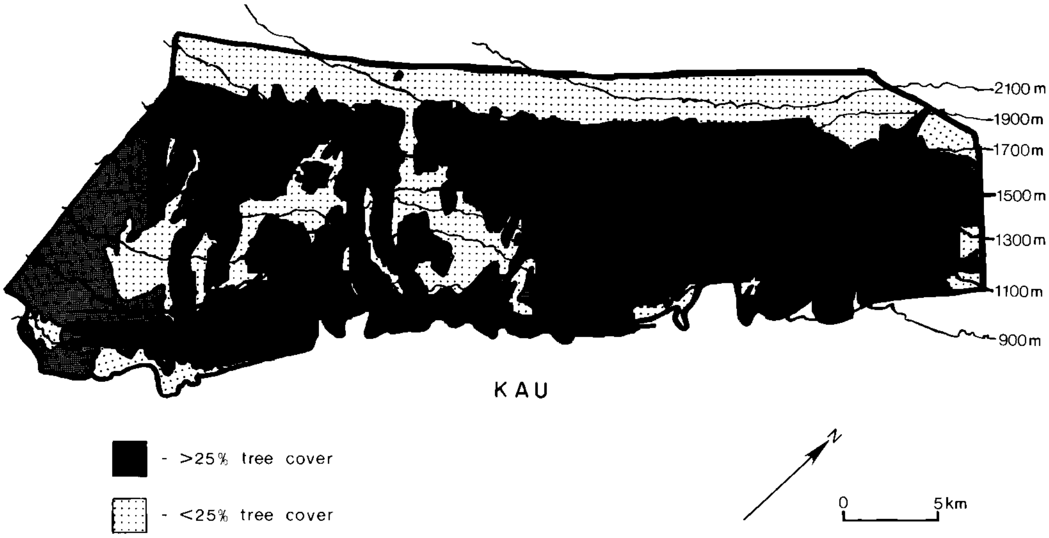


FIGURE 18. Canopy cover in the Kau study area.

at two localities, and tree ferns only at Kipuka Ki and Kipuka Puaulu (Fig. 20). The Kipukas study area includes the upper half of the Mauna Loa transect of the International Biological Program study in Hawaii (Mueller-Dombois et al. 1981). Canopy cover is scattered throughout much of this area (Fig. 21). An exceptionally intact mature mesic forest remnant (Table 2; Mueller-Dombois and Lamoureux 1967) at Kipuka Puaulu once supported the Greater Koa-Finch, Hawaiian Akialoa, Akiapolaau, Hawaii Creeper, and Akepa (Perkins 1903, Baldwin 1953, Banko and Banko 1980).

KONA

Kona, the largest area studied, is situated on Hualalai and Mauna Loa on western Hawaii (Figs. 9 and 22). The study area covers 1265 km^2 and extends from 200 to 2500 m elevation. Forests reach their best development in convection cells on the south and west slope of Hualalai and on the slopes of Mauna Loa in south Kona. Elsewhere the habitat is generally dry. Mostly treeless areas on the high eastern slopes of Hualalai and parts of the Hualalai-Mauna Loa saddle were omitted from the study area.

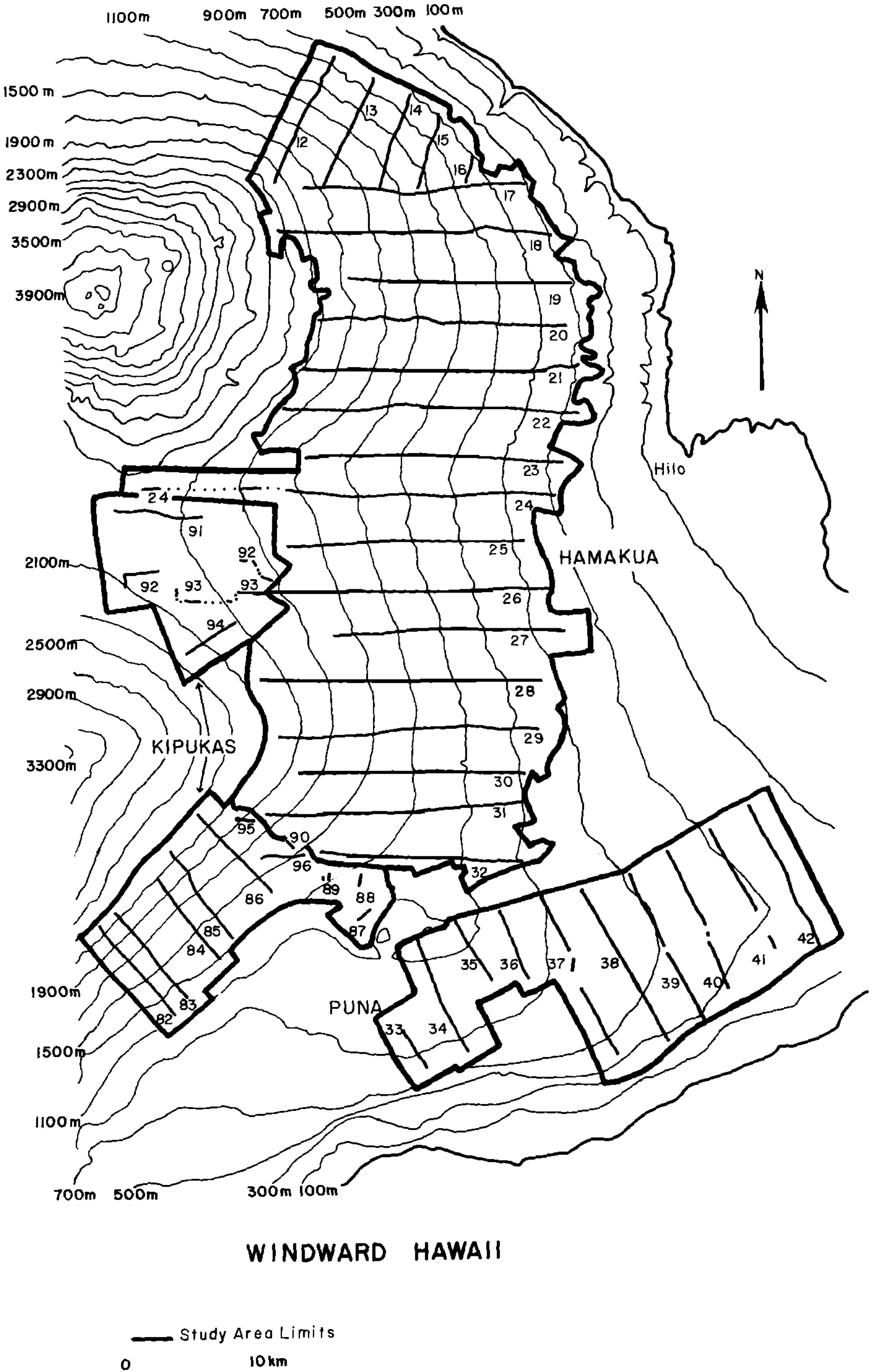


FIGURE 19. Transect locations in the windward Hawaii study areas (Hamakua, Puna, and Kipukas).

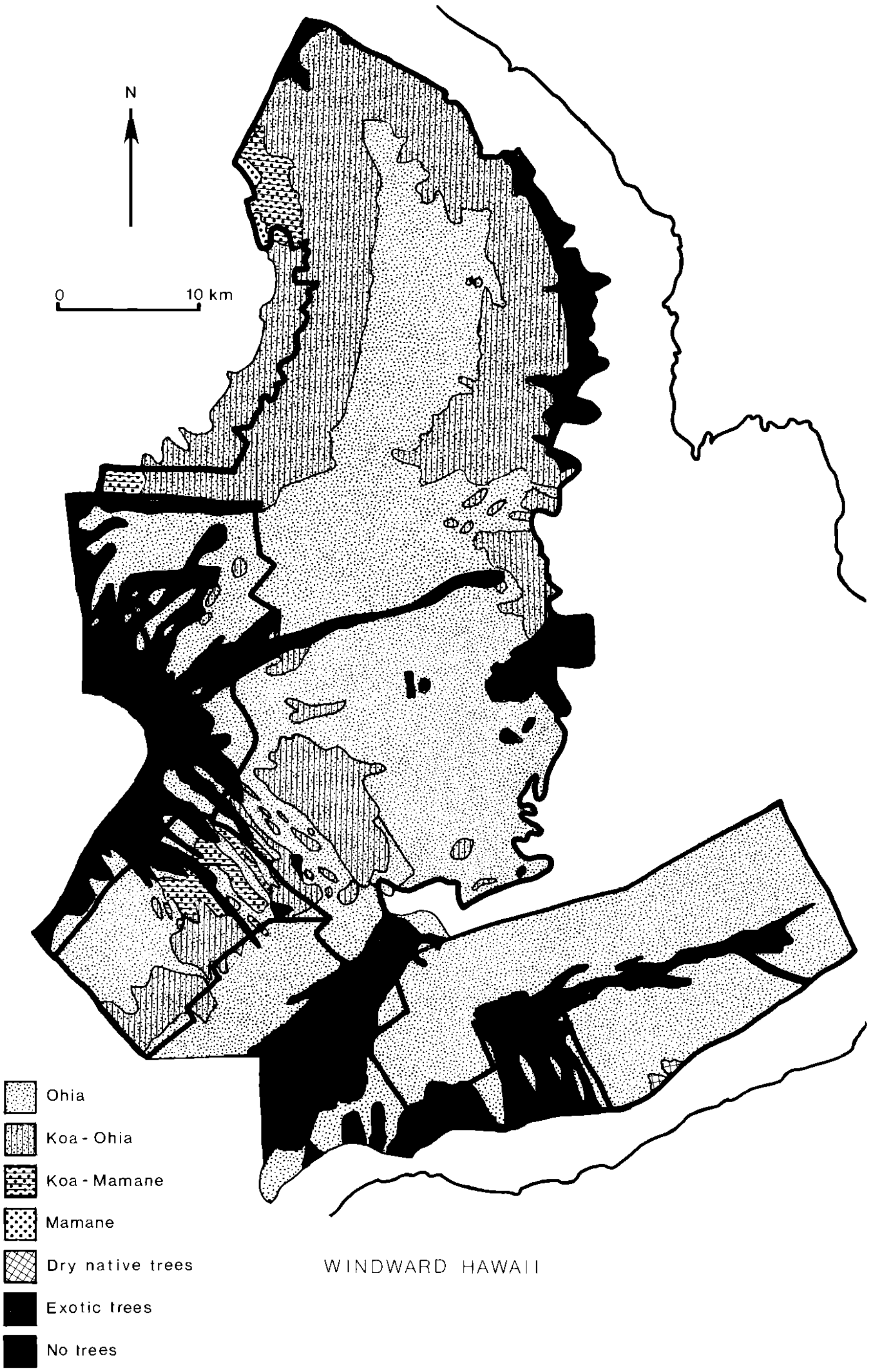


FIGURE 20. Habitat types in the windward Hawaii study areas (Hamakua, Puna, and Kipukas).

FIGURE 21. Canopy cover in the windward Hawaii study areas (Hamakua, Puna, and Kipukas).

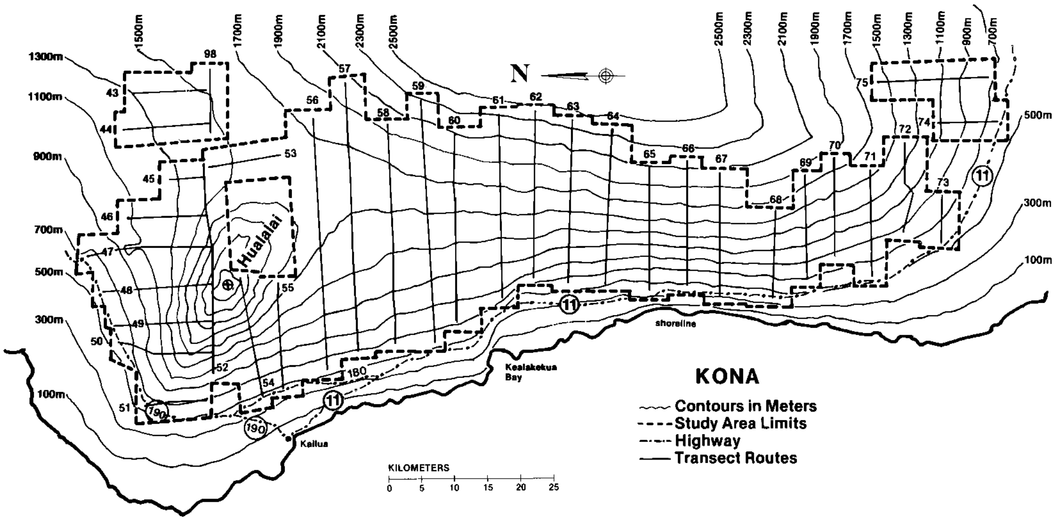


FIGURE 22. Transect locations in the Kona study area.

Koa occurs over much of the region, but is absent from dry areas at high elevations. Introduced trees, particularly guava and Christmas-berry, are common at low elevations; eucalyptus and conifer plantations are also frequent. Around the base of Hualalai, many introduced tree species occur (Fig. 23). Banana poka outbreaks occur on the mesic and wet areas of Hualalai. Ieie, matted ferns, and tree ferns are frequent in most mesic and wet areas, particularly at low elevations in south Kona. Introduced grasses are abundant in the dry areas north of Hualalai and on several large ranches in the northern half of the Mauna Loa shield. The forests have been fragmented by lumbering, grazing, and numerous historic lava flows, especially in south Kona (Fig. 24). Mature dry forest remnants occur below Puu Waawaa and on the Kapua Tract (Table 2).

Several species of extinct finch-like honeycreepers are known solely or primarily from Kona collecting stations (Berger 1981). Omao are absent from vast areas of Kona where they were formerly abundant (van Riper and Scott 1979) and Hawaiian Crows are now limited to Kona. The lower north slopes of Hualalai support many species of introduced birds (Lewin 1971).

MAUNA KEA

The Mauna Kea study area encompasses the ring of open subalpine woodlands on the east, south, and west slopes of Mauna Kea (Figs. 9 and 25). This area covers 139 km^2 and extends from 1900 to 3100 m elevation. The area generally lies above the inversion layer and supports dry habitat. Mamane is found throughout the area, and naio is dominant on the arid southwest slopes (Fig. 26). Native shrubs and introduced grasses are the most frequent understory cover, although native grasses predominate towards treeline. The canopy cover is far more open in this study area than in others (Fig. 27). Detailed descriptions of the area have been given by Hartt and Neal (1940) and Scott et al. (1984).

KOHALA

Kohala Mountain is the remnant of an old volcanic system forming the northern projection of the island of Hawaii (Figs. 9 and 28). The study area covers 124 km^2 and extends from 300 m to the highest peak, Kaunu o Kaleioohie, 1670 m elevation. Large deep valleys with steep sides (Waipio, Waimanu, Honokane, Pololu) run to the northeast dissecting the volcanic shield. The trade wind pattern of precipitation predominates. Southwest of the study area lies a rainshadow, where the native vegetation has been almost entirely replaced by introduced grasses. Over 95% of the study area is classified as wet habitat, and bogs are frequent. The central portion has the greatest precipitation, the highest values for tree biomass, tree ferns, and matted ferns, and the lowest proportion of introduced plants. Introduced trees, principally conifers, eucalyptus, and guava, are most common on the northwest and southwest edges (Fig. 29). Introduced grasses are common along forest margins. Passiflora was restricted to one locality on the southwest margin. No koa, naio, mamane, or ieie were recorded at any station. The canopy cover is primarily closed to open (Fig. 30). Kohala Mountain is the last known locality for the presumably extinct Ula-ai-hawane, *Ciridops anna* (Munro 1944).

EAST MAUI

The East Maui study area covers 404 km^2 and extends from 200 to 2800 m elevation on Haleakala, a massive shield volcano with a high elevation cinder desert in the summit "crater" (Figs. 10 and 31). The rainfall pattern on East Maui is typical for a high island: heavy trade wind precipitation on windward slopes below the inversion layer, several small convection cells, and dry leeward and high elevation areas. Ohia rainforest covers windward slopes. The zone of mesic habitat is much narrower than on Hawaii due to the smaller size and steeper slopes of East Maui. Pockets

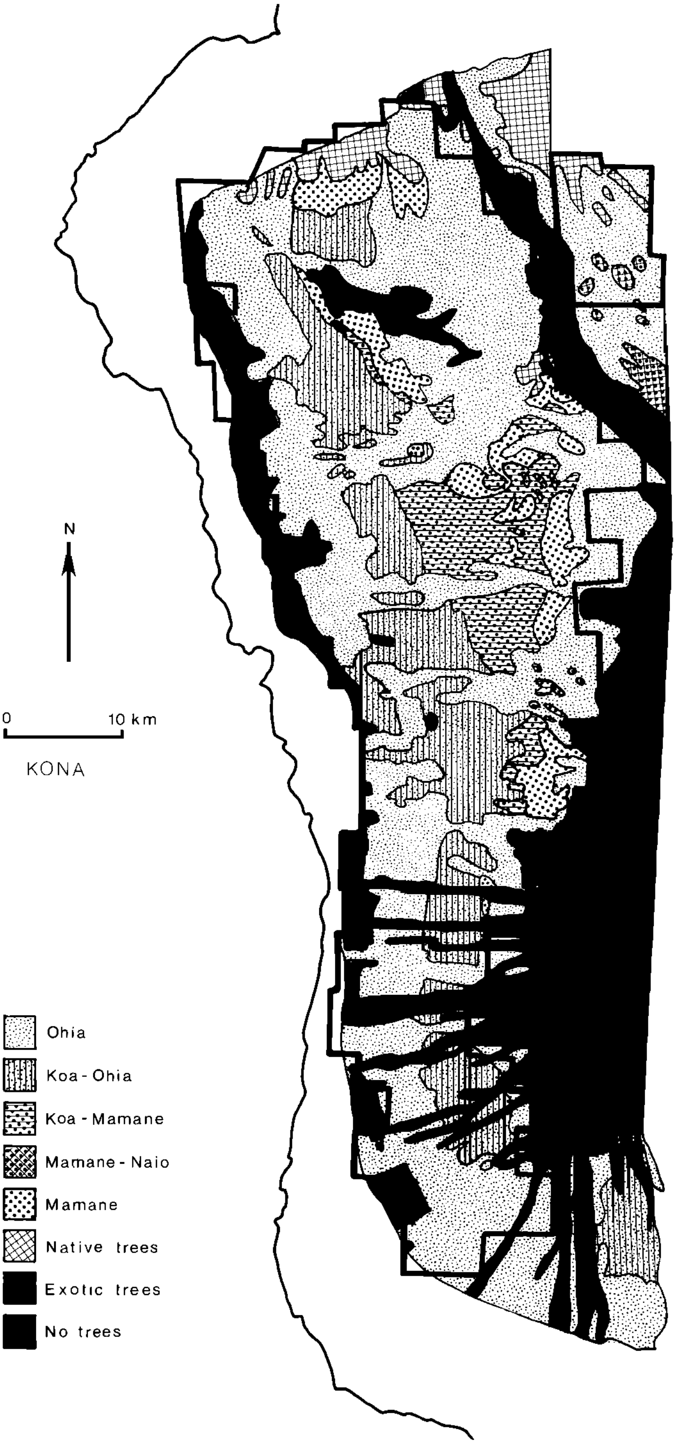


FIGURE 23. Habitat types in the Kona study area.

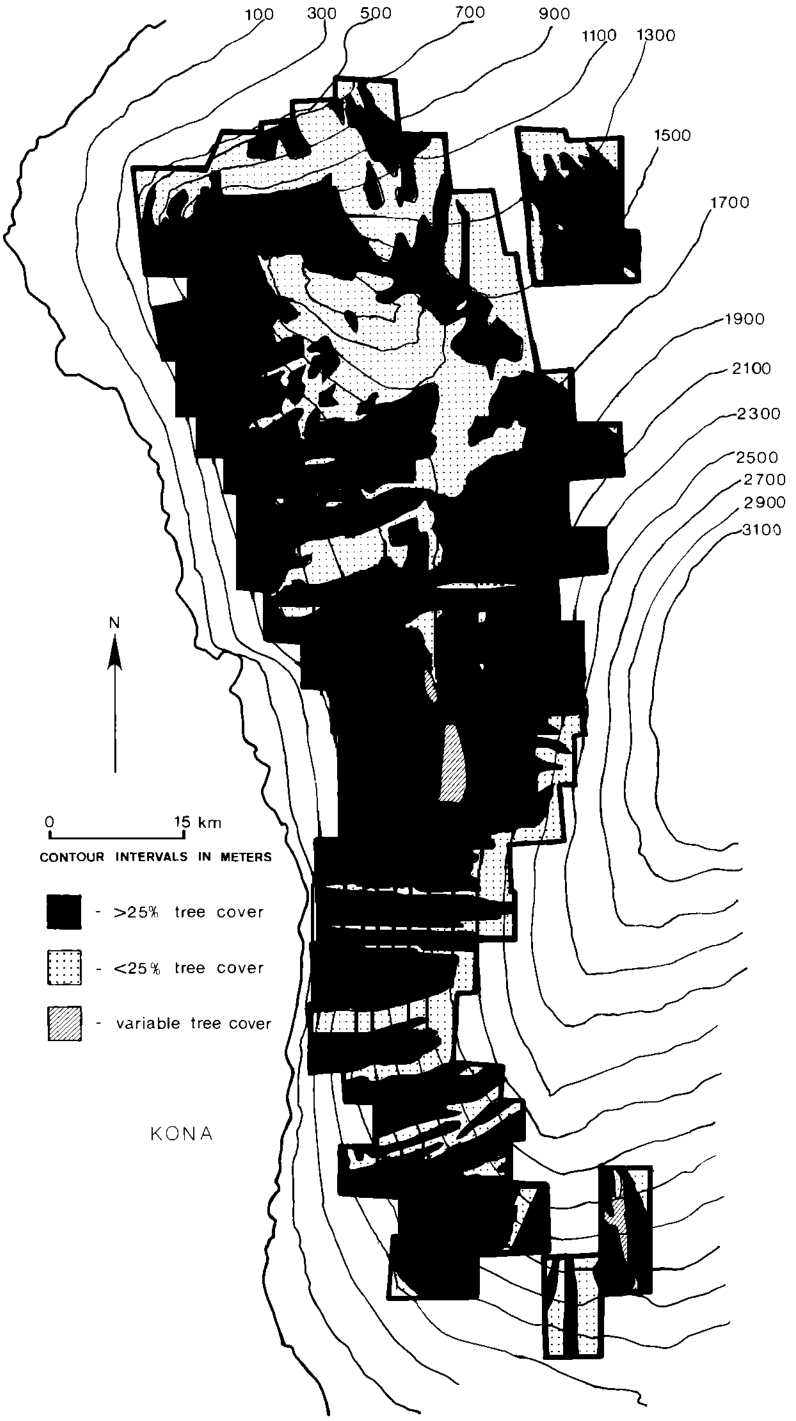


FIGURE 24. Canopy cover in the Kona study area.

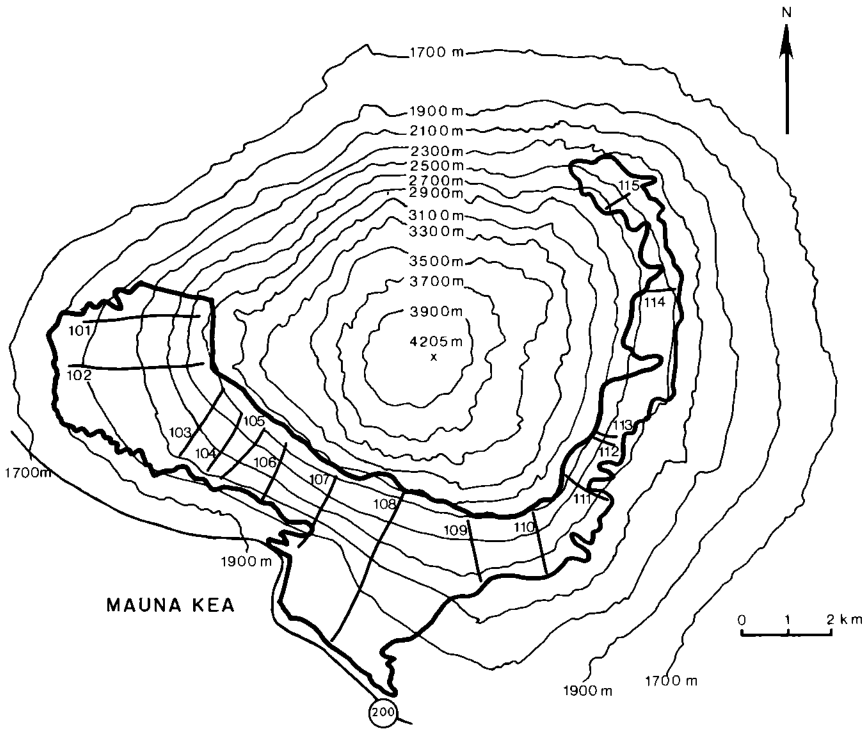


FIGURE 25. Transect locations in the Mauna Kea study area.

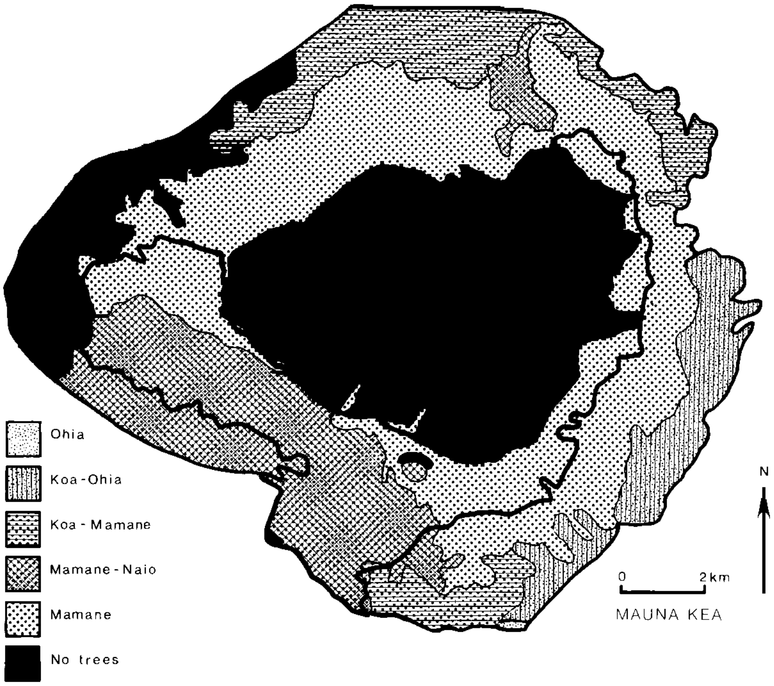


FIGURE 26. Habitat types in the Mauna Kea study area.

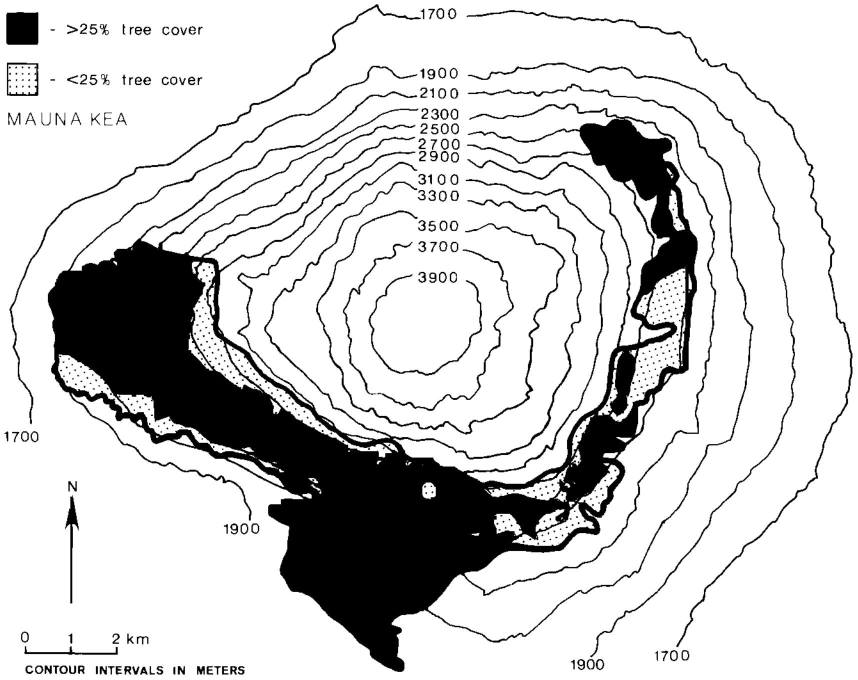


FIGURE 27. Canopy cover in the Mauna Kea study area.

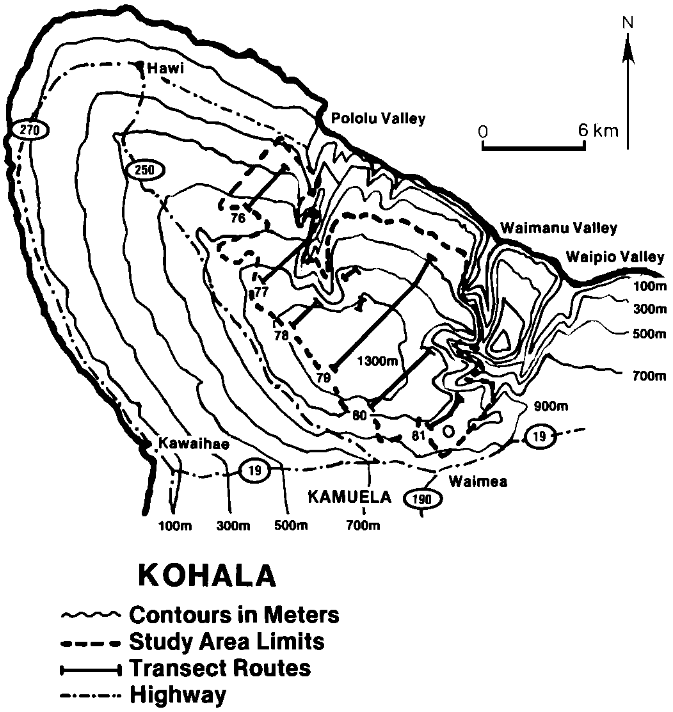


FIGURE 28. Transect locations in the Kohala study area.

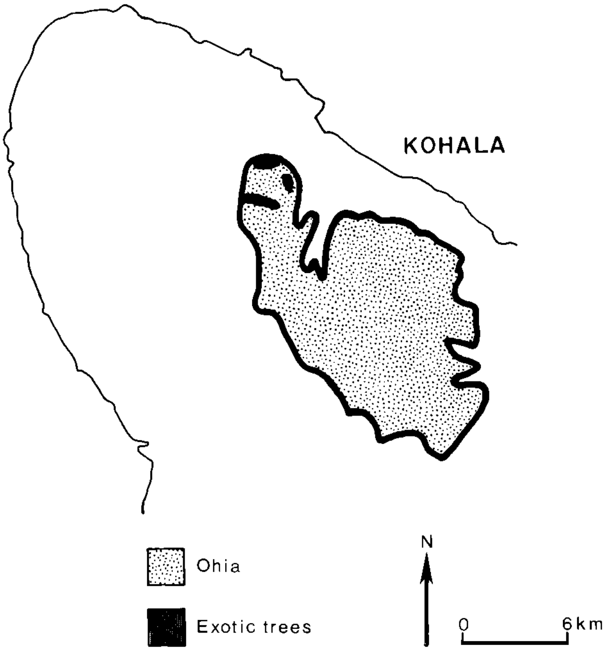


FIGURE 29. Habitat types found in the Kohala area.

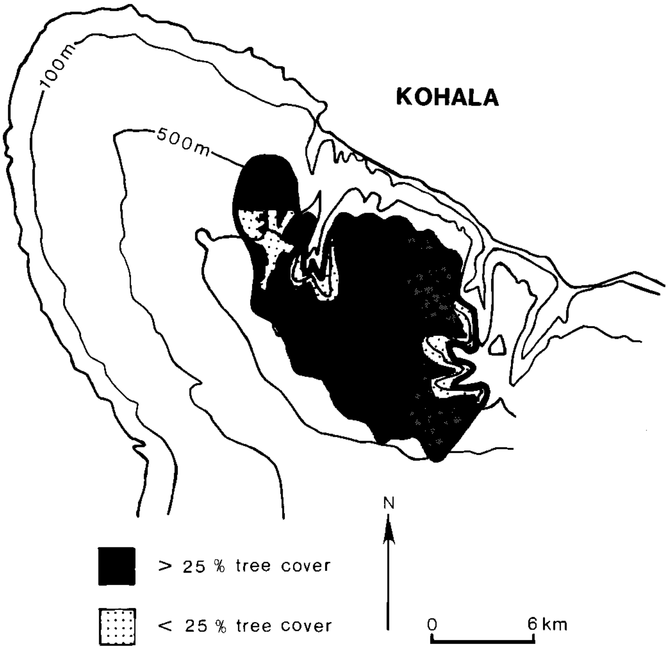


FIGURE 30. Canopy cover in the Kohala study area.

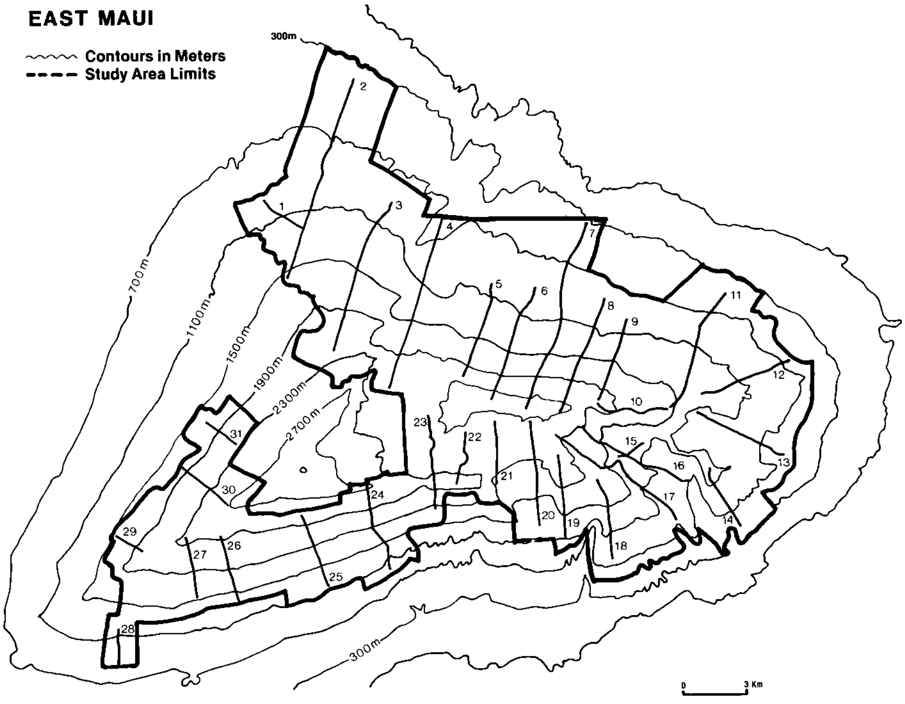


FIGURE 31. Transect locations in the East Maui study area.

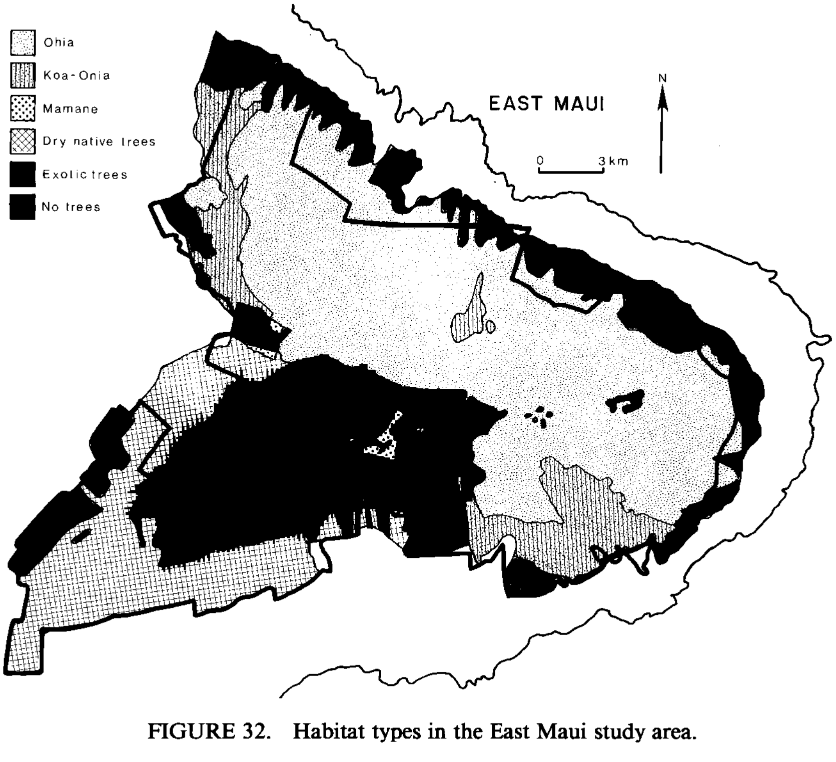


FIGURE 32. Habitat types in the East Maui study area.

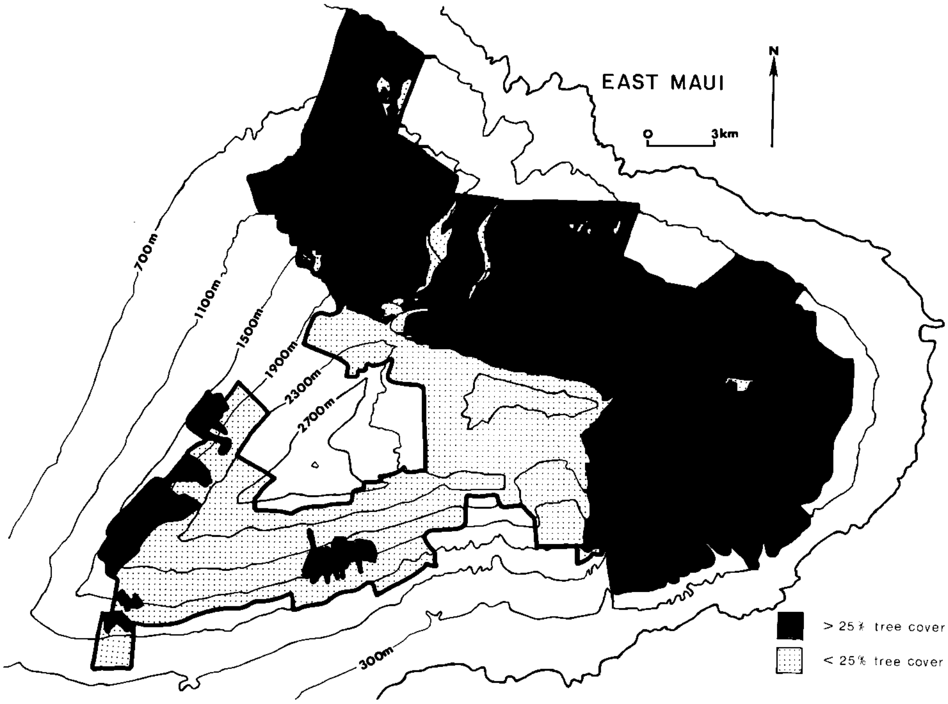


FIGURE 33. Canopy cover in the East Maui study area.

of koa-ohia forest occur northwest of Koolau Gap, in Kipahulu Valley, in Kaupo Gap, and as vestiges on the Kahikinui Tract. The western dry slopes of Haleakala formerly had extensive koa and sandalwood forests that were greatly disturbed by logging and grazing. One remnant area, the Auwahi Tract, is exceptionally rich in endemic dry forest plants (Table 2, Figs. 13, 32). The leeward slopes and crater district of East Maui have a much reduced canopy cover compared to the windward forests (Fig. 33).

Mamane is fairly common on the leeward side and in the cinder desert of the crater. Introduced trees, mainly guava, eucalyptus, and conifers, occur at lower elevations and along disturbed forest edges. Matted ferns are common in ohia dieback areas. Tree ferns are less common than on Hawaii, but still widespread. Passiflora outbreaks are small and confined to localized areas. Introduced grasses are common and widespread on ranchlands. Well-developed bogs occur locally near Lake Wai Anapanapa.

Many endemic birds occur only in the high montane rainforest on the northeast slopes of Haleakala. The Ou and Olomao were the only species lost from East Maui in historic times.

WEST MAUI

The West Maui study area covers 44 km^2 and extends from 250 m to the highest peak, Puu Kukui, 1764 m elevation (Figs. 10 and 34). The West Maui Mountains, a volcanic system separate from Haleakala, are incised by deep amphitheater-headed valleys (Stearns 1966). Puu Kukui does not rise above the inversion layer, and very wet ohia rainforest covers most of the study area (Fig. 35). The many ridges, gulches, and bogs in the study area result in a variable canopy cover (Fig. 36).

We recorded no koa, mamane, or naio on West Maui. Forests of introduced trees, sugar cane fields, disturbed dry scrub, and pineapple fields border the area below. Bogs occur on Puu Kukui, its subsidiary ridges, and Eke Crater. Although West Maui has lost all except three native passerines common in historic times, evidence suggests the avifauna was originally as rich as on East Maui.

MOLOKAI

The Molokai study area is located in the forests on the eastern half of the island (Figs. 10 and 37). The area covers 131 km^2 and extends from 250 m to the highest peak, Kamakou, 1515 m elevation. East Molokai consists of eroded lava flows that slope southward and are bounded by sheer seacliffs along the northern shore; these cliffs are punctuated by deep amphitheater-headed canyons. An interior plateau, Olokui, is bounded by cliffs on all sides and is virtually inaccessible to feral ungulates. Molokai does not rise above the inversion layer, and windward areas support rainforest. A rainshadow occurs toward the southwest part of the study area, where mature dry forest remnants occur (Table 2). Naio, mamane, and koa are restricted to this area. Conifers and eucalyptus are common in the western half of the study area. Guava and other introduced trees are common in Pelekunu and Wailau Valleys (Fig. 38), but passiflora was found only in Wai-

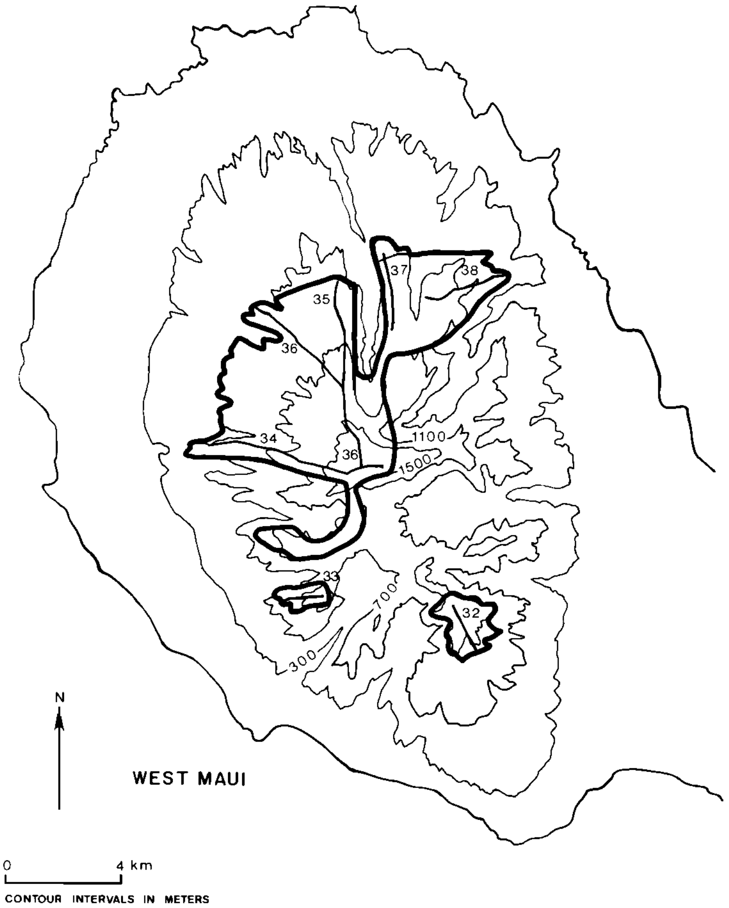


FIGURE 34. Transect locations in the West Maui study area.

lau. Canopy cover in the study area is most open in the southwest and in the east (Fig. 39), where axis deer, feral pigs, and cattle have completely devastated large forest tracts. Many bird species have been lost in historic time, including the Bishop's Oo, Black Mamo, Crested Honeycreeper, and perhaps the Molokai Creeper.

LANAI

The Lanai study area is situated on the slopes of the high north caldera rim (Figs. 10 and 40) where a small remnant of native forest occurs (Fig. 41). The study area covers 20 km^2 and extends from 300 m to the highest peak, Lanaihale, 1027 m elevation. The crest of the caldera has wet forest due to fog interception (Blumenstock and Price 1967) and a weak trade wind effect, but the forest sharply grades into arid habitat at lower elevations. No significant amounts of koa, naio, mamane, tree ferns, ieie, passiflora, or native grasses were recorded. Canopy cover on Lanai (Fig. 42) has been greatly influenced by past land use practices and the impacts of cattle, goats, deer, and sheep, although the low cover on Lanaihale corresponds to an intact native shrub community. All native passerines are extinct except the Apapane and possibly the Common Amakihi.

KAUAI

The Kauai study area is located in the Alakai Swamp region, a high montane plateau dissected by numerous valleys and bordered by sheer canyons (Figs. 11 and 43). The area covers 25 km^2 and extends from 1000 to 1500 m elevation. Mount Waialeale, elevation 1569 m, lies 1 km east of the study area and has the highest mean annual precipitation on earth, exceeding 1500 cm in some years. The study area vegetation consists of very wet, dense ohia forest, and includes few introduced species. Ohia is the only forest type within the study area, although bogs are scattered throughout and a large area of mesic koa-ohia forest occurs northwest of the study area. The canopy cover in the study area is dense (Fig. 44). No koa, naio, mamane, introduced trees, or passiflora were recorded. All 10 bird forms endemic to Kauai occur in the study area, but the Kauai Akialoa may have become extinct since the last sighting in 1965 (Berger 1981, Sincock et al. 1984).

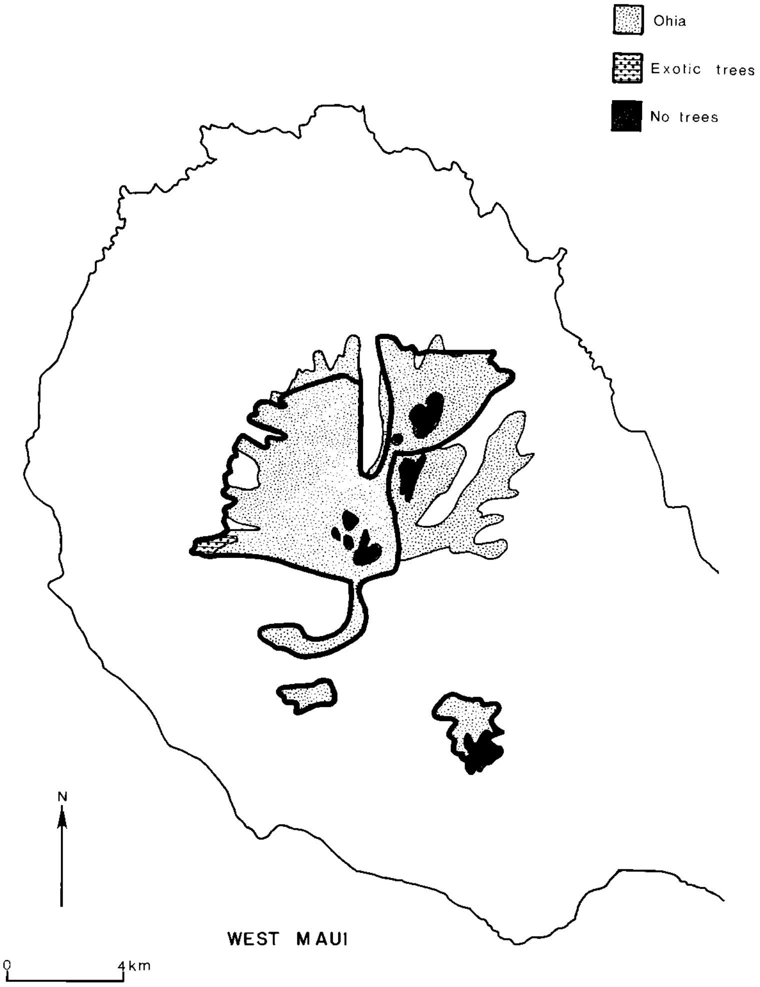


FIGURE 35. Habitat types in the West Maui study area.

FIELD METHODOLOGY

Establishment of Transects

A survey of the scope required to sample all Hawaiian forest bird habitat has never been attempted (Scott, Jacobi, and Ramsey 1981). The analysis presented in this monograph is based on 9940 stations surveyed during 20,789 count periods that recorded over 240,000 birds of 57 species across 4114 km^2 in 12 study areas on 5 islands (Tables 3, 4). Except for the Mauna Kea study area, we chose May–August as our sampling period because it provided reasonably fair weather, birds were conspicuous and vocal, and we were assured of a supply of experienced birders. We selected areas small enough so that they could be surveyed in three months. Our survey of the Mauna Kea study area was designed to maximize efficiency in determining densities of Palila (Scott et al. 1984).

Variation of bird behavior and plant phenology within a season was considered minor in comparison with geographic variation within a study area. The boundaries of each study area were determined from our knowledge of the distribution of native vegetation. The upper elevational limits for the study areas were determined by tree line or the highest point on the island. Lower and lateral boundaries were imposed by such factors as agricultural development, urbanization, or other habitat discontinuities. Because the forests of windward Hawaii were too extensive to survey in a single season, we surveyed the low elevation forest southeast of Route 11, the belt highway (Puna study area) and the dry forest west of Kilauea Crater (Kipukas study area) separately from the main block of generally wet forest that extended from Kilauea Crater to the northeast slopes of Mauna Kea (Hamakua study area).

The map locations of the initial transect in each study area were determined randomly and subsequent transects were systematically placed 1.6 or 3.2 km apart

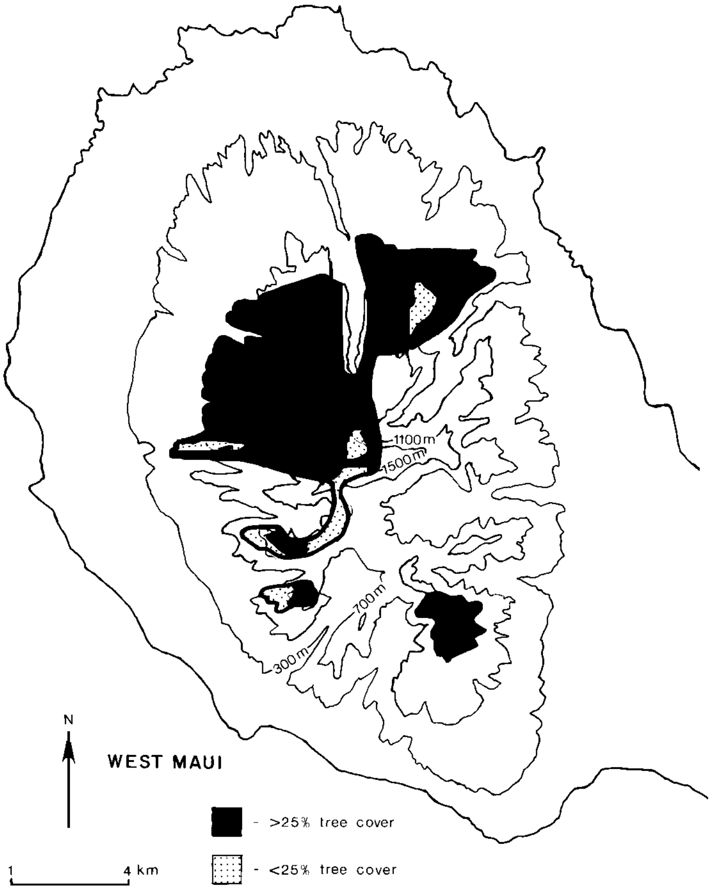


FIGURE 36. Canopy cover in the West Maui study area.

perpendicular to elevational contours. We deviated from this design only on Kauai and Mauna Kea where all transects were randomly located within the known distributional area of endangered species. The distance between transects was 1.6 km in areas where birds were known to have very localized distributions. Transect field locations were placed as close as possible to actual map positions. Two- and three-person teams laid the transects and established sampling stations using measuring tapes and compasses (for details see Ramsey et al. 1979 or Scott, Jacobi, and Ramsey 1981). We placed stations 100 m apart in Kau, 200 m apart on Mauna Kea, 250 m apart on Lanai, and 134 m apart in all other study areas (Table 3). The distance in Kau was based on preliminary estimates of effective detection distances. We increased the station distance to 134 m after analyzing the 1976 data. The greater distances on Mauna Kea and Lanai reflected the more open habitat in these areas. Stations were marked with numbered metal tags and flagging tape. Additional flagging was placed 9 and 18 m before and after each station. These flags alerted team members to an approaching station and were frequently used in calibrating distance estimates. The distance between stations was approximately twice the effective detection distance of the Omao, one of the most vocally conspicuous passerines, in order to provide a high degree of statistical independence among stations.

Observer Training

Ornithologists

We developed a training program to reduce variation among field ornithologists in their ability to detect and identify birds (Kepler and Scott 1981). In 1976 field workers were selected for their familiarity with Hawaiian birds: all but one had two or more years of experience. The least experienced individual underwent rigorous training prior to the survey. All observers spent one week immediately preceding the survey reviewing the forest birds that were more difficult to identify. We gave particular attention to the Hawaii Creeper, whose accurate identification had presented problems for years (Scott et al. 1979). In subsequent years we selected observers based on general birding experience, motivation, temperament, academic background, and physical condition. These ornithologists took part in two to three weeks of training that involved laboratory

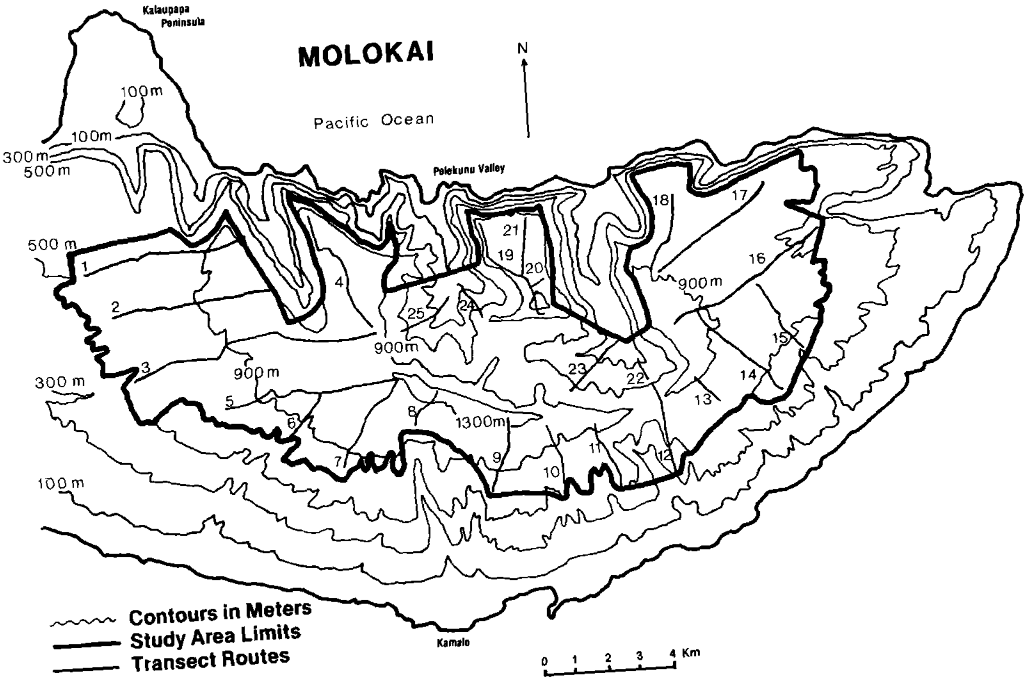


FIGURE 37. Transect locations in the Molokai study area.

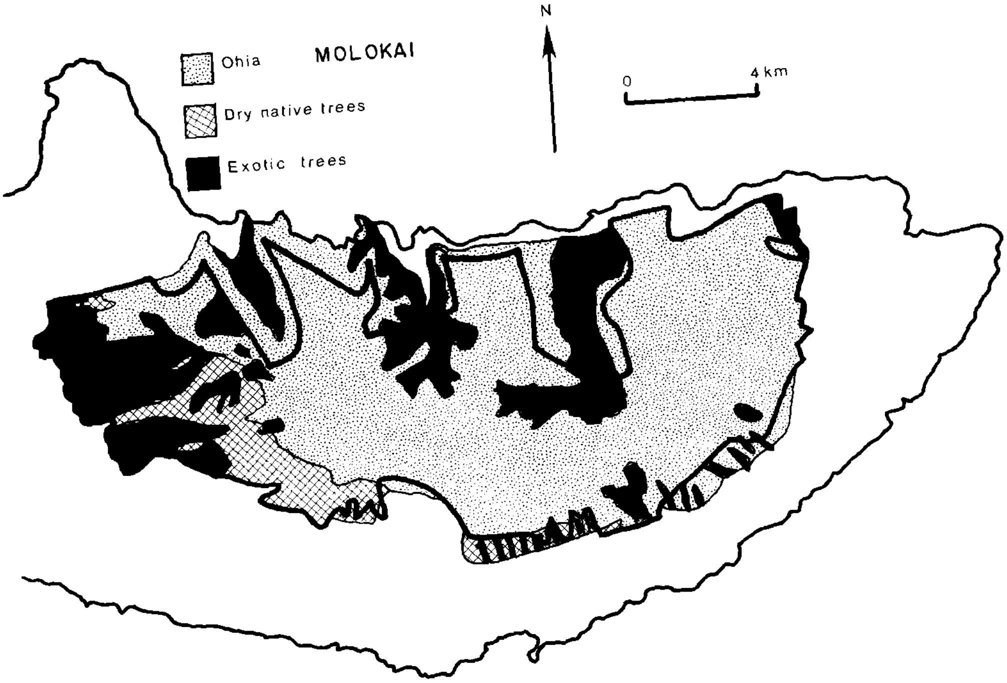


FIGURE 38. Habitat types in the Molokai study area.

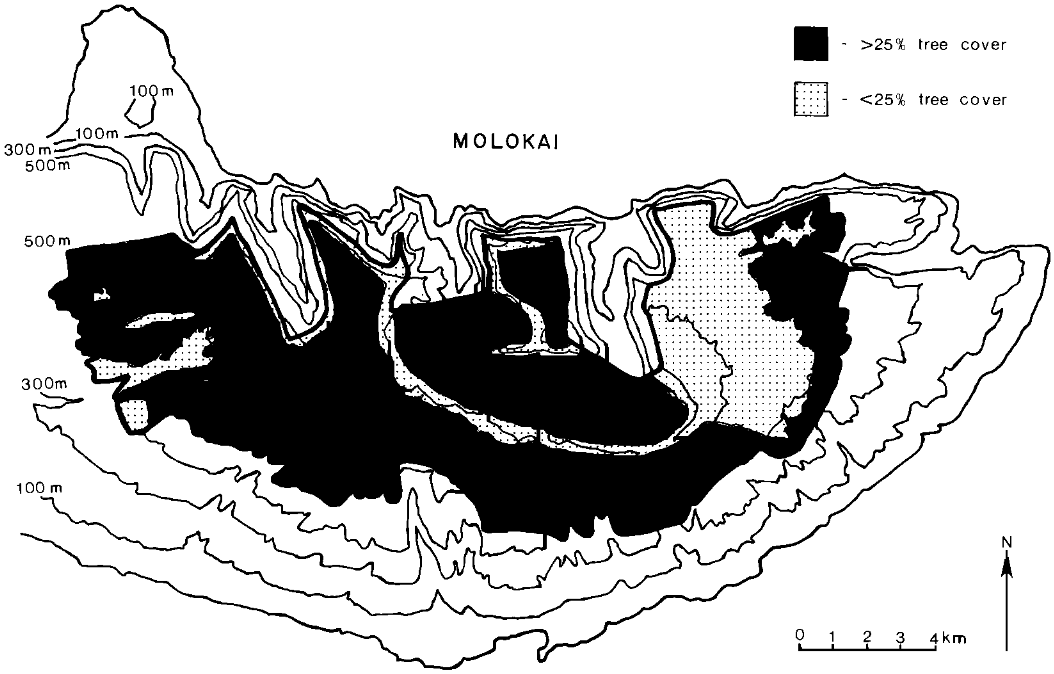


FIGURE 39. Canopy cover in the Molokai study area.

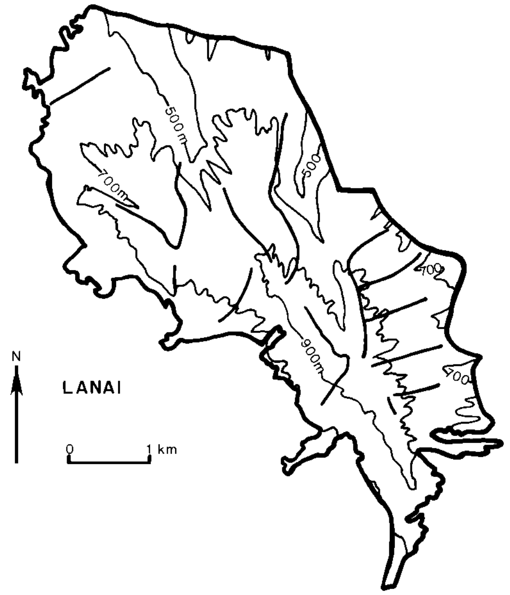


FIGURE 40. Transect segments in the Lanai study area.

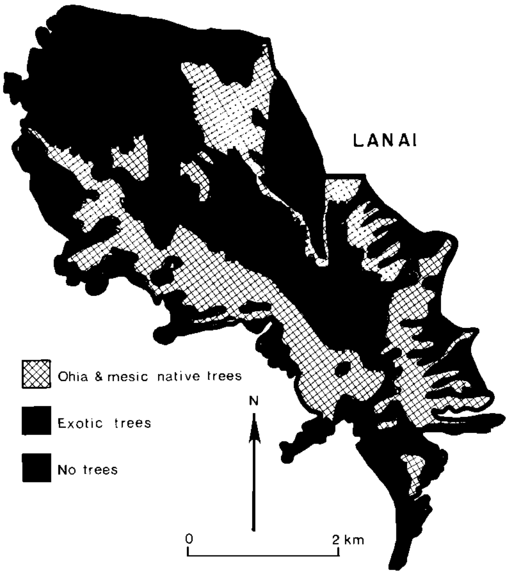


FIGURE 41. Habitat types in the Lanai study area.

TABLE 3
Hawaiian Forest Bird Survey Study Areas

Study area	Survey dates	Distance between transects (km)	Length (km) of transects	No. of stations	No. of count periods	Distance between stations (m)	Observer sequences[a]
Kau	6/22/76–7/23/76	3.2	93	871	1742	100	1
Hamakua	6/18/77–9/1/77	3.2	357	2478	5598	134	2
Puna	5/17/79–6/14/79	3.2	90	669	1338	134	2
Kipukas	5/17/79–8/10/79	3.2	62	460	920	134	2
Kona	5/24/78–7/26/78	3.2	382	2847	5694	134	2
Mauna Kea	2/25/83–3/4/83	random placement, minimum 500 m	65	317	378	150	3
Kohala	7/28/79–8/9/79	3.2	29	215	430	134	2
East Maui	5/22/80–8/17/80	1.6 and 3.2	148	1104	2208	134	4
West Maui	7/27/80–8/21/80	1.6	26	194	388	134	4
Molokai	7/9/79–7/21/79; 8/2/80–8/8/80	1.6	76	568	1136	134	2 and 4
Lanai	5/2/79–5/10/79	N/A	10	77	154	250	2
Kauai	5/12/81–5/24/81	random placement, minimum 500 m	63	140	803	134	2 and 5
Totals			1401	9940	20,789		

[a] Observer sequence codes: 1 = second observer followed first with 5–15 min. delay; 2 = second observer followed first with 10–15 min delay; 3 = single observer 6 min. count period; 4 = specialists and generalists, 18 m apart; and 5 = 18 m apart and back to back.

training, simultaneous counts, pairing with experienced observers, and distance estimation (Kepler and Scott 1981; Scott, Ramsey, and Kepler 1981). The training program became more efficient and thorough with each passing year.

We tested all observers for hearing ability; all but two observers the first year and one in subsequent years met the criteria of Emlen and DeJong (1981) and Ramsey and Scott (1981b). Those with slightly impaired hearing were among the most experienced observers.

Thirty-four observers participated in the HFBS and individuals remained with the program from one to six years. The number of individuals participating in any given year ranged from six to twelve.

Ornithologists carried all their food and equipment in packs when working down a transect (Fig. 45) and remained in the forest until a transect was completed. This ordinarily took five to six days, but one transect took twelve days. Birds were counted only during periods of good weather when the wind registered no more than 4 on the Beaufort Scale (21 km/hr) and there was no appreciable noise from rain or water dripping from vegetation.

Botanists

As with the ornithologists, botanists underwent training prior to each field season. During training, emphasis was placed on calibrating plant cover, phenology categories, and height estimates. Field note formats were standardized to facilitate data transcription.

BIRD SAMPLING

We conducted bird counts during a four-hour sampling period (05:15–09:15 HST). The period was extended one hour on Maui where rainy weather often prevailed, but birders were not required to count for more than four hours.

The sampling period represented a compromise among the vocal conspicuousness of several bird species. As an example, Omao were more conspicuous during the first two daylight hours, whereas Akepa and other species were more conspicuous in the second half of the period. To compensate for this, observers spent four hours after the sampling period looking for endangered birds, observing their behavior, and recording the locations of species not found earlier in the day.

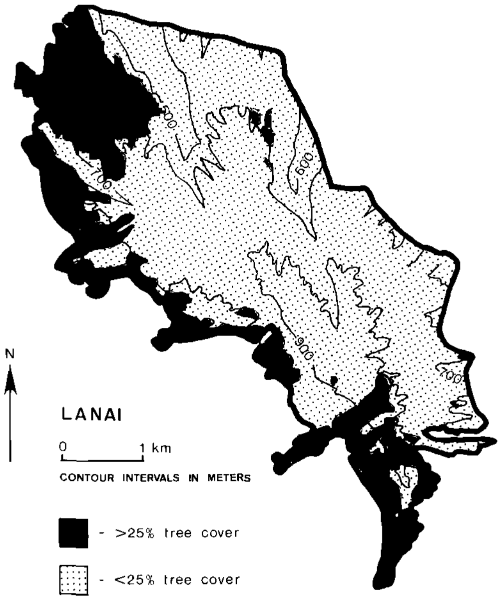


FIGURE 42. Canopy cover in the Lanai study area.

These data were used in determining species ranges and in constructing habitat response graphs.

Observers worked in pairs during the actual survey work. This permitted comparisons between observers and was necessary for safety reasons due to extremely hazardous terrain and volcanic activity in the Puna District of Hawaii. Ornithologists alternated daily being first down a transect. Results of studies of observer variability and sequence effects will be presented elsewhere.

The variable circular-plot method was used to record the occurrence of birds (Reynolds et al. 1980). All birds heard or seen during a count period were recorded as being an aural, visual, or combined detection. The estimated distance to each bird when it was first detected was also recorded. Birds judged not to be utilizing the area surveyed (e.g., flying high over the area) were not recorded (Reynolds et al. 1980). In test conditions, the variable circular-plot method compared in accuracy with spot-map and transect techniques (Anderson and Ohmart 1981, DeSante 1981, Edwards et al. 1981, Szaro and Jakle 1982).

We selected eight minutes as our count period. This period was short enough that our assumption of an instantaneous count was not seriously violated but still long enough to allow an observer to accurately record all birds observed (Scott and Ramsey 1981a).

We used three different sampling designs to avoid

TABLE 4

NUMBER OF STATIONS SAMPLED BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevational strata												
100–300 m	···	···	···	···	···	···	···	···	···	12	···	···
300–500 m	···	25	138	···	18	···	4	13	···	44	···	···
500–700 m	5	205	189	···	171	···	14	58	18	96	10	···
700–900 m	66	383	181	···	335	···	20	112	53	149	41	···
900–1100 m	135	428	134	···	322	···	42	147	39	150	26	···
1100–1300 m	155	449	26	28	402	···	66	148	44	105	···	75
1300–1500 m	158	423	···	72	565	···	55	126	20	17	···	65
1500–1700 m	142	300	···	94	448	···	14	114	18	···	···	···
1700–1900 m	136	161	···	109	266	···	···	111	11	···	···	···
1900–2100 m	66	54	···	148	198	43	···	121	···	···	···	···
2100–2300 m	4	5	···	33	117	39	···	97	···	···	···	···
2300–2500 m	···	···	···	···	24	74	···	38	···	···	···	···
2500–2700 m	···	···	···	···	···	85	···	10	···	···	···	···
2700–2900 m	···	···	···	···	···	65	···	2	···	···	···	···
2900–3100 m	···	···	···	···	···	11	···	···	···	···	···	···
Habitat types												
Ohia	610	1295	642	294	1593	···	204	532	183	424	···	139
Koa-ohia	257	925	···	74	652	···	···	158	···	···	···	···
Koa-mamane	···	32	···	82	209	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	27	163	···	···	···	···	···	···
Mamane	···	···	···	···	195	154	···	7	···	···	···	···
Other natives	···	45	···	30	62	···	···	127	···	45	16	···
Intro. trees	···	126	···	···	89	···	11	88	2	99	54	···
Treeless	···	10	26	4	39	···	···	185	18	5	7	1

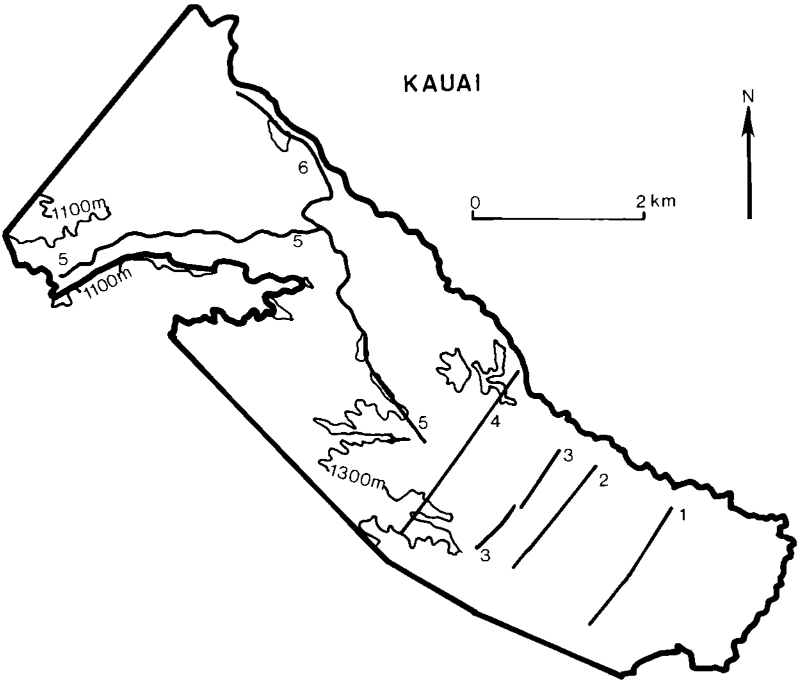


FIGURE 43. Transect locations in the Kauai study area.

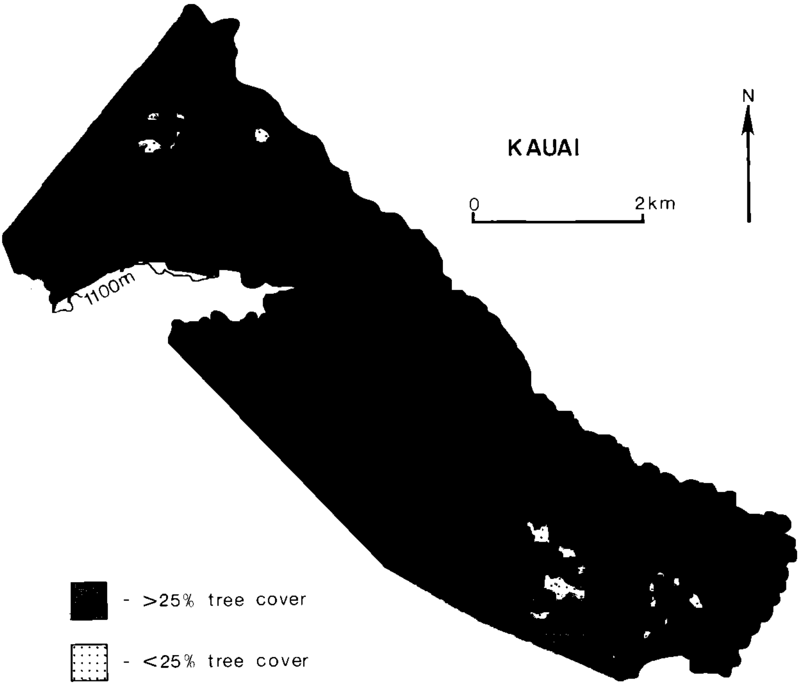


FIGURE 44. Canopy cover in the Kauai study area.

FIGURE 45. Observer at top of transect prepared for ten-day bout in the rainforest in Hamakua study area. Note dense matted fern vegetation. (Photograph by C. B. Kepler)

bias resulting from sequence effects, observer boredom, or observers that were overwhelmed by the number of birds (Scott and Ramsey 1981b): (1) two observers separated by 5–15 min, observers recording all birds observed on all stations; (2) observers placed 9 m before and 9 m after a station, recording simultaneously, and comparing species lists and numbers at the conclusion of counts but making no changes on the data sheets; and (3) observers as in 2, but each observer recording all of the species except one of the two most common species. In all three designs observers counted birds independently of each other (Scott and Ramsey 1981b).

VEGETATION SAMPLING

Botanical survey

We sampled the vegetation in each study area to determine the habitat requirements of the bird species and the factors that affected the distribution and stability of their habitats.

The vegetation was described in three ways. First, detailed descriptions of the vegetation and habitat features were made at each station. Then, at irregular intervals, the vegetation structure and floristic composition were described in intensive detail. Finally, detailed vegetation maps were prepared for each study area.

Field vegetation sampling was done by two-person teams. Vegetation structure was usually sampled at each station within two weeks of the date that bird populations were censused to minimize temporal change in vegetation structure, particularly in flowering and fruiting phenology. Botanists quantified vegetation structure within an estimated 50 m of the station. Since the botanical teams were not limited to a four-hour sampling period, they covered about twice as many stations daily as the bird survey teams. A ratio of one botanical team to two bird survey teams was therefore ideal for this survey.

Detailed habitat description

A habitat description format was developed for the survey, which allowed a rapid, detailed, and consistent assessment of the major habitat features in the field. Habitat information recorded along the transects included (1) general description of the vegetation type;

FIGURE 46. Ecotone between wet ohia forest and mesic native subalpine scrub dominated by *Sadleria, Vaccinium, Styphelia,* and *Coprosma* at 2100–2200 m elevation on East Maui. Note isolated patches of alpine *Deschampsia* grassland, steepness of terrain, and cloud formation marking inversion layer. Entire range of Poouli lies in back and to the right of oval-shaped grassy area. (Photograph by T. L. C. Casey)

FIGURE 47. Dry ohia woodland with native shrub understory at 1500 m elevation near Puu Lehua, Hawaii, with Hualalai in the background. (Photograph by C. B. Kepler)

FIGURE 48. Aerial view of kipukas of mesic ohia forest surrounded by dry ohia scrub pioneering 1852 lava flow from Mauna Loa in background. (Photograph by W. E. Banko)

FIGURE 49. Dry mamane woodland with patchy introduced grass understory at 2400 m elevation on south slope of Mauna Kea. (Photograph by J. D. Jacobi)

FIGURE 50. Closed canopy ohia rainforest with olapa, *Vaccinium,* and *Dubautia* understory at 2000 m elevation along [Lake] Wai Ele'ele on East Maui. (Photograph by J. D. Jacobi)

(2) phenological data for selected plant species; (3) a detailed description of the vegetation structure and floristic composition at selected stations; (4) estimates of maximum, minimum, and modal tree diameter at selected stations; (5) tree stand vigor; (6) occurrence of aggressive weedy plant species; (7) signs of feral ungulate presence and damage to the vegetation; and (8) substrate type.

The vegetation type description included categories for tree crown cover, tree height, tree species composition, and ground cover or understory type (Jacobi 1978). Crown cover was estimated in the following classes: closed canopy (>60% cover), open canopy (25–60% cover), scattered trees (5–25% cover), and very scattered trees (<5% cover, trees widely spaced). Tree canopy height was estimated in three classes: tall stature (>10 m), medium stature (5–10 m), and low stature (2–5 m). When the canopy was distinctly multi-layered, the cover, height, and species composition were noted separately for individual stories.

Vegetation structure and floristic composition were sampled at irregular intervals along the transects using the relevé method (Mueller-Dombois and Ellenberg 1974). Sampling points were taken at the start of each transect and additionally wherever a major change in the vegetation occurred. Total plant cover was estimated to the nearest 10% for all recognizable vegetation layers: ground cover (0–0.5 m), small shrubs (0.5–2 m), tall shrubs (2–5 m), small or sub-canopy trees (5–10 m), and tall trees (>10 m). Additionally, all species within a vegetation layer were listed and their cover rated, using a modification of the Braun-Blanquet (1932) cover-abundance scale. Although our method was based on estimation rather than actual measurement, semiquantitative methods have sufficient accuracy and far greater efficiency compared with more detailed measurements for characterizing vegetation profiles (Braun-Blanquet 1932, Moore et al. 1970, Mueller-Dombois and Ellenberg 1974, Barbour et al. 1980) and are effective in analyzing avian habitat response (Sabo 1980).

Vegetation mapping

Vegetation maps of the study area were prepared in order to relate the bird survey information to the distribution of plant communities. Vegetation map units described the vegetation in a similar but less detailed

FIGURE 51. Dieback of wet ohia forest showing tree fern understory on east slope of Mauna Loa in Hamakua study area. (Photograph by J. D. Jacobi)

FIGURE 52. Remnant dry forest dominated by koa, ohia, mamane, and sandalwood, confined to vicinity of gulch, and surrounded by open eroded pasture at 1400 m elevation on Kahikinui Tract of East Maui. Area formerly inhabited by Maui Parrotbill, Nukupuu, and Akepa. (Photograph by J. D. Jacobi)

FIGURE 53. Mesic koa-ohia forest in Waikamoi Preserve, East Maui, at 1600 m elevation. This forest was more extensive 100 years ago and harbored Ou, Maui Parrotbill, and Nukupuu. The Ou is now extinct on Maui. (Photograph by C. B. Kepler)

manner than field descriptions along transects. Moisture regime, tree canopy cover, tree height, tree species composition, and ground cover type were distinguished.

The distributions of the vegetation units were initially interpreted on aerial photographs at the approximate scale of 1:45,000 using a mirror stereoscope with 3 × and 6 × magnification. These preliminary map units were then verified on the ground during the field season by the botanical teams. An overview of the area from a small airplane or helicopter helped resolve interpretation problems in areas not covered on the ground. Finally, the corrected map unit boundaries from the aerial photographs were compiled on a U.S. Geological Survey 7.5′ quadrangle topographic map base using a Kern PG-2 plotter.

Vegetation map units were the foundation for the habitat response graphs and for determining areas within the range of a species. From the vegetation map units we also constructed eight general habitat types reflecting dominant tree species (ohia, koa-ohia, koa-mamane, mamane, mamane-naio, other native trees, introduced trees, treeless; see Figs. 46–60) for use in stratifying population estimates.

Phenology

We determined the flowering and fruiting phenology for three tree species that were important sources of food for native birds: ohia, olapa, and mamane (Perkins 1903). The 10 trees of each species nearest to the sampling station were scored on a 0–4 scale for the presence of flowers (ohia, mamane) or fruit (olapa, mamane) as follows: 0 = none; 1 = <1% of crown covered; 2 = 1–5% covered; 3 = 5–25% covered; 4 = >25% covered. On Mauna Kea we also determined the phenology of naio fruit.

INSECT OBSERVATIONS

Stations were baited and visual searches made for the carnivorous ant *Pheidole megacephala* at each camp site on Hawaii (approximately every 15th station), because this species may compete for food with insectivorous birds (Perkins 1903, Banko and Banko 1976). During the 1976 survey, light traps and casual obser-

FIGURE 54. Dry lama-ohia woodland with understory completely dominated by fire-adapted fountain grass at 1000 m elevation near Puu Waawaa, Hawaii. Hawaiian Crow formerly bred in this area. (Photograph by J. D. Jacobi)

FIGURE 55. Remnant arid *Erythrina-Reynoldsia* woodland at 150 m elevation, Ulupalakua area, East Maui. Once extensive before Polynesian and western disturbance, woodlands like this one hosted over a dozen species of extinct honeycreepers. (Photograph by C. B. Kepler)

FIGURE 56. Greensword (*Argyroxiphium virescens*, Compositae) bog with native sedges surrounded by ohia rainforest at 1650 m elevation on East Maui. (Photograph by C. B. Kepler)

FIGURE 57. Alpine *Deschampsia* grassland with admixture of introduced grass (*Holcus lanatus*) and native shrubs on ridge at 2300 m elevation on windward East Maui. (Photograph by C. B. Kepler)

FIGURE 58. Remnant woodland on the Auwahi Tract, an area at 1200 m elevation on East Maui with an exceptionally rich assemblage of xerophytic species. Arborescent monocot in foreground is halapepe (*Dracaena aurea*). (Photograph by R. Hobdy)

vation at campsites were used to document the occurrence of *Culex quinquefasciatus* and other mosquito species. We used only casual observations at campsites in subsequent years.

DATA ANALYSIS

ESTIMATION OF EFFECTIVE AREA SURVEYED

Bird densities were determined from the field data using "plotless" or "variable area" survey procedures, where estimation of the area surveyed poses a statistical problem. The theory of variable area techniques originated with studies of line transect surveys (Emlen 1971, Seber 1973, Burnham and Anderson 1976, Ramsey 1979), and was extended to more general survey methods (Ramsey et al. 1979, Ramsey and Scott 1981a), including the variable circular-plot method (Reynolds et al. 1980). Ramsey and Scott (1979, 1981a) outlined the methods to obtain smoothed estimates.

Raw estimates of effective area

Each station was assigned to one of 13 detectability classes (Table 5) based on canopy and understory conditions that affected visibility. Twelve of these classes represented the factorial combinations of crown cover (closed, open, scattered), canopy height (tall, short), and understory (closed, open); class 13 designated treeless stations. Detections were grouped into data cells by species, observer, detectability class, and study area.

Detection distances D were converted to the area X that was searched to obtain that detection as $X = \pi D^2$. Detection areas in each cell were arranged in order of increasing magnitude from 1 to N and then used to construct a cumulative distribution curve (Fig. 61). A line from any point P_1 at (x_1, y_1) to another point P_2 at (x_2, y_2) on the cumulative distribution function has slope equal to the density of detections in area (see Ramsey and Scott 1981a). We constructed the convex envelope of the cumulative distribution function by drawing a straight line from the origin (0, 0) to the point P_1 at (x_1, y_1) that gave the greatest slope of all

TABLE 5

ADJUSTMENT FACTORS FOR THE EFFECTS OF HABITAT CONFIGURATION ON EFFECTIVE AREA

Detectability class	Multiplicative factor
Closed canopy (>60% cover)	
Open understory, height >10 m	1.00
Open understory, height 2–10 m	1.46
Closed understory, height >10 m	0.87
Closed understory, height 2–10 m	0.98
Open canopy (20–60% cover)	
Open understory, height >10 m	1.24
Open understory, height 2–10 m	1.89
Closed understory, height >10 m	1.02
Closed understory, height 2–10 m	1.10
Scattered canopy (<20% cover)	
Open understory, height >10 m	1.84
Open understory, height 2–10 m	3.38
Closed understory, height >10 m	0.85
Closed understory, height 2–10 m	1.16
Treeless	6.79

FIGURE 59. Elfin woodland in Hana Forest Reserve at 1500 m elevation on East Maui. Note dense bryophyte and fern cover on all surfaces. (Photograph by C. B. Kepler)

points on the curve, and extending the envelope from P_1 to the point P_2 that gave the greatest slope beyond P_1, and so forth to P_3, P_4, etc.

The slope of the envelope curve is constant over sections and does not increase as the area searched increases. We used a likelihood ratio rule to decide when the decline in slope (density) from point P_r (x, y) to P_{r+1} (x', y') was significant. Letting M be the slope from the origin to P_r, M' the slope from the origin to P_{r+1}, and m the slope from P_r to P_{r+1}, we considered that the decline in slope from P_r to P_{r+1} was significant at (x^*, y^*), the first point with $y > \sqrt{n}$ (see Ramsey and Scott 1979), such that

$$y\cdot\ln(M) + (y' - y)\cdot\ln(m) - y'\cdot\ln(M') < -2.$$

The raw estimate of effective area surveyed A could then be found graphically by extending the line from the origin through (x^*, y^*) to intersect the line $y = n$, and dropping from there to the horizontal axis (Fig. 61). Therefore, $A = nx^*/y^*$ (see Wildman 1983).

Burnham et al. (1981) suggested that a cell size of $n \geq 30$ was desirable for nonparametric estimates of effective area. We used $n \geq 25$ as a limit with the HFBS data. Even with this cutoff, the majority of cells had too few detections to produce raw estimates.

One potential source of error in estimating effective area was inaccurate estimation of detection distance. Rigorous observer training increased accuracy (Kepler and Scott 1981), and in field tests our observers estimated the distance to birds heard but not seen to within ±10% (range of observer averages, −9.1% to +6.3%) (Scott, Ramsey, and Kepler 1981). The error thus introduced into the area surveyed and the population estimates from inaccurate distance estimates varied from −17.4% to +13.0%, with an average absolute deviation of 9.2%.

Smoothed estimates

Missing cell values were estimated and available cell estimates were smoothed by fitting a model that represented the influence of species, observer, and detectability code on the effective area. Examination of the residuals from a preliminary model justified the inclusion of terrain dissection in the final model.

Let y_{fzod} be the natural logarithm of the raw estimate of effective area in the cell with study area f, species z,

FIGURE 60. Introduced strawberry guava forest typical of wet lowland habitat, 800 m elevation on windward East Maui. (Photograph by C. B. Kepler)

observer *o*, and detectability code *d*, and let n_{fzod} be the number of detections in that cell. The logarithmic transformation stabilized the variance, produced a scale in which factors had negligible interaction effects, but did not yield normally distributed residuals.

The expected effective area was given by:

$$\mathrm{Exp}(y_{fzod}) = a_z + b_o + c_d + g_f, \qquad [1]$$

with a_z as the average log-transformed effective area of species *z*, b_o as the effect of observer *o*, c_d as the effect of detectability code *d*, and g_f as the effect of topography in study area *f*. The model was fit by weighted least squares, with the weights being the square roots of cell sample sizes. Sufficient data were collected on 1747 cells to estimate effects for 28 observers and 13 detectability classes on detecting the 20 most abundant species.

A full examination of all possible interactions was not possible. We fit models with the Kau, Hamakua, and Kona data that allowed for observer-by-detectability interactions and for different effects by seven abundant species (Elepaio, Omao, Red-billed Leiothrix, Japanese White-eye, Common Amakihi, Iiwi, and Apapane). The effects of observers and detectability codes were remarkably consistent among species and were independent of each other. When this analysis was extended to Hawaii Creeper and Akepa, however, the data suggested that one observer was more efficient at locating rare birds than common ones (Scott and Ramsey 1981b). Several other anomalies were found and had rational explanations but they were rather unimportant in comparison with the major factor effects.

To illustrate the relative importance and consistency of effects, we fit separate models like model [1] within each study area (without g_f) and compared the results with the overall model in an analysis of variance (Table 6). The sums of squares and the degrees of freedom are not precisely additive because of the sparseness and imbalance of the cells used. Species differences account for about 37% of the total variation in the logarithms of effective area. Significant variation occurs among study areas in the effective areas for certain species. However, variation in observer adjustments among

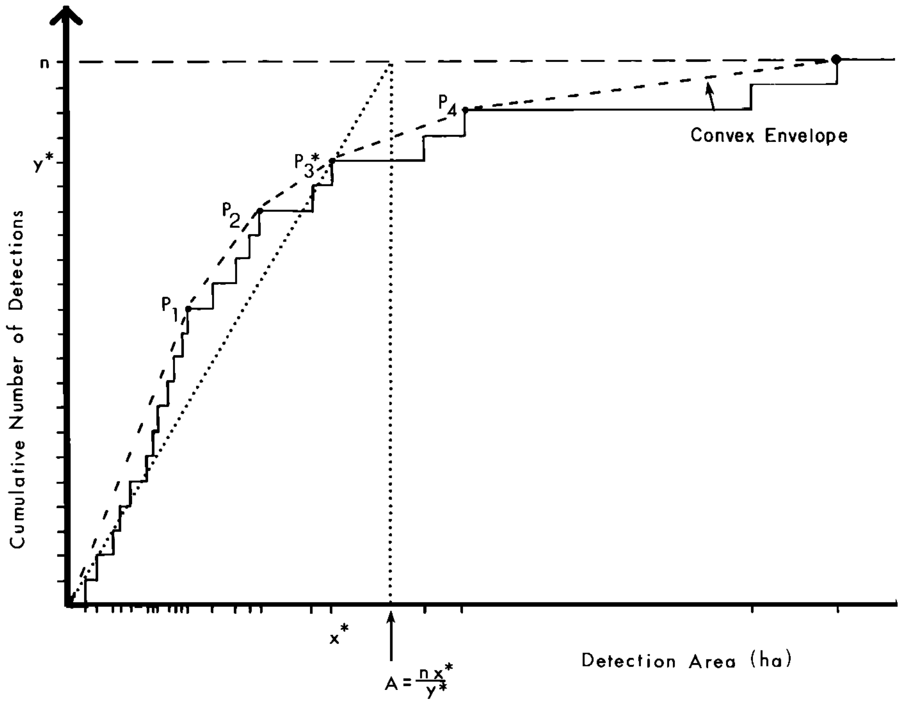


FIGURE 61. The cumulative detection curve and its envelope. In this example a significant decline in slope occurs at P_3. (See pages 48–49 for explanation.)

study areas is nonsignificant, and variation in habitat configuration effects among study areas has relatively minor significance.

The multiplicative factors for observer effects in the general model varied from 0.57 to 2.09 ($\bar{x} = 1.08$, SD = 0.44), suggesting that the best observer covered about four times as much area as the worst. The effects of detectability classes (Table 5) had greater statistical significance than those of observers. Detectability class effects were not satisfactorily explained in terms of a main-effect factorial model of canopy cover, canopy height, and understory cover. The effect of canopy cover depended on the understory: with a closed understory the effective area surveyed was about the same for closed canopy and scattered trees. Where the understory was sparse, however, the increase in effective area surveyed from open canopy to scattered trees was dramatic. This suggested that a single index of visibility might serve as well as our detectability classes. With such an index, observers would classify detectability conditions according to how much total vegetation occurred within a certain distance.

After fitting the preliminary model, we calculated residuals for Japanese White-eye, Common Amakihi,

TABLE 6

ANALYSIS OF VARIANCE FOR THE EFFECT OF SPECIES, OBSERVER, AND HABITAT CONFIGURATION ON EFFECTIVE DETECTION DISTANCE

Source	df	Sum of squares	Mean square	F^a
Species	19	792.67	41.72	157.49***
Obervers	27	15.49	0.57	2.17**
Habitat configuration	12	33.63	2.80	10.58***
Between study areas				
Species	60	830.14	13.84	52.23***
Observers	54	13.37	0.25	0.93
Habitat configuration	52	19.69	0.38	1.43*
Residual	1532	405.84	0.26	
Total	1746	2076.56	1.19	

[a] *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

TABLE 7
EFFECTIVE DETECTION DISTANCES FOR HAWAIIAN BIRDS

Species	Effective detection distance (m)	Method of determination[a]
Hawaiian Goose	200	2
Black Francolin	186	2
Erckel's Francolin	163	2
Gray Francolin	136	2
Chukar	51	1
Japanese Quail	60	2
Kalij Pheasant	42	2
Red Junglefowl	557	2
Ring-necked Pheasant	269	2
Common Peafowl	434	2
Wild Turkey	183	2
California Quail	125	2
Lesser Golden-Plover	53	2
Spotted Dove	150	2
Zebra Dove	124	2
Mourning Dove	150	3
Eurasian Skylark	76	1
Hawaiian Crow	282	2
Japanese Bush-Warbler	73	2
Elepaio	37	1
White-rumped Shama	78	2
Omao	60	1
Kamao	60	1
Olomao	23	3
Puaiohi	50	3
Melodious Laughing-thrush	95	1
Red-billed Leiothrix	56	1
Northern Mockingbird	77	1
Common Myna	89	1
Kauai Oo	150	3
Japanese White-eye	27	1
Northern Cardinal	71	1
Saffron Finch	28	2
House Finch	43	1
Yellow-fronted Canary	31	2
Ou	66	2
Palila	60	2
Maui Parrotbill	50	2
Common Amakihi	32	1
Anianiau	38	1
Nukupuu	39	2
Akiapolaau	80	2
Kauai Creeper	29	1
Hawaii Creeper	44	2
Maui Creeper	28	1
Akepa	34	1
Iiwi	36	1
Crested Honeycreeper	46	1
Apapane	35	1
Poo-uli	23	3
House Sparrow	43	2
Red-cheeked Cordonbleu	28	3
Lavender Waxbill	28	3
Warbling Silverbill	32	2
Nutmeg Mannikin	23	1

[a] Method of determination: 1 = species used in fitting the full model; 2 = species means found by pooling data groups; 3 = distance estimate based on extrapolation from similar species.

Iiwi, and Apapane, and determined the percent of positive residuals within each forest. These ranged from a high of 90% in Kipukas to a low of 30% in Molokai. This wide variability was probably due to topography, particularly the degree of topographic dissection in each study area. A crude measure of the topographic dissection of each study area was strongly correlated with the percent of positive residuals ($r = 0.80$). Our results suggested that steep rugged terrain increased the observer-bird distances required to achieve the same horizontal distances as on flat areas and also concealed some birds in topographic relief. This resulted in reduced detectability and smaller effective areas surveyed. We incorporated this topographic effect into the model by introducing a single variable (g_f) to indicate three general levels of topographic dissection: +1 for Kona and Kipukas; −1 for Molokai, Kohala, and West Maui; and 0 for the other study areas. The estimate of the effect of different terrain translated to 49% higher effective areas in Kona and Kipukas and to 33% lower effective areas in Molokai, Kohala, and West Maui, compared to the other study areas.

Density estimates derived by our procedures may have been subject to other occasional sources of error: field mis-identifications, inaccurate distance estimates, movement of birds, and multiple sightings. Nonetheless, density estimates were preferable to raw numbers because the density estimates statistically accounted for the differential conspicuousness of different bird species, the effect of habitat structure on detectability, and observer variability.

The assumptions behind the density estimates were best met by the native passerines and non-flocking introduced passerines. For most Hawaiian forest passerines at least one and usually several vocal cues were given in an eight-minute period during the morning hours (Ralph 1981; J. M. Scott, unpub. data). We shortened the count period to six minutes on Mauna Kea because Palila gave several cues per six-minute count and such counts detected 95% of the individuals of other species that were detected during simultaneous eight-minute counts (J. M. Scott, S. Mountainspring, unpub. data).

BIRDS PER COUNT PERIOD

Researchers interested in comparing their results with ours may find it useful to convert the density values given in our tables to corresponding birds per eight-minute count period. This can be done by multiplying bird density by the effective area surveyed per count. The effective area surveyed per count is computed from the effective detection distance for a species (Table 7) and the mean multiplicative detectability factor for the appropriate stratum and study area (Table 8). As an example, the density of Elepaio at 1500–1700 m elevation in the Hamakua study area is 226 birds/km^2 (see Table 16). The effective detection distance for Elepaio from Table 7 is 37 m. The raw value of the effective area surveyed would be πr^2, or 4301 m^2. According to Table 8, stations in the 1500–1700-m stratum of the Hamakua study area have a mean multiplicative detectability factor of 1.02, i.e., the actual effective area that was surveyed during the HFBS averaged 1.02 times greater than the raw value due to habitat and observer effects. Thus the effective area surveyed per count would

TABLE 8
Multiplicative Factors for Effective Areas by Elevation, Habitat, and Study Area

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevational strata												
100–300 m	···[a]	···	···	···	···	···	···	···	···	0.90	···	···
300–500 m	···	1.03	1.79	···	1.91	···	0.81	0.66	···	1.17	···	···
500–700 m	2.15	1.20	1.16	···	1.42	···	1.07	1.15	1.43	1.19	1.29	···
700–900 m	0.88	1.15	1.06	···	1.66	···	1.07	1.19	1.38	1.30	2.04	···
900–1100 m	0.89	1.10	1.22	···	1.85	···	1.28	1.23	0.94	1.29	1.24	···
1100–1300 m	1.01	1.12	2.23	2.30	1.98	···	1.17	1.31	1.07	1.13	···	0.97
1300–1500 m	0.97	1.13	···	2.90	2.10	···	0.98	1.54	0.97	1.14	···	1.19
1500–1700 m	0.86	1.02	···	2.49	2.19	···	0.92	1.55	1.19	···	···	···
1700–1900 m	0.84	1.03	···	2.56	2.23	···	···	1.96	1.37	···	···	···
1900–2100 m	1.14	1.55	···	2.67	2.53	2.19	···	2.63	···	···	···	···
2100–2300 m	0.81	2.15	···	3.13	3.11	2.10	···	2.73	···	···	···	···
2300–2500 m	···	···	···	···	2.33	2.12	···	4.02	···	···	···	···
2500–2700 m	···	···	···	···	···	2.16	···	4.30	···	···	···	···
2700–2900 m	···	···	···	···	···	2.19	···	6.45	···	···	···	···
2900–3100 m	···	···	···	···	···	2.19	···					
Habitat types												
Ohia	1.00	1.12	1.31	2.81	1.98	···	1.09	1.31	1.10	1.24	···	1.05
Koa-ohia	0.79	0.96	···	2.24	1.85	···	···	1.09	···	···	···	···
Koa-mamane	···	1.95	···	2.31	2.27	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	2.95	2.19	···	···	···	···	···	···
Mamane	···	···	···	···	2.51	2.12	···	1.84	···	···	···	···
Other natives	···	1.95	···	2.65	2.67	···	···	2.23	···	1.72	2.28	···
Intro. trees	···	1.67	···	···	1.47	···	0.98	1.81	1.07	0.87	1.35	···
Treeless	···	3.22	1.41	5.91	5.29	···	···	3.44	1.79	2.58	2.76	4.30

[a] ··· indicates stratum not sampled in study area.

be 1.02 × 4301 m^2, or 0.0044 km^2. A density of 226 birds/km^2 surveyed over 0.0044 km^2 yields a value of 0.99 birds/count period for Elepaio in the indicated stratum. By an identical procedure, the standard error of 14 birds/km^2 converts to 0.06 birds/count period.

Range Determination

Bird populations and densities in a study area were calculated for those areas within the geographic range of a species. To determine the range, study areas were first divided into geographic cells using 200 m elevational contours and the midpoint lines between transects. We then determined the distributional area for each species using the following criteria.

1) If a bird species occurred in a given vegetation map unit along a transect, its range was interpreted as extending to the limits of that vegetation type within the geographic cell.
2) If a vegetation map unit was sampled within a geographic cell and the bird species did not occur in that vegetation type, then it was omitted from the range for that cell, unless it was adjacent to occupied range on at least three sides and occupied less than 20 ha.
3) If a vegetation map unit was not sampled within a geographic cell but the species occurred in that cell or in the same elevational stratum on an adjacent transect, then we included that vegetation type within the range, unless the species did not occur elsewhere in that vegetation type.
4) If a species was not found within a vegetation type that was sampled in a geographic cell, but was found in the same vegetation type at a lower elevation (for native birds), in the same elevation on an adjacent transect, or as a result of incidental observations, then we included that vegetation type within the range.

If a particular vegetation type was not surveyed in the study area, then density estimates were not determined and the area of that vegetation type was not used in determining population estimates. Density values were plotted by hand and smoothed by eye from seven-point moving averages for the Kau study area maps and from averages over 2–9 stations for other study areas, the exact numbers being a function of sampling intensity. Continuous declines and increases in density were assumed between widely scattered values.

Population Estimates

Determination of population estimates began with the weighted mean densities and the effective areas surveyed at each station. The effective area surveyed for the Kau study area was based on observations made only in that area. All other analyses used pooled samples for all years. Stations were stratified by the eight general habitat types and by 200-m elevational intervals. Within each stratum we calculated the average density and its variance for those stations that fell within the species range. The average densities were mul-

TABLE 9
HABITAT AND AREA IN ASSUMED ORIGINAL RANGE OF NATIVE BIRDS

Species	Habitat types occupied[a]									Original range (km²)[b]				
										Hawaii	Maui	Molo-kai	Lanai	Kauai
Hawaiian Goose	A	D_1	D_2					S	G	4084	809	410	332	336
Hawaiian Hawk	A	D_1	D_2	M_1	M_2	W_1	W_2			7720	···	···	···	···
Hawaiian Rail				M_1		W_1				2417	···	···	···	···
Short-eared Owl	A	D_1	D_2	M_1	M_2	W_1	W_2	S	G	9033	1824	672	365	1429
Hawaiian Crow	A	D_1	D_2	M_1	M_2					5028	···	···	···	···
Elepaio	A	D_1	D_2	M_1	M_2	W_1	W_2			7720	···	···	···	1429
Kamao	A		D_2	M_1	M_2	W_1	W_2			···	···	···	···	1429
Olomao	A	D_1	D_2	M_1	M_2	W_1	W_2			···	1805	672	365	···
Omao	A	D_1	D_2	M_1	M_2	W_1	W_2			9033	···	···	···	···
Puaiohi				M_1	M_2	W_1	W_2			···	···	···	···	1094
Kauai Oo	A	D_1		M_1	M_2	W_1	W_2			···	···	···	···	1429
Bishop's Oo	A	D_1	D_2	M_1	M_2	W_1	W_2			···	1805	672	···	···
Hawaii Oo	A	D_1	D_2	M_1	M_2	W_1	W_2			7720	···	···	···	···
Kioea				?						?	···	···	···	···
Ou		D_1	D_2	M_1	M_2	W_1	W_2			7043	1485	501	186	1368
Palila	A	D_1	D_2							2771	683	410	332	336
Lesser Koa-Finch	A	D_1	D_2	M_1	M_2					4543	···	···	···	···
Greater Koa-Finch	A	D_1	D_2	M_1	M_2					4543	···	···	···	···
Kona Grosbeak	A	D_1	D_2	M_1	M_2					4543	···	···	···	···
Maui Parrotbill	A	D_1	D_2	M_1	M_2	W_1	W_2			···	1805	672	365	···
Common Amakihi	A	D_1	D_2	M_1	M_2	W_1	W_2	S		9033	1815	672	365	1429
Anianiau		D_1		M_1	M_2	W_1	W_2			···	···	···	···	1368
Greater Amakihi						W_1	W_2			3178	···	···	···	···
Akialoa	A	D_1	D_2	M_1	M_2	W_1	W_2			7720	···	672	365	···
Kauai Akialoa	A	D_1		M_1	M_2	W_1	W_2			···	···	···	···	1429
Nukupuu	A	D_1	D_2	M_1	M_2	W_1	W_2			?	1805	672	365	1429
Akiapolaau	A	D_1	D_2	M_1	M_2	W_1	W_2			7720	···	···	···	···
Kauai Creeper	A	D_1		M_1	M_2	W_1	W_2			···	···	···	···	1429
Hawaii Creeper				M_1	M_2	W_1	W_2			4949	···	···	···	···
Maui Creeper	A	D_1	D_2	M_1	M_2	W_1	W_2			···	1805	513	365	···
Molokai Creeper				M_1	M_2	W_1	W_2			···	···	262	···	···
Akepa				M_1	M_2	W_1	W_2			4949	1015	···	···	1094
Ula-ai-hawane						W_1	W_2			3178	···	···	···	···
Iiwi			D_2	M_1	M_2	W_1	W_2			5730	1122	262	33	1094
Hawaii Mamo						W_1	W_2			3178	···	···	···	···
Black Mamo						W_1	W_2			···	···	159	···	···
Crested Honeycreeper				M_1	M_2	W_1	W_2			···	1015	262	···	···
Apapane		D_1	D_2	M_1	M_2	W_1	W_2			5730	1122	262	185	1094
Poo-uli				M_1	M_2	W_1	W_2			···	1015	···	···	···
15 species extinct honeycreepers	A	D_1								1990	683	410	332	336

[a] Habitat types: A = arid low elevation woodland, D_1 = dry lowland forest, D_2 = dry montane forest, M_1 = mesic lowland forest, M_2 = mesic montane forest, W_1 = wet lowland forest, W_2 = wet montane forest, S = alpine scrub, G = alpine grassland.

[b] ··· indicates species assumed not to have occurred originally on this island.

tiplied by the total areas of the strata within the species range, and these were added to obtain a population estimate. A confidence interval for the population estimate was computed from the pooled estimate of variance (Ramsey and Scott 1978, 1979, 1981a).

UNRECORDED SPECIES

The status of some native Hawaiian forest birds has been the subject of much speculation. Since 1950 several species believed extinct have been rediscovered (Richards and Baldwin 1953; Pekelo 1963a, 1963b; Richardson and Bowles 1961, 1964; Banko 1968; Shallenberger and Vaughn 1978; Sabo 1982).

It is possible that species that occur in areas we surveyed were missed by our sampling efforts. We assumed that the effective detection distance for each of the possibly undetected species was similar to related extant species, and that the current range was similar to that of extant species with similar habitat preferences. These values were used to determine the probability of detecting at least one individual in randomly distributed populations of 10, 50, and 100 birds within the presumed range.

Using similar extant species, we estimated an effective area surveyed for the unrecorded species at each station, taking into account observer and detectability effects. The sum of effective area over all stations in the range gave *a*, the total area effectively surveyed for the species. Given a total area A in the species range, the probability of recording at least one individual of a species with a population of N was approximated as

$$P = 1 - (1 - a/A)^N.$$

We considered the probability statements to be extremely conservative because they assumed each point was sampled only once (we sampled each one at least twice) and ignored the many hours spent by us and others looking for these species outside the eight-minute count periods.

ORIGINAL RANGES

In order to compare the present range of a species with the original range prior to Polynesian contact, we constructed maps (Figs. 4–8) that show in a general way the probable vegetation zonation before human disturbance, using maps modified from Ripperton and Hosaka (1942). We then turned to early historical accounts of ranges and habitat preferences (primarily Palmer in Rothschild 1893–1900, Henshaw 1902, Perkins 1903, and Munro 1944) and fossil records (Olson and James 1982b) to infer the vegetation zones and islands that we assumed species originally inhabited. We then computed the area of the species range on each island (Table 9). It should be realized that this procedure gave at best an approximation of the original ranges, because of the selective and incomplete nature of fossil deposits and of the areas studied by early workers (remote montane areas had few fossil deposits and were often neglected by workers; Hawaii had fewer lowland fossil deposits than other islands because of its comparative geological recency). Nonetheless, we felt the attempt to "reconstruct" original ranges provided valuable insights into the present status of a species.

ANALYSIS AND INTERPRETATION OF HABITAT RESPONSE

From the HFBS data base we developed a landscape perspective (Whittaker 1967, Whittaker et al. 1973) for habitat response patterns; that is, we attempted to describe the response of a species in terms of habitat elements that varied between the communities that constituted the landscape of the study area. Whenever the responses of several species have been compared across a range of habitats, they have been found to be individualistic, with their modal responses scattered along landscape gradients, and their distributions overlapping broadly (Whittaker 1972). The principle of species individuality, first articulated by Ramensky (1924, 1983) and later emphasized by Gleason (1926, 1939), prompted us to focus the analysis on individual species and then to infer the underlying limiting factors of a species from repeating themes in the habitat response patterns.

The study of habitat response required a multivariate approach because many components were involved in habitat structure (Green 1971). Beals (1960), James (1971), Shugart and Patten (1972), and Anderson and Shugart (1974) were among the first to apply to birds the classical multivariate techniques that are widely used in describing habitat response patterns. Equally important to interpreting habitat response patterns have been studies on physiological and morphological adaptations, reproductive biology, wintering habits, predation, food limitation and competition, plant-insect-bird interactions, historical factors, etc.

The objectives of habitat analysis were to (1) evaluate the strength of association of individual habitat variables with species habitat response, (2) compare variation in habitat response of a species across different study areas, (3) evaluate the effect of interspecific competition between ecologically similar species in modifying habitat response, and (4) analyze the habitat response of synthetic variables that describe community structure in terms of species richness (number of species), and bird species diversity.

Although the term "habitat selection" appears frequently in the literature of bird-habitat relationships, we preferred the more neutral term "habitat response," in the sense of a statistical association with an underlying stimulus factor.

Habitat variables

Each station was classified into one of three moisture classes on the basis of the field description of floristic components: dry, mesic, and wet. An extensive series of indicator species was used to determine the appropriate moisture class for a station. Initially we sought to include precipitation, as given by standard rainfall maps, to indicate moisture, but the maps were inaccurate in some areas and other factors interfered. The moisture classes that we used integrated precipitation with the water-holding capacity of the soil, fog drip, local drainage, relative humidity, and other factors. Dry forests pioneering recent lava flows, for example, lie adjacent to wet forests in areas of heavy rainfall.

Because of our on-going development of techniques for quantifying habitat structure, habitat structure was characterized differently in the Kau and Hamakua study areas (1976–1977) compared with later work. In Kau and Hamakua, individual understory components were not recorded unless present as substantial cover (>20%), usually leading to an underestimate for sparse ground cover types. Although the difference did not affect analyses of habitat response within a study area, it affected comparisons of responses in Kau and Hamakua with responses in study areas surveyed later.

The habitat, or independent, variables that entered the habitat analysis as primary data for each station, together with comments on their measurement and justification for their inclusion, follow. (The mean and standard error for these variables, stratified by elevation, habitat type and study area, may be found in the Appendix).

Moisture.—A score of 2 was given to stations classified as dry, 4 to mesic, and 6 to wet. A small number (<1%) of stations were classified as intermediate to the main groups. The use of a mid-value for the mesic group assumed that bird response to mesic habitat was about midway between habitat responses to dry and wet habitat. An initial analysis using two dummy variables (dry/not dry and wet/not wet) showed that this assumption was generally appropriate.

Elevation.—Elevation above mean sea level in meters was determined from the standard U.S. Geological Survey 1:24,000 topographic map series and from readings made at each station with an altimeter calibrated to control points on the U.S.G.S. topographic map.

Tree biomass.—An index of forest development was calculated as crown cover in percent times canopy height in meters. Tree biomass also indexed foliage volume. Vegetation and canopy volume were used in analyzing avian habitat response by Sturman (1968), Karr and Roth (1971), Sabo (1980), and Rice et al. (1983).

Crown cover.—Crown cover was entered as percent cover. Observers were trained to divide classes at 5%, 25%, 60%, and 80% cover values. In the analysis, cover was entered as the midpoint value for the cover class to which the station was assigned. In the field some stations were given cover values intermediate to the designated classes, and the analysis preserved such values. In some cases cover values summed to $>100\%$ due to multi-layering in dense canopies.

Canopy height.—Canopy height was entered as the height in meters of the highest canopy layer. Observers were trained to divide classes at 2, 5, 10, and 25 m heights. In the analysis, height was entered as the midpoint value for the height class to which the station was assigned. In the field some observers designated intermediate heights to the established classes, and the analysis preserved such data.

Dominant tree species.—Five dominant tree types were used as separate variables in the analysis: koa, ohia, naio, mamane, and introduced trees (mainly guavas, eucalyptus, and Christmas-berry). The values entered were the tree biomass for that tree type.

Understory summaries.—Shrub cover was computed as the total cover of plants with shrub-like habit above 50 cm height; ground cover as the total cover of plants with stature below 50 cm height.

Understory components.—Eleven understory types were entered as variables in the analysis as percent cover: native shrubs, introduced shrubs, ground ferns (sum of native and introduced species), matted ferns, tree ferns, ieie, passiflora, native herbs, introduced herbs, native grasses, and introduced grasses. Due to methodological differences mentioned earlier, ground fern, ieie, and native herbs were not recorded in Kau or Hamakua.

Flowers and fruit phenology.—The mean phenology scores for the 10 trees nearest to the station of ohia (flowers), olapa (fruit), mamane (flowers, fruit), and naio (fruit) were multiplied by the tree biomass variables; these variables indexed the total amount of flowers and fruit of those species in the area.

Community variables

For each station three variables were computed from the bird data to estimate properties of community structure and the relative role of native and introduced species. The variables used and their construction are given below.

Species richness.—Two variables, native species richness and introduced species richness, summarized the number of native and introduced bird species occurring at a station. Originally we also examined total species richness and bird densities for native, introduced, and all species. Our analysis of total species richness and total bird density indicated that these variables behaved like composites of their native and introduced components. This made comparisons between study areas difficult, because the study areas differed greatly in the relative dominance of native and introduced elements. Separate analyses of the native and introduced components were more instructive. Similar questions were raised in our analysis of bird density. By its nature, density weighted individual species disproportionately. We found that composite density variables were strongly influenced by one or two dominant species. In every study area the habitat response of introduced bird density was almost identical to that of the extremely common Japanese White-eye. Where two or three species contributed 80–90% of the native bird density, it was almost impossible to make meaningful comparisons between study areas, because of the idiosyncratic effect of different proportions of the major species. This problem was especially severe in interpreting the effect of tree species and understory variables. Our preliminary analysis suggested that the complexity of community structure was more meaningfully indexed by species richness than by density because richness tended to maintain its integrity between study areas, whereas density was frequently overwhelmed by the responses specific to particular species.

Bird species diversity.—The reciprocal of Simpson's (1949) index of heterogeneity was taken as an estimate of the diversity and dominance of the bird populations at each station. This variable was computed as $1/\Sigma\, p_i^2$, where p_i was the density of species i divided by the total bird density at the station. This measure was interpreted as the number of equally common species required to produce the same heterogeneity as observed at the station (Peet 1974). Simpson's index was better suited to our data than the Shannon-Wiener information index ($-\Sigma\, p_i \log_e p_i$) because the latter was biased for samples with small (10 vs. 50–100) number of individuals (Routledge 1980) and was more sensitive to changes in rare species, which were more likely to be missed during eight-minute counts. The reciprocal Simpson index, however, was more sensitive to changes in the most abundant species (Peet 1974), and thus reflected the degree of dominance by the most common species.

Preliminary screening

Before we constructed habitat response models, the bird and habitat variables were carefully examined for a number of potential problems. Univariate distributions of each variable were examined for outliers and departures from the normal probability function. Each variable was mapped in geographic space to determine inconsistencies in measurement and to identify variables unsuitable for further analysis. Multiple regression was performed on random subsets of the data and the residuals examined for nonlinear trends and heteroscedasticity (variance of subsamples changing with the mean). These preliminary analyses were useful in focusing on key issues and in realizing the limitations of the analysis.

The variance tended to increase with the mean for many variables in the screening process, and therefore all bird densities and all habitat variables except elevation and moisture were transformed by $x' = \log_{10}(x + 1)$ to stabilize the variance. The log transformation brought most variables into reasonable conformance with the multivariate normal distribution and corrected many problems evident in the analysis of residuals. Use of the log transformation has also been appropriate and customary for analyzing population fluctuations as percent changes (Whittaker 1975).

Another result of the preliminary screening was the determination that many bird species demonstrated a curvilinear response to two important variables, elevation and tree biomass. Quadratic (x^2) terms for these variables were therefore included in the analyses to represent curvilinearity. Nonlinear response to other variables occasionally appeared in the analysis of residuals but was relatively rare. Screening also showed that in many Hamakua and Kipukas models, the tree fern and moisture variables usually took on surrogate relations, where one variable served as a proxy for another presumably causal variable (see also the section on interpreting habitat response). Tree fern was eliminated from these models to facilitate interpretation.

Regression models

We sought to implement a multivariate model that (1) accounted for the intercorrelations among habitat variables in order to avoid confounding, (2) could be uniformly applied to all dependent variables in order to facilitate objective comparisons of species, and (3) could be interpreted by readers with a moderate statistical background.

Regression models were constructed from a multiple regression design. The predicted density y of a bird species took the form of

$$y = a_0 + \Sigma\, b_i x_i,$$

where a_0 was the constant term, x_i was the value and b_i the coefficient of habitat variable i. This multiple regression model was based on the analysis of variance (ANOVA) paradigm and permitted statistical significance tests of the overall equation and of individual effects (Draper and Smith 1981). The regression equation took into account not only the effect of the habitat variables on the birds, but also intercorrelations among the habitat variables. This reduced spurious and confounding relations due to surrogate effects. Community variables were subjected to the same analysis as bird densities. Multiple linear regression has been effective in analyzing the responses of individual species (Sturman 1968, Abbott et al. 1977, Dyer 1978, Westman 1981) and community variables (Glenn-Lewin 1976).

Multiple regression equations may be constructed in many different ways, depending on the criteria for entering or deleting variables. We developed a model design that could be implemented on standard statistical packages such as the Biomedical Computer Programs P-series (BMDP, Dixon and Brown 1979) or the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975); an updated version of the latter was used for portions of this analysis.

The model design used was a structured stepwise procedure that worked down through a series of hierarchical levels, adding significant variables to the regression equation and deleting variables that became insignificant as others were added. The process ended at the bottom level when no more variables could significantly enter the model and only significant ones remained in the model; this was the "final model." The final model was therefore arrived at through a series of inclusion and deletion steps (as many as 36 steps were needed in fitting the final model). At each step, the only difference between our procedure and standard forward stepwise regression was that the variables at hierarchical levels below the current entry level were not available for inclusion. The criterion for entry of a variable to the model was a minimum F-to-enter value of 5.00, corresponding approximately to the 0.025 significance level. For variables in the model, deletion occurred when F-to-exit dipped below 3.84, the 0.05 significance level. The significance levels to enter were more stringent than those to exit to ensure that the model with the entering variable (often the pool of potential candidates was large) actually "explained" habitat response better than the model without the variable.

The key feature of this procedure was the organization of variables into hierarchical levels. The hierarchical organization we used (1) gave certain variables perceived as more important, or more extensive, the opportunity to enter the model before more localized variables that may have had trivially higher F values; (2) represented the notion that most birds responded more strongly to a gross habitat feature (e.g., tree biomass) than to a fine one (e.g., native herbs) if the final equation could have included only one of the two variables; (3) organized the entry of correlated variables so that specific interpretations could be made (e.g., tree biomass was entered first as an index of forest development, then canopy height as a particular forest feature, then ohia as one element of the forest, and then ohia flowers as a food resource); and (4) considered linear terms of elevation and tree biomass before quadratic ones.

Following fundamental considerations on the architecture and description of complexity (Simon 1962, Gauch 1982), the hierarchy worked from the general to the specific by proceeding from extensive abiotic variables to increasingly intensive and small-scale variables, down through this series of levels:

1) elevation and moisture—represent abiotic elements such as temperature, moisture, exposure, and precipitation;
2) [elevation]^2;
3) tree biomass—as a general index of forest development;
4) [tree biomass]^2;
5) crown cover and canopy height—specific aspects of forest structure after general forest development has been considered;
6) the five tree types: koa, ohia, etc.—specific dominant floristic elements of the forest;
7) shrub cover and ground cover—general aspect of the understory;
8) the eleven understory types: native shrubs, matted ferns, etc.—specific growth forms and taxa of the understory; and
9) the five flowers and fruit variables—included for passerines as potential food sources.

Habitat response models were computed for each bird species for which we had sufficient data, and for the three community variables in each study area. Because of the small size of the West Maui study area

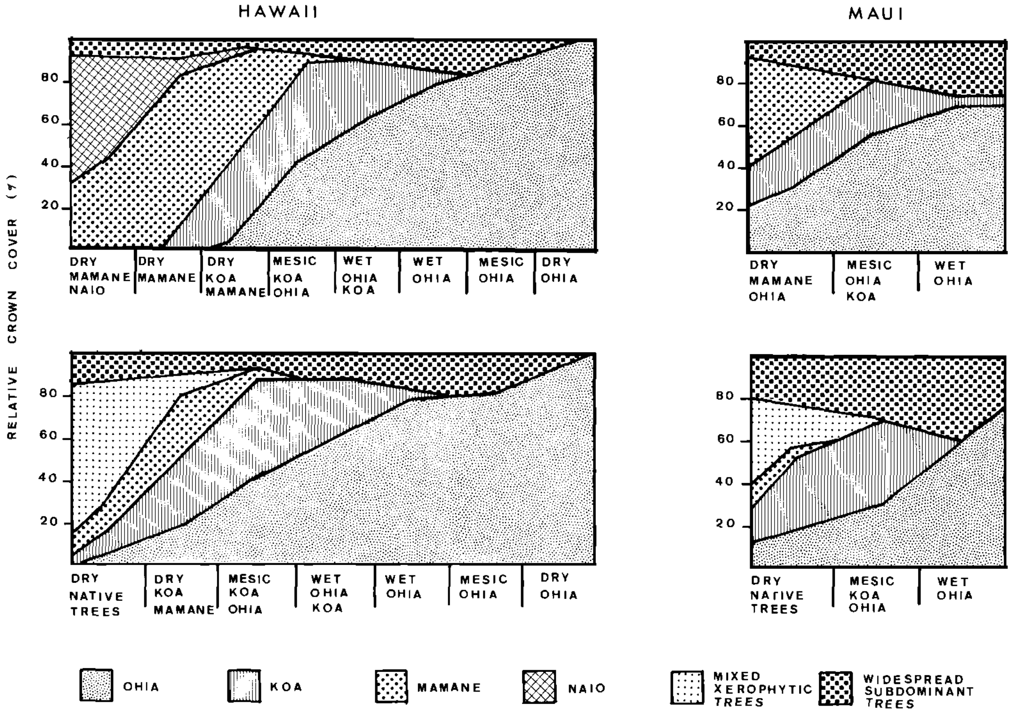


FIGURE 62. Relative abundance of dominant tree species in forest and woodland habitat types on Hawaii and Maui.

and the similarity of bird response patterns on East and West Maui, the two areas were combined in the regression analysis.

Habitat response graphs

Contour graphs of habitat response were used to complement the multiple regression models. Because habitat response graphs require a fairly large number of data points that are well distributed across the habitat space, we constructed contour graphs only for Hawaii and Maui (Figs. 62 and 63). Although the graphs are only two dimensional and thus could not display species response to every habitat component, contour graphs are more sensitive than regression models to nonlinear response and variable interaction, and are straightforward in interpretation once their design is grasped. Contour mapping of the population response to environmental gradients is a form of direct gradient analysis and is one of the best ordination techniques for giving detailed information on the distributions of species (Margalef 1963, Whittaker and Gauch 1978). The technique was pioneered by Whittaker (1952, 1956, 1960), and has been frequently applied to bird distributions in habitat space (Sabo 1980, Rotenberry and Wiens 1981, James and Warner 1982).

The choice of axes for the contour graphs was based on the general results of the habitat response models. The axes represented (1) elevation and mosquito presence, (2) forest development, and (3) moisture and dominant tree composition. A summary of habitat response models presented later (Table 70) showed that the habitat variables representing these axes had significant entries in over half the models.

To represent elevation and mosquito presence, we constructed separate contour graphs for areas above and below 1500 m elevation, the approximate upper limit of mosquitoes in the Hawaiian Islands (see Goff and van Riper 1980). Forest development was represented on the Y-axis by tree biomass (m-%), the product of crown cover (%) and canopy height (m) (as described in the *Habitat variables* section above). The Y-axis was labeled in physiognomic terms: forest (tree biomass >500 m-%—, equivalent to >10 m high, closed canopy); woodland (150–500 m-%—5–10 m high, open canopy); savanna (50–150 m-%— <5 m high, very open canopy, or 5–10 m high, scattered trees); and scrub (<50 m-%— <5 m high, scattered trees, shrubland, grassland, or barren).

Moisture was represented on the X-axis by a gradient from dry to wet. A detailed hierarchical classification of the vegetation types on Hawaii showed two parallel series of vegetation types along this axis that were differentiated mainly by substrate age. On the immature substrates of younger lava flows and ash deposits, ohia dominated dry, mesic, and wet moisture classes. On older lava and ash substrates, mamane, koa, and other native trees dominated dry and mesic areas; ohia dominated the wettest sites. To represent the complex effect of substrate age on vegetation along the X-axis, we pivoted the younger dry and mesic ohia sites away from dry and mesic sites on older substrates. Hence, the

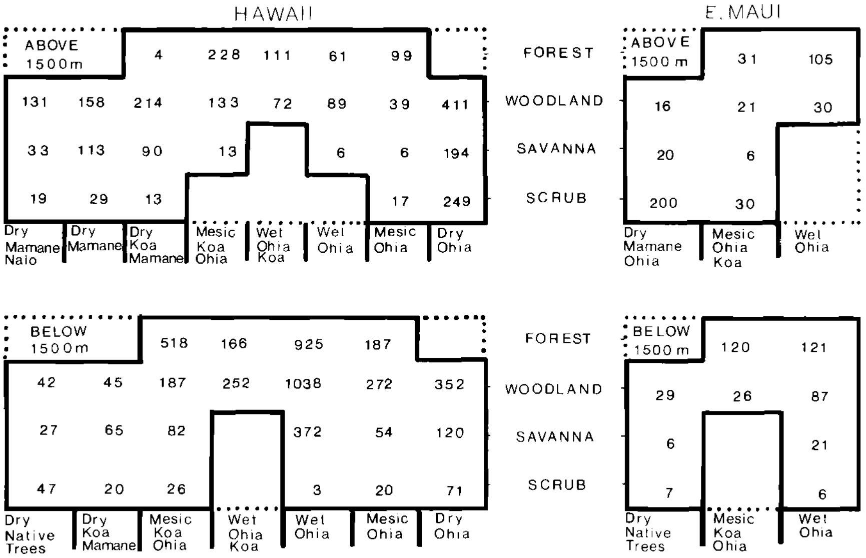


FIGURE 63. Sample sizes for cells on the habitat response graphs.

X-axis extended from drier mamane and koa-ohia sites, through wet ohia sites, to drier ohia sites (Fig. 62). On Maui, recent substrates covered a negligible portion of the study area and did not require differentiation. The X-axis on the Maui graphs thus corresponded to the left half on Hawaii graphs (Fig. 62).

Once the axes were defined, each vegetation type was positioned on the graph. Although some subjectivity was necessary in placing units along the X-axis, tree species composition for the units was recorded below the X-axis to permit objective comparisons. Some differences in tree species composition occurred along the X-axes between areas above and areas below 1500 m elevation, mainly reflecting the replacement of mamane and naio above by a dry native tree association dominated by lama and halapepe below 1500 m. Also notable was the rarity of dry closed forests (especially below 1500 m) and wet scattered forests. On Maui, the narrowness of the mesic zone and its widespread destruction resulted in few samples in mesic areas.

Contour graphs for habitat response were constructed as follows: (1) the location of each detailed vegetation type on the habitat graph was determined; (2) the mean and standard deviation of bird density for the stations in each vegetation type were computed; (3) the mean and standard deviation were plotted on the habitat graph; (4) incidental observations were used to determine the range limits of a species in habitat space; and (5) isopleths were drawn by hand and smoothed, taking sample sizes (Fig. 63) of the vegetation types into account.

Interpreting habitat response

Although multivariate analyses of habitat response frequently appear in the literature, rarely are the bases for interpreting analytical results explicitly described. Because regression models require care in their interpretation, this section describes the main procedures for interpreting habitat response and may be useful to other investigators applying regression or discriminant function analysis to large data sets.

The final equation of the structured regression procedure, the regression model, is a major source of statements on bird response. Each of the 164 regression models has a suite of descriptive and ancillary statistics. The most useful statistics in interpreting these models are the signed t tests for the coefficients of the habitat variables in the final models. These t values usually give a fair indication of the habitat response of a species. The coefficients of the regression equation are useful but sensitive to transformations and the other variables in the model. Due to space limitations, the coefficients and other statistics are not included in the tables that follow but are available at the Mauna Loa Field Station. In addition to the above variables, the partial correlations of variables not in the model, the simple bivariate correlations, and the habitat response graphs were consulted in interpreting response patterns and comparing patterns between study areas.

Quadratic terms for elevation and tree biomass indicate response patterns modeled as parabolas (see also Meents et al. 1983). When the x^2 term is positive, the parabola opens upward (bimodal), and when negative, it opens downward to approximate a bell-shaped curve. The relation of the parabola's axis of symmetry to the actual range of values of the habitat variable is helpful in interpreting a model. The position of the axis is determined by the ratio of the linear coefficient to the quadratic coefficient. When the axis lies below the actual range of values, then the habitat response resembles a linear function (of the same sign from the x^2 term), but leveling off at high values. An axis within the actual range represents bimodal (rare) or bell-shaped response. We use the contour graphs and densities tabulated by elevation to interpret nonlinear habitat response to elevation and tree biomass.

Because of the high dimensional configuration of habitat space, our interpretation of bird response attempts to distinguish the most important effects among many interrelated factors acting simultaneously. In many models a gestalt-like response to several related variables is apparent. Surrogate relations appear among variables that are moderately to highly correlated and are a source of discord when comparing regression models across several study areas. We could not arrange orthogonal contrasts to avoid this as in classic ANOVA, because the distribution of vegetation types was unknown prior to sampling. In models where surrogate relations appear between variables such as tree biomass, crown cover, and canopy height, the relative magnitudes of the *t* tests and the regression coefficients are useful in interpreting the habitat response, as are bivariate correlations with the dependent variable and the habitat response graph.

Methodological differences between study areas in quantifying ground cover in the field may have caused discrepancies for these variables when Kau and Hamakua models are compared with other areas. Another problem is sampling error of the dependent variable when most stations have a value of zero. For rare species, unoccupied areas may still be suitable habitat (Wiens 1981), and the effect of this sort of sporadic rarity on regression analysis is usually a reduction in statistical significance. In many models R^2 values are less than 0.10, i.e., the model explains less than 10% of the total variance. Although such models have low predictive value, R^2 is not the appropriate criterion for judging the usefulness of the model in identifying factors that affect habitat response (Draper and Smith 1981). For this purpose we used the *t* statistics for the individual variables included in the model. As explained below, the importance of individual *t* statistics is interpreted by comparison with other *t* statistics in that model, in other models for the same species, and in models for other species. For rare species we therefore tended to place greater emphasis on the habitat effects identified in a model than the low R^2 values would otherwise seem to warrant.

In addition to the assumptions and mechanics of model construction, the relation of the study area to the geographic range of a species also affects interpretation. If only the periphery of a species range was sampled (e.g., many introduced birds common at low elevations), the patterns sometimes give a misleading impression of the species habitat preferences taken as a whole because the edge of the range represented marginal or sporadically occupied habitat. For some recently introduced species (e.g., Kalij Pheasant and Yellow-fronted Canary on Hawaii), range boundaries are still dynamic, and the regression models may better indicate the habitat currently occupied than the range of habitat that these birds may eventually find optimal.

Significant variation in habitat structure is necessary in the landscape sampled to determine habitat response patterns. The Kauai and Kohala study areas are rather homogeneous, and some models based on these areas show weak or no patterns of habitat response, i.e., not statistically different from sampling within a uniform cluster.

Our data did not exactly meet the assumptions underlying the statistical tests associated with the ANOVA model. The significance levels for the *F* and *t* tests, although often astronomical, were interpreted as indicators of the relative importance of variables, not as exact tests, due to stepwise variable selection and deviation of the data from strict multivariate normality (Draper et al. 1971, Pope and Webster 1972, Johnson 1981a). Variables having large numbers of stations with a value of zero usually deviate from the normal distribution; in such cases the regression model still provides the best unbiased linear estimator (Draper and Smith 1981) even though the significance tests are inaccurate (Bradley 1968).

Comparison of the regression models for a given species across different study areas shows that each area has unique peculiarities that tend to reappear when examining the regression models for other bird species. It was therefore appropriate to interpret a particular habitat response model in a relativistic manner, i.e., the relation of species *X* to habitat variable *Y* in a given area was indicated not only by significance tests but also by *X*'s response to other variables in that model, the nature of that model compared with other models for species *X*, and the patterns of the models for species *X* compared with the models for other species. Thus a *t* value of 5 (highly significant) was of great importance in some models (e.g., those for study areas with smaller sample sizes or for very rare species) and of relatively little importance in others (e.g., a model with large sample size that included six variables with $t > 10$). For each species we noted the principal effects along with the basis for their interpretation. We attempted to reconcile major discrepancies between study areas in each species account in terms of model mechanics, geographical pattern, and historical context.

In many habitat analyses, correlated variables "compete" as possible explanations for a habitat response pattern. In this analysis we impose an ordering from extensive geographic-scale variables (elevation, moisture) to more detailed-scale habitat components because the resulting explanation (1) reflects the role of large scale components as determinants of the small scale ones, (2) is of greater use in developing habitat management strategy, and (3) seems to parallel the conceptualizing faculty of the human mind (Simon 1962). A similar structured approach is found in the technique of path analysis (Turner and Stevens 1959, Overton and Florschutz 1962, Duncan 1966). Although in some instances the imposed ordering may not reflect the biological mechanisms determining the habitat response patterns, important lower level variables still have high significance values in the final model due to the least squares algorithm. When several highly correlated hypotheses compete to explain a particular pattern (e.g., whether a response is due to tree biomass, or to crown cover and canopy height, or to the sum of differentially preferred tree species), our approach is inadequate to distinguish the true "cause" behind the pattern, which in all probability is a complex, unmeasurable gestalt variable. The variable hierarchy then offers a pragmatic first approximation to understanding the pattern.

It must also be recognized that an indefinitely large number of appropriate analyses are possible for identifying habitat response patterns. We were prevented from examining a broader range of techniques because of the time and cost constraints inherent in analyzing large data sets. For example, although nonparametric techniques are preferable to parametric ones (Bradley 1968), for our data set parametric methods were far more cost-efficient. The analysis chosen met our needs and was applied uniformly to all species to facilitate objective comparison. If one or two species were of special interest, a model (and the study itself) could be tailored to reflect current knowledge of habitat requirements.

The vocalizations of some species, such as Red Junglefowl, Ring-necked Pheasant, Common Peafowl, California Quail, Spotted Dove, Hawaiian Crow, Kauai Oo, and Ou, carry long distances. Such birds were sometimes in a different habitat than the observer and could mislead efforts to determine habitat requirements (e.g., gamebirds calling at water), but the usual effect of including these birds in the analysis is to inflate the estimate of variance in habitat response. A solution to the problem would be to instruct the observers to note birds they believed were calling from a different habitat type, and then exclude these records from the analysis of habitat response.

INTERSPECIFIC COMPETITION

The analysis of interspecific competition presented here is a condensed summary of a treatment presented elsewhere (Mountainspring and Scott 1985). We tested for prima facie evidence that competition modified the distribution of the species by statistically removing the effect of the habitat variables on bird distributions and then evaluating the association (negative, neutral, or positive) between each species pair by using partial correlation analysis (see development by Schoener 1974, Crowell and Pimm 1976, and Hallett and Pimm 1979).

SPECIES-AREA RELATIONSHIPS

To approach in a general way the relationship between the number of extant native species and habitat area, we assembled a sample set of 20 major "habitat islands" of montane rainforest. These habitat islands were relatively isolated from one another by degraded and non-rainforest habitat. Data from the HFBS, Sincock's 1968–1973 Kauai survey, Shallenberger's 1977–1978 Oahu surveys, and the open literature were used to tabulate for each area: (1) the probable number of extant native passerine species, (2) the maximum elevation of rainforest, and (3) the approximate area of the habitat island. Multiple regression was used to quantify the statistical relationships among these variables.

COMPARISONS WITH EARLIER SURVEYS

The Hawaiian avifauna has been surveyed with varying intensities a number of times in the past, most notably by Wilson and Evans (1890–1899), Palmer (in Rothschild 1893–1900), Henshaw (1902), Munro (1944), Baldwin (1953), Richardson and Bowles (1964), Berger (1972, 1981), and Conant (1975, 1980, 1981), by Caum (1933) and Schwartz and Schwartz (1949) for introduced species, and by Olson and James (1982b) for fossils. In the species accounts we attempt to compare the present distribution, abundance, and habitat response of native birds with their status as indicated in earlier accounts in order to document historical trends and gain further insight on limiting factors.

A particularly useful study for these purposes was J. L. Sincock's 1968–1973 survey of Kauai. Because the results of this survey were partly unpublished, not widely available (Sincock et al. 1984), and Sincock has kindly granted us access to them, we briefly outline his research to give an idea of the techniques and magnitude of that survey. J. L. Sincock (pers. comm.) recorded all birds seen within a constant distance along a transect of known length that he slowly walked during a 30 min period. He censused 866 transects at 50 sites that were randomly located within seven strata that represented all native forests above 300 m elevation on Kauai. Densities were estimated for each stratum from the transect data and extrapolated to population sizes based on the stratum area. Ranges were calculated from transect data and incidental observations. To facilitate comparison between his study and ours, we sampled an area in 1981 for which Sincock estimated bird population sizes during 1968–1973.

SURVEY LIMITATIONS

In the studies of Perkins (1903), Munro (1944), Baldwin (1953), MacMillen and Carpenter (1980), and van Riper (1984), attention was drawn to mass movements of nectarivorous species (Iiwi, Apapane) and more localized movements of Common Amakihi. Conant (1981) documented a similar distributional shift of Crested Honeycreeper to lower elevations in winter in Kipahulu Valley. Because the nectarivores in particular fly long distances to patchily distributed, locally abundant nectar sources, their distributions and areas of high density shift markedly throughout the year. Population sizes of Hawaiian birds have wide annual variations (Ely and Clapp 1973, Clapp et al. 1977, Scott et al. 1984), even though non-nectarivorous species tend to have the same distribution and habitat response patterns from year to year (Scott et al. 1984). These phenomena should serve to note that our survey represented a "snapshot" of bird distribution at a moment in time: densities, population sizes, habitat response, and, to a lesser extent, distributions can be expected to change in the seasons and years that follow this survey.

NATIVE SPECIES ACCOUNTS

Our discussion of the distribution, abundance, and habitat response of Hawaiian forest birds focuses on individual species in order to facilitate comparisons between the populations of different forests and islands, and to infer historical and contemporary limiting factors for native species. Native and introduced birds are treated in separate sections; phylogenetic order within each section follows the A.O.U. *Check-list* (1983) and its 35th supplement (1985). Established Hawaiian names not used by the A.O.U. are given in parentheses in the headings for the species accounts, while other frequently used alternate names are given at the beginning of the accounts.

(*Continued on page 68*)

TABLE 10
Summary Statistics for Native Birds in the Study Areas on Hawaii

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Hawaiian Goose (Nene)							
Range (km²)	64	148	...	111	91	...	...
Stations in range	95	224	...	178	146	...	...
Stations occupied	8	19	...	26	16	...	...
Birds recorded	24	52	...	82	41	...	...
% pop. above 1500 m	100	100	...	100	87	...	...
Total population	59	93	...	112	76	...	...
SE	25	25	...	38	28	...	...
Pop. by habitat type							
Ohia	59	87	...	105	53	...	...
Koa-ohia	...	6	...	1	11	...	...
Koa-mamane	...	...	...	2	3	...	...
Mamane	...	...	...	...	9	...	...
Other natives	...	...	...	4	...	...	...
Hawaiian Hawk (Io)							
Stations occupied	7	36	1	2	56	1	...
Birds recorded	7	52	1	5	78	1	...
Lesser Golden-Plover (Kolea)							
Stations occupied	...	8	...	10	4	2	1
Birds recorded	...	10	...	18	2	4	1
Short-eared Owl (Pueo)							
Stations occupied	11	4	...	4	21	3	...
Birds recorded	11	5	...	4	23	3	...
Hawaiian Crow (Alala)							
Range (km²)	...	...	...	...	253	...	...
Stations in range	...	...	...	...	613	...	...
Stations occupied	...	...	...	...	103	...	...
Birds recorded	...	...	...	...	259	...	...
% pop. above 1500 m	...	...	...	...	20	...	...
Total population	...	...	...	...	76	...	...
SE	...	...	...	...	9	...	...
Pop. by habitat type							
Ohia	...	...	...	...	23	...	...
Koa-ohia	...	...	...	...	52	...	...
Elepaio							
Range (km²)	252	1014	219	100	988	97	79
Stations in range	706	2226	547	233	2313	234	159
Stations occupied	250	1201	168	68	1239	38	121
Birds recorded	404	3513	380	163	4187	64	372
% pop. above 1500 m	15	36	0	78	49	100	9
Total population	12,181	112,570	857	2737	62,782	2501	13,642
SE	846	3054	689	202	1698	443	1030
Pop. by habitat type							
Ohia	4474	62,028	8576	365	24,673	...	13,098
Koa-ohia	7708	49,536	...	786	20,075	...	...
Koa-mamane	...	408	...	512	9474	...	...
Mamane-naio	...	...	...	...	33	1792	...
Mamane	...	...	...	...	5353	709	...
Other natives	...	219	...	747	29	...	...
Intro. trees	...	378	...	...	2765	...	544
Treeless	...	...	...	327	378	...	...
Omao							
Range (km²)	327	978	227	204	19	...	...
Stations in range	863	2134	558	361	57	...	...
Stations occupied	752	1678	429	132	34	...	...
Birds recorded	3436	8116	1987	554	151	...	...
% pop. above 1500 m	31	34	0	98	16	...	...

TABLE 10
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Total population	56,443	95,662	15,509	2106	732	...	...
SE	1342	1488	503	111	55	...	...
Pop. by habitat type							
Ohia	38,716	65,391	15,508	1268	68	...	...
Koa-ohia	17,728	28,984	...	301	664	...	...
Koa-mamane	...	138	...	110	...	...	...
Other natives	...	204	...	11	...	...	...
Intro. trees	...	827	...	...	...	...	...
Treeless	...	119	1	417	...	...	...
Ou							
Range (km^2)	...	92	53	...	...	...	...
Stations in range	...	212	145	...	...	...	...
Stations occupied	...	10	1	...	...	...	...
Birds recorded	...	32	1	...	...	...	...
% pop. above 1500 m	...	0	0	...	...	...	...
Total population	...	385	9	...	...	...	...
SE	...	157	9	...	...	...	...
Pop. by habitat type							
Ohia	...	385	9	...	...	...	...
Palila							
Range (km^2)	...	...	...	...	...	139	...
Stations in range	...	...	...	...	...	317	...
Stations occupied	...	...	...	...	...	51	...
Birds recorded	...	...	...	...	...	97	...
% pop. above 1500 m	...	...	...	...	...	100	...
Total population	...	...	...	...	...	2268	...
SE	...	...	...	...	...	342	...
Pop. by habitat type							
Mamane-naio	...	...	...	...	...	1669	...
Mamane	...	...	...	...	...	599	...
Common Amakihi							
Range (km^2)	329	870	245	268	1133	139	107
Stations in range	868	1876	618	469	2665	317	202
Stations occupied	604	1050	144	413	2233	272	158
Birds recorded	2587	3878	1034	3298	20,350	1378	645
% pop. above 1500 m	74	57	0	89	48	100	18
Total population	157,408	172,741	32,465	41,556	348,879	87,624	29,175
SE	7377	4920	2461	1280	5324	3777	1632
Pop. by habitat type							
Ohia	111,098	59,321	32,253	26,274	210,118	...	27,730
Koa-ohia	155,896	104,429	...	7032	77,019	...	...
Koa-mamane	...	2490	...	5063	30,391	...	...
Mamane-naio	...	...	...	...	1983	37,057	...
Mamane	...	...	...	...	19,497	50,567	...
Other natives	...	2645	...	1229	2076	...	...
Intro. trees	...	3831	...	...	2895	...	1445
Treeless	1589	24	212	1957	4901	...	...
Akiapolaau							
Range (km^2)	60	314	...	5	61	139	...
Stations in range	199	669	...	12	129	317	...
Stations occupied	19	70	...	1	6	3	...
Birds recorded	30	126	...	1	7	3	...
% pop. above 1500 m	53	69	...	100	73	100	...
Total population	533	891	...	2	22	46	...
SE	163	118	...	2	9	26	...
Pop. by habitat type							
Ohia	2	180	...	...	2	...	...
Koa-ohia	531	711	...	2	20	...	...
Mamane	...	...	...	...	...	46	...

TABLE 10
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Hawaii Creeper							
Range (km²)	189	439	...	...	102	...	...
Stations in range	582	898	...	...	246	...	...
Stations occupied	31	166	...	...	20	...	...
Birds recorded	40	393	...	...	33	...	...
% pop. above 1500 m	78	77	...	...	81	...	...
Total population	2102	10,102	...	...	297	...	...
SE	540	827	...	...	73	...	...
Pop. by habitat type							
Ohia	1472	2792	...	...	...	...	...
Koa-ohia	630	7299	...	...	289	...	...
Koa-mamane	...	11	...	...	8	...	...
Akepa							
Range (km²)	180	268	...	...	32	...	...
Stations in range	503	489	...	...	69	...	...
Stations occupied	63	93	...	...	24	...	...
Birds recorded	108	195	...	...	43	...	...
% pop. above 1500 m	81	83	...	...	86	...	...
Total population	5293	7938	...	...	661	...	...
SE	780	919	...	...	126	...	...
Pop. by habitat type							
Ohia	4160	1908	...	...	...	...	...
Koa-ohia	1134	6030	...	...	661	...	...
Iiwi							
Range (km²)	280	792	109	126	753	42	56
Stations in range	770	1681	347	283	1748	83	131
Stations occupied	451	1096	8	63	789	5	12
Birds recorded	1623	6133	10	151	2902	7	23
% pop. above 1500 m	74	59	0	99	42	100	16
Total population	56,561	228,034	191	2339	52,008	482	802
SE	1968	5460	70	427	1875	219	286
Pop. by habitat type							
Ohia	31,979	90,058	191	682	21,672	...	780
Koa-ohia	24,581	129,599	...	540	24,640	...	...
Koa-mamane	...	1936	...	714	2465	...	...
Mamane-naio	...	...	...	...	65	...	...
Mamane	...	...	...	...	550	483	...
Other natives	...	252	...	279	...	...	...
Intro. trees	...	6188	...	...	2367	...	22
Treeless	...	...	...	125	248	...	...
Apapane							
Range (km²)	329	1050	264	278	1132	42	108
Stations in range	869	2316	652	482	2637	83	207
Stations occupied	789	1750	529	422	1912	3	136
Birds recorded	6376	11,905	5469	3468	12,741	3	517
% pop. above 1500 m	65	34	0	74	28	100	12
Total population	273,477	408,852	132,023	37,665	225,338	219	20,374
SE	6514	8881	3452	1526	5125	123	1737
Pop. by habitat type							
Ohia	180,892	214,254	129,782	19,288	129,351	...	20,052
Koa-ohia	92,585	188,554	...	10,427	69,871	...	...
Koa-mamane	...	705	...	5581	6183	...	...
Mamane-naio	...	...	...	...	90	...	...
Mamane	...	...	...	...	3047	219	...
Other natives	...	2058	...	1320	33	...	...
Intro. trees	...	3201	...	...	11,585	...	322
Treeless	...	81	2241	1048	5178	...	...

TABLE 11

SUMMARY STATISTICS FOR NATIVE BIRDS IN THE STUDY AREAS ON MAUI, MOLOKAI, LANAI, AND KAUAI

	East Maui	West Maui	Molokai	Lanai	Kauai
Hawaiian Goose (Nene)					
Range (km²)	35	...	...	...	...
Stations in range	138	...	...	...	...
Stations occupied	20	...	...	...	...
Birds recorded	62	...	...	...	...
% pop. above 1500 m	90	...	...	...	...
Total population	49	...	...	...	...
SE	12	...	...	...	...
Pop. by habitat type					
Ohia	7	...	...	...	...
Mamane	2	...	...	...	...
Other natives	7	...	...	...	...
Treeless	33	...	...	...	...
Lesser Golden-Plover (Kolea)					
Stations occupied	4	8	1	...	...
Birds recorded	6	14	1	...	...
Short-eared Owl (Pueo)					
Stations occupied	12	...	...	3	8
Birds recorded	27	...	...	4	12
Elepaio					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	139
Birds recorded	...	...	...	...	1332
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	5929
SE	...	...	...	...	250
Pop. by habitat type					
Ohia	...	...	...	...	5928
Treeless	...	...	...	...	1
Kamao					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	9
Birds recorded	...	...	...	...	23
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	24
SE	...	...	...	...	10
Pop. by habitat type					
Ohia	...	...	...	...	24
Olomao					
Range (km²)	...	...	16	...	...
Stations in range	...	...	120	...	...
Stations occupied	...	...	1	...	...
Birds recorded	...	...	1	...	...
% pop. above 1500 m	...	...	0	...	...
Total population	...	...	19	...	...
SE	...	...	19	...	...
Pop. by habitat type					
Ohia	...	...	19	...	...
Puaiohi					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	3
Birds recorded	...	...	...	...	13

TABLE 11
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	20
SE	...	...	...	...	17
Pop. by habitat type					
Ohia	...	...	...	...	20
Kauai Oo (Ooaa)					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	3
Birds recorded	...	...	...	...	6
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	2
SE	...	...	...	...	1
Pop. by habitat type					
Ohia	...	...	...	...	2
Ou					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	1
Birds recorded	...	...	...	...	1
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	3
SE	...	...	...	...	3
Pop. by habitat type					
Ohia	...	...	...	...	3
Maui Parrotbill					
Range (km²)	50	...	...	...	...
Stations in range	193	...	...	...	...
Stations occupied	26	...	...	...	...
Birds recorded	57	...	...	...	...
% pop. above 1500 m	71	...	...	...	...
Total population	502	...	...	...	...
SE	116	...	...	...	...
Pop. by habitat type					
Ohia	502	...	...	...	...
Common Amakihi					
Range (km²)	340	36	37	...	25
Stations in range	1001	177	178	...	140
Stations occupied	601	58	48	...	101
Birds recorded	2077	138	95	...	381
% pop. above 1500 m	39	0.4	0	...	0
Total population	43,930	2762	1834	...	2257
SE	1725	421	363	...	217
Pop. by habitat type					
Ohia	28,549	2762	922	...	2257
Koa-ohia	4104	...	...	...	...
Mamane	27	...	...	...	...
Other natives	6287	...	...	...	...
Intro. trees	3638	...	912	...	...
Treeless	1323	...	...	...	...
Anianiau					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	134
Birds recorded	...	...	...	...	1546

TABLE 11
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	6077
SE	...	...	...	...	277
Pop. by habitat type					
Ohia	...	...	...	...	6072
Treeless	...	...	...	...	5
Nukupuu					
Range (km²)	7	...	...	...	25
Stations in range	35	...	...	...	140
Stations occupied	1	...	...	...	0
Birds recorded	2	...	...	...	0
% pop. above 1500 m	38	...	...	...	0
Total population	28	...	...	...	?
SE	28	...	...	...	...
Pop. by habitat type					
Ohia	28	...	...	...	...
Kauai Creeper					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	65
Birds recorded	...	...	...	...	341
% pop. above 1500 m	...	...	...	...	0
Total population	...	...	...	...	1649
SE	...	...	...	...	214
Pop. by habitat type					
Ohia	...	...	...	...	1649
Maui Creeper					
Range (km²)	135	...	...	...	...
Stations in range	462	...	...	...	...
Stations occupied	221	...	...	...	...
Birds recorded	990	...	...	...	...
% pop. above 1500 m	76	...	...	...	...
Total population	34,839	...	...	...	...
SE	2723	...	...	...	...
Pop. by habitat type					
Ohia	30,484	...	...	...	...
Koa-ohia	1096	...	...	...	...
Intro. trees	2324	...	...	...	...
Treeless	934	...	...	...	...
Akepa					
Range (km²)	23	...	...	...	25
Stations in range	84	...	...	...	140
Stations occupied	4	...	...	...	92
Birds recorded	8	...	...	...	349
% pop. above 1500 m	88	...	...	...	0
Total population	227	...	...	...	1674
SE	146	...	...	...	168
Pop. by habitat type					
Ohia	199	...	...	...	1674
Koa-ohia	28	...	...	...	...
Iiwi					
Range (km²)	207	16	18	...	25
Stations in range	654	81	120	...	140
Stations occupied	336	6	7	...	139

TABLE 11
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Birds recorded	1488	9	12	···	1214
% pop. above 1500 m	38	1	0	···	0
Total population	18,812	176	80	···	5400
SE	1006	74	33	···	264
Pop. by habitat type					
Ohia	16,392	176	80	···	5397
Koa-ohia	2156	···	···	···	···
Other natives	79	···	···	···	···
Intro. trees	93	···	···	···	···
Treeless	93	···	···	···	3
Crested Honeycreeper (Akohekohe)					
Range (km²)	58	···	···	···	···
Stations in range	215	···	···	···	···
Stations occupied	102	···	···	···	···
Birds recorded	415	···	···	···	···
% pop. above 1500 m	99	···	···	···	···
Total population	3753	···	···	···	···
SE	373	···	···	···	···
Pop. by habitat type					
Ohia	3551	···	···	···	···
Koa-ohia	86	···	···	···	···
Treeless	117	···	···	···	···
Apapane					
Range (km²)	370	41	118	20	25
Stations in range	1069	184	565	77	140
Stations occupied	772	160	404	21	140
Birds recorded	4422	973	2362	47	5781
% pop. above 1500 m	40	3	0	0	0
Total population	93,818	15,825	38,643	540	30,327
SE	3511	1129	2360	213	716
Pop. by habitat type					
Ohia	70,106	15,684	27,868	···	30,303
Koa-ohia	9825	···	···	···	···
Mamane	32	···	···	···	···
Other natives	5562	···	717	68	···
Intro. trees	3802	···	10,055	472	···
Treeless	4491	141	3	···	24
Poo-uli					
Range (km²)	13	···	···	···	···
Stations in range	53	···	···	···	···
Stations occupied	1	···	···	···	···
Birds recorded	3	···	···	···	···
% pop. above 1500 m	73	···	···	···	···
Total population	141	···	···	···	···
SE	141	···	···	···	···
Pop. by habitat type					
Ohia	141	···	···	···	···

(*Continued from page 61*)

Population estimates have been rounded to an appropriate number of significant digits in the text; exact computed values may be found in Tables 10 and 11. After each estimate the 95% confidence interval (abbreviated as "95% CI") is given in text; approximate values of these may be obtained by doubling the standard errors (SE) given in Tables 10 and 11. For unrecorded endemic species we estimated the probability of having detected at least one bird during our survey (Table 12).

TABLE 12
Probability of Detecting at Least One Bird of Species Unrecorded During the HFBS

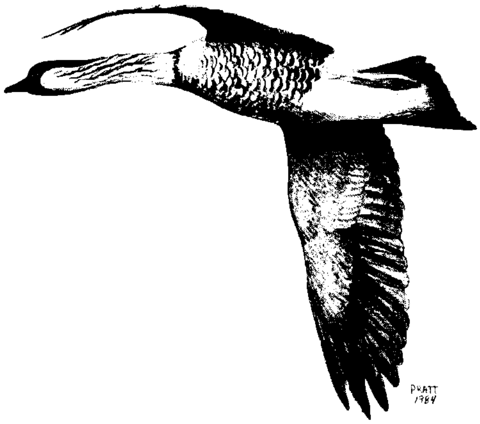
		Probability of detection											
		Study areas											
Species	Population	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Hawaiian Rail	10	0.074	0.056	0.086	0.048	0.066		0.064					
	50	0.318	0.252	0.364	0.218	0.288		0.288					
	100	0.535	0.440	0.595	0.388	0.494		0.494					
Omao	10							0.235					
	50							0.731					
	100							0.931					
Olomao	10								0.348	0.445		0.359	
	50								0.882	0.948		0.892	
	100								0.986	0.997		0.988	
Bishop's Oo	10								0.492	0.608	0.759		
	50								0.966	0.991	0.999		
	100								0.999	0.999	0.999		
Hawaii Oo	10	0.387	0.308	0.440	0.267	0.351	0.337	0.344					
	50	0.913	0.841	0.945	0.789	0.885	0.872	0.879					
	100	0.992	0.975	0.996	0.955	0.987	0.984	0.985					
Kioea	10	0.387	0.308	0.440	0.267	0.351		0.344					
	50	0.913	0.841	0.945	0.789	0.885		0.879					
	100	0.992	0.975	0.996	0.955	0.987		0.985					
Ou	10	0.314				0.284		0.278	0.406	0.512	0.661	0.418	
	50	0.848				0.811		0.803	0.926	0.972	0.996	0.933	
	100	0.977				0.964		0.961	0.995	0.999	0.999	0.996	
Palila	10					0.240							
	50					0.747							
	100					0.936							
Lesser Koa-Finch	10		0.059		0.007	0.058							
	50		0.261		0.033	0.260							
	100		0.454		0.066	0.453							
Greater Koa-Finch	10		0.059		0.007	0.058							
	50		0.261		0.033	0.260							
	100		0.454		0.066	0.453							
Kona Grosbeak	10					0.058							
	50					0.260							
	100					0.453							

TABLE 12
CONTINUED

		Probability of detection											
		Study areas											
Species	Population	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Maui Parrotbill	10									0.334			
	50									0.868			
	100									0.983			
Common Amakihi	10											0.117	
	50											0.464	
	100											0.712	
Greater Amakihi	10		0.064										
	50		0.281										
	100		0.483										
Hawaiian Akialoa	10	0.074	0.056	0.086	0.007	0.066		0.064				0.104	
	50	0.318	0.252	0.364	0.033	0.288		0.282				0.421	
	100	0.535	0.440	0.595	0.066	0.494		0.485				0.665	
Kauai Akialoa	10												0.148
	50												0.550
	100												0.797
Nukupuu	10									0.217			0.238
	50									0.706			0.742
	100									0.914			0.934
Akiapolaau	10			0.484				0.382					
	50			0.964				0.910					
	100			0.999				0.992					
Hawaii Creeper	10			0.178	0.015			0.134					
	50			0.624	0.070			0.511					
	100			0.858	0.136			0.761					
Maui Creeper	10									0.118		0.091	
	50									0.466		0.379	
	100									0.715		0.614	
Molokai Creeper	10										0.170		
	50										0.606		
	100										0.845		
Akepa	10			0.110	0.009			0.082		0.169			
	50			0.441	0.043			0.347		0.605			
	100			0.687	0.083			0.547		0.844			

TABLE 12
CONTINUED

Species	Population	Probability of detection											
		Study areas											
		Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Ula-ai-hawane	10		0.056	0.086		0.066		0.064					
	50		0.252	0.364		0.288		0.282					
	100		0.440	0.595		0.494		0.485					
Iiwi	10											0.146	
	50											0.546	
	100											0.794	
Hawaii Mamo	10	0.128	0.098	0.149	0.012	0.114	0.109	0.112					
	50	0.495	0.404	0.554	0.059	0.455	0.438	0.446					
	100	0.745	0.644	0.801	0.114	0.703	0.684	0.694					
Black Mamo	10										0.319		
	50										0.854		
	100										0.979		
Crested Honeycreeper	10									0.290	0.400		
	50									0.819	0.922		
	100									0.967	0.994		
Poo-uli	10									0.081			
	50									0.345			
	100									0.570			



HAWAIIAN GOOSE
Nesochen sandvicensis

HAWAIIAN GOOSE [NENE]
(*Nesochen sandvicensis*)

Hawaiian Geese, or Nene, have unique anatomical adaptations for living on rugged arid lava flows (Miller 1937), where they feed on the leaves, buds, flowers, and seeds of *Hypocharis radicata,* grasses, and other herbs, and on the fruits of *Vaccinium* spp., *Coprosma ernodeoides,* and other plants (Baldwin 1947b, Kear and Berger 1980).

Fossil remains suggest that Hawaiian Geese originally occurred on all the main islands (Olson and James 1982b). Historically they occurred on Hawaii from near sea level to 2400 m elevation in the subalpine scrublands of Mauna Loa, and probably on Maui in the subalpine zone (Baldwin 1945a). Presently they are restricted to upland areas on Hawaii and Maui; the Maui population is the result of a translocation effort begun in 1962 (Kear 1975, Kear and Berger 1980). The lowlands, however, may have been the most important breeding area (Perkins 1903).

Prior to the 20th century, Hawaiian Geese were common on Hawaii (Baldwin 1945a). The numbers decreased significantly as a result of hunting, habitat modification, introduced predators, diseases, and competitors (Baldwin 1945a), so that by 1951 the wild population was estimated at no more than 30 birds (Smith 1952). Since then, a captive propagation and release program by state, federal, and private agencies has resulted in increased numbers (Walker 1966, Kear and Berger 1980).

Surveys conducted by the Hawaii Division of Fish and Game suggest that the number of Hawaiian Geese in the wild began to decline when the number of captive-reared birds released to the wild was sharply reduced (Devick 1981a, 1981b). The population estimates for our study areas (Tables 10, 11) were less than the number released in sanctuaries during the seven years prior to our survey (Kear and Berger 1980), suggesting a population maintained mostly by captive-reared birds (Banko and Manuwal 1982).

Hawaiian Geese occur in the Hamakua, Kipukas, Kona, and Kau study areas on Hawaii and on East Maui (Table 13). The highest densities on Hawaii are on the upper slopes of Hualalai, the upper Kau study area, and the saddle area of Mauna Loa. Hawaiian Geese do not occur in the mamane and mamane-naio woodlands of Mauna Kea. They occur at middle elevations in Hawaii Volcanoes National Park as a result of captive releases (Banko and Manuwal 1982) and are frequently seen on the Volcano Golf Course (HFBS data). Areas near 2400 m elevation, the upper limit for this species, were not fully surveyed on Hawaii; in Kau and Kona, birds undoubtedly occur higher than we found them (maximum elevation 2100 m). The lower limits, about 1300 m, are usually bounded by closed canopy forest.

The 390 ± 120 (95% CI) Hawaiian Geese estimated to live in the wild (Tables 10, 11) comprise three distinct populations. Above 260 ± 100 (95% CI) birds occur at upper elevations in Kau (Fig. 64) and windward Hawaii (Fig. 65). Birds occasionally fly across the Kapapala Tract (transects 82–86) between the upper Hamakua and Kau areas, but Hawaiian Geese do not breed there. A second population of 75 ± 55 (95% CI) birds occurs on the south to southwest slopes of Hualalai (Fig. 66). The two Hawaii populations use pastures opened by ranching and some birds are attracted to stock ponds. The third population consists of 50 ± 25 (95% CI) birds confined to scrub and grasslands on the crater and upper slopes of Haleakala (Fig. 67). Vagrant birds occasionally occur at low elevations on both islands.

TABLE 13
DENSITY [MEAN (SE)] OF THE HAWAIIAN GOOSE (NENE) AND HAWAIIAN CROW (ALALA) BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Hawaiian Goose					Hawaiian Crow
	Kau	Hamakua	Kipukas	Kona	E. Maui	Kona
Elevation						
100–300 m	···	···	···	···	···	···
300–500 m	···	0	···	0	0	0
500–700 m	0	0	···	0	0	0
700–900 m	0	0	···	0	0	0
900–1100 m	0	0	···	0	0	+ (+)
1100–1300 m	0	0	0	+ (+)	0	+ (1)
1300–1500 m	0	0	0	1 (1)	1 (1)	+ (+)
1500–1700 m	1 (1)	+ (+)	+ (+)	1 (+)	*	+ (+)
1700–1900 m	+ (+)	1 (1)	1 (+)	+ (+)	2 (1)	+ (+)
1900–2100 m	1 (1)	5 (2)	1 (+)	+ (+)	3 (1)	0
2100–2300 m	+ (+)	0	+ (+)	0	2 (1)	0
2300–2500 m	···	···	···	0	+ (+)	0
2500–2700 m	···	···	···	···	1 (1)	···
2700–2900 m	···	···	···	···	+ (+)	···
2900–3100 m	···	···	···	···	···	···
Habitat						
Ohia	1 (+)	1 (+)	1 (+)	1 (+)	2 (1)	+ (+)
Koa-ohia	+ (+)	1 (+)	+ (+)	1 (+)	+ (+)	1 (+)
Koa-mamane	···	0	1 (+)	+ (+)	···	+ (+)
Mamane-naio	···	···	···	0	···	+ (+)
Mamane	···	···	···	1 (1)	2 (1)	0
Other natives	···	0	6 (3)	0	1 (1)	0
Intro. trees	···	0	···	0	0	0
Treeless	···	0	0	0	2 (1)	0

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area; * indicates stratum was not sampled in range but was sampled elsewhere in study area.

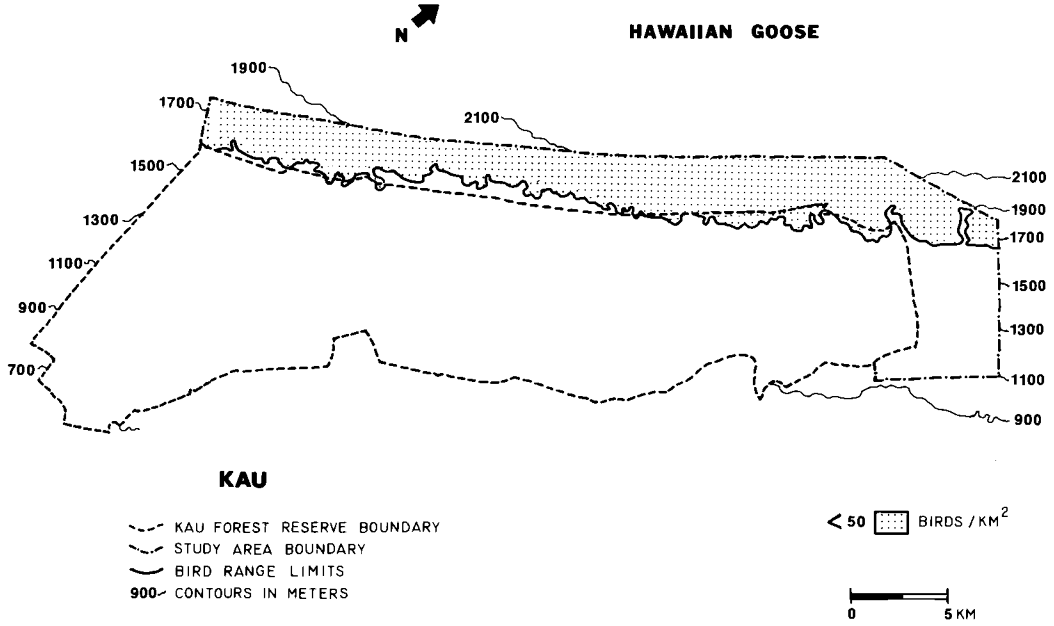


FIGURE 64. Distribution and abundance of the Hawaiian Goose (Nene) in the Kau study area.

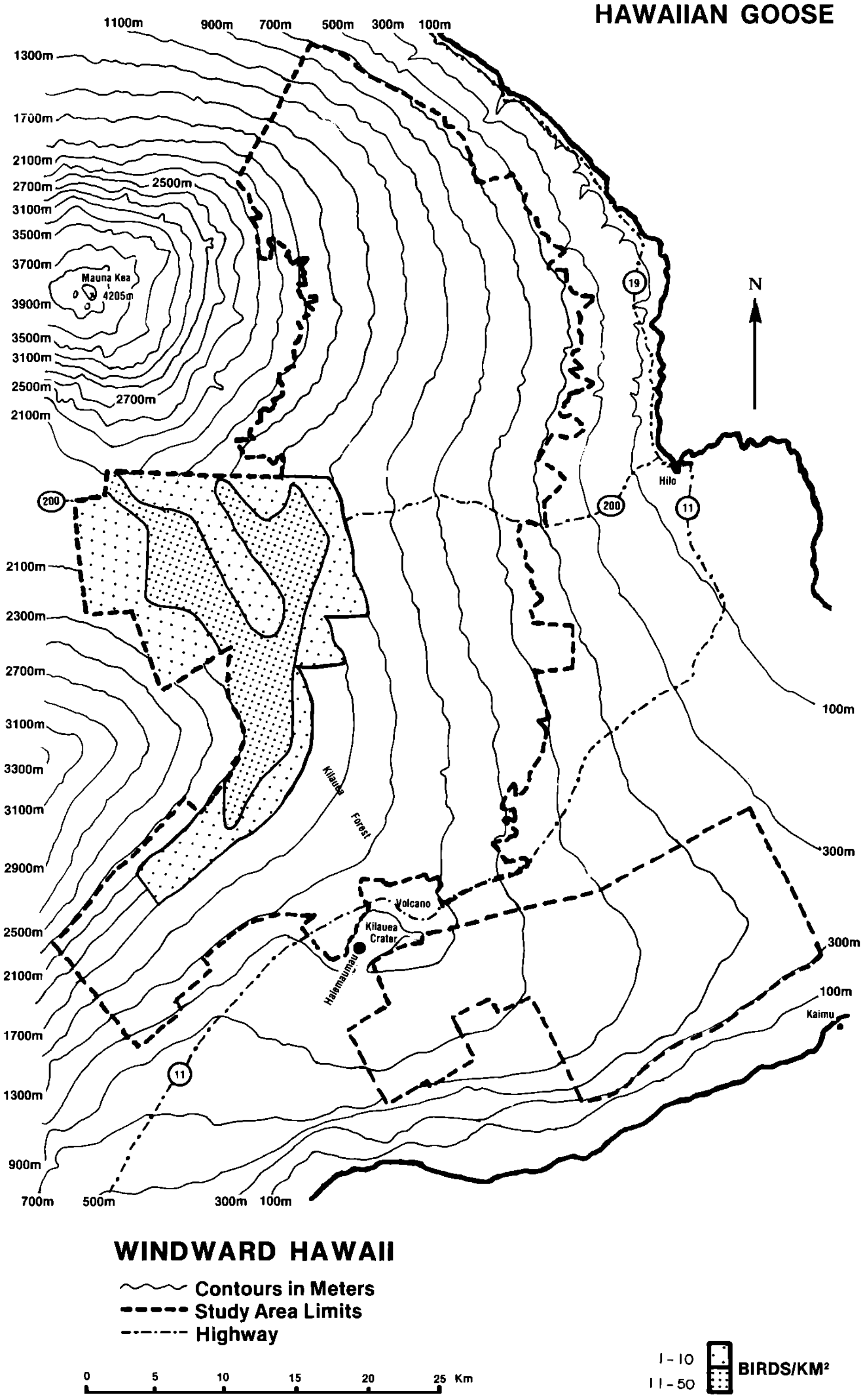


FIGURE 65. Distribution and abundance of the Hawaiian Goose (Nene) in the windward Hawaii study areas.

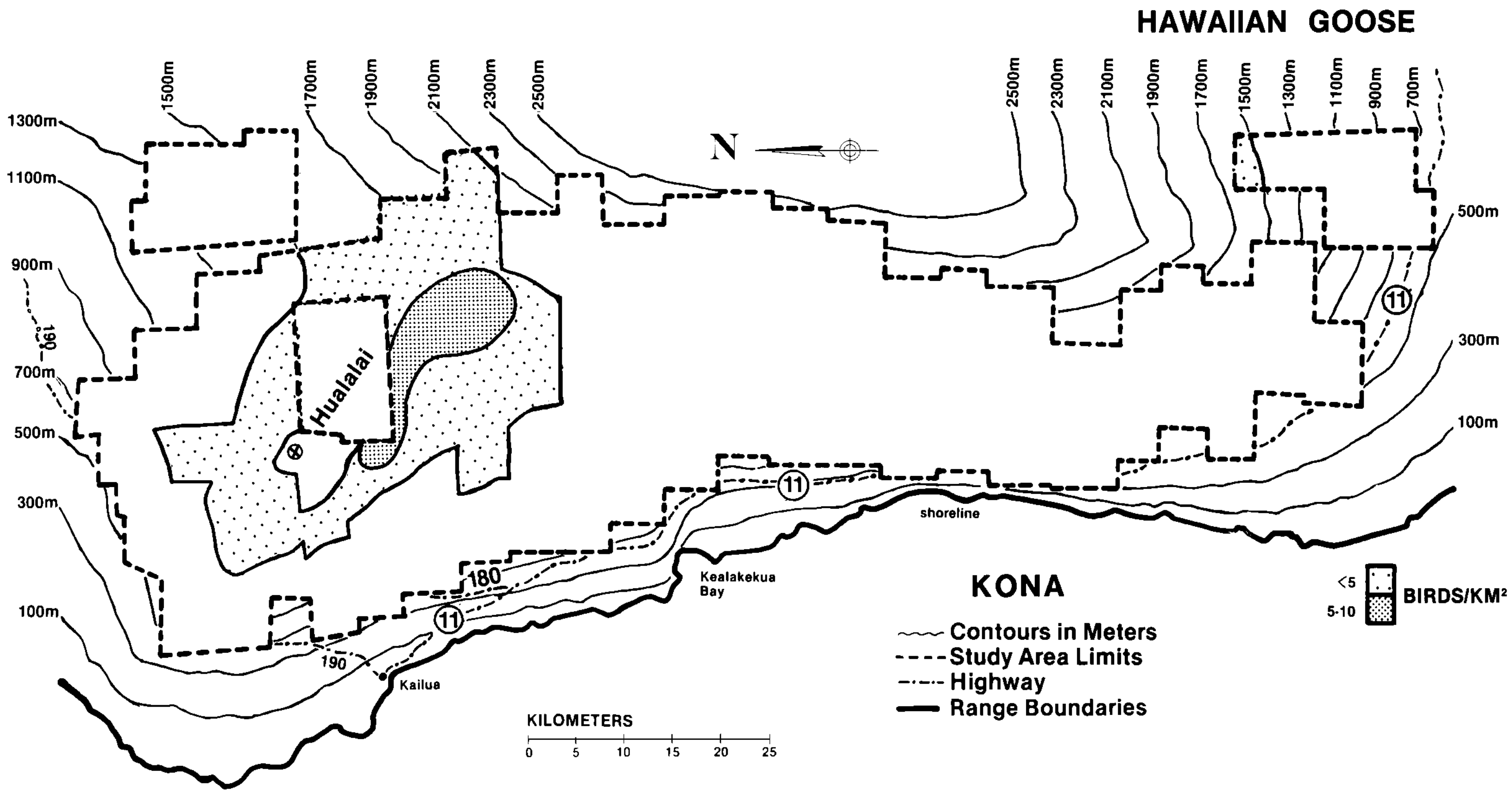


FIGURE 66. Distribution and abundance of the Hawaiian Goose (Nene) in the Kona study area.

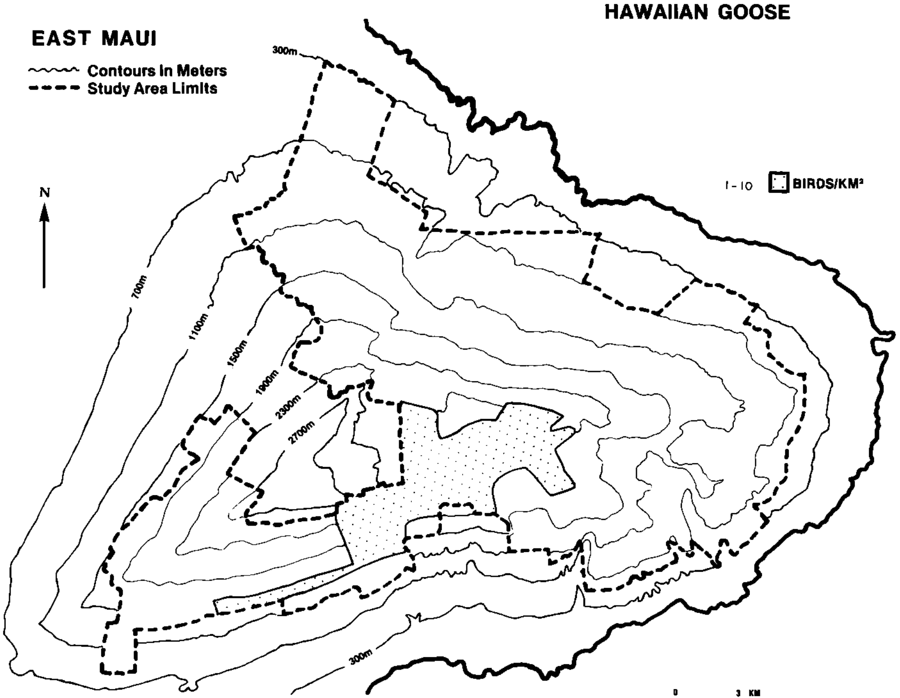


FIGURE 67. Distribution and abundance of the Hawaiian Goose (Nene) in the East Maui study area.

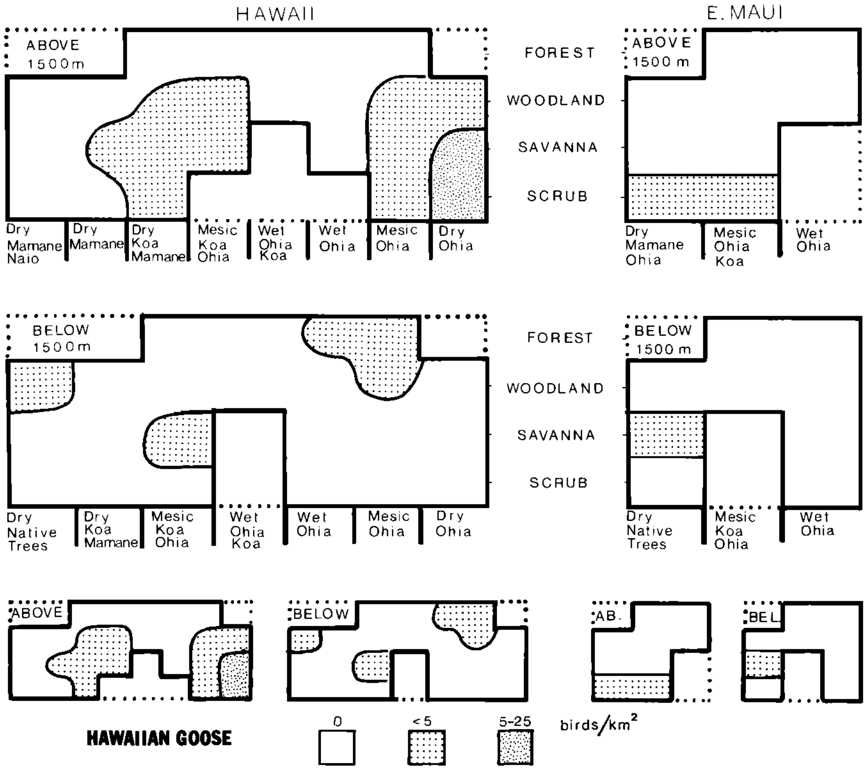


TABLE 14

REGRESSION MODELS FOR HABITAT RESPONSE OF THE HAWAIIAN GOOSE (NENE) AND HAWAIIAN CROW (ALALA)[a]

	Hawaiian Goose					Hawaiian Crow
	Kau	Hamakua	Kipukas	Kona	Maui	Kona
R^2	0.41*	0.11*	0.41*	0.02*	0.03*	0.11*
Moisture	···	−3.7*	−2.6	···	···	2.4
Elevation	···	−5.4*	···	2.6	2.3	3.0
(Elevation)^2	···	5.9*	···	···	···	−2.8
Tree biomass	−2.3	···	···	−4.5*	2.2	···
(Tree biomass)^2	15.1*	···	···	2.9	···	···
Crown cover	−3.2	2.7	···	···	−2.9	···
Canopy height	−2.2	−2.8	···	···	···	···
Koa	···	−6.1*	···	···	···	5.4*
Ohia	2.8	4.8*	···	···	···	···
Naio	X	X	···	···	X	···
Mamane	X	···	···	···	···	···
Intro. trees	X	···	X	···	···	···
Shrub cover	···	···	···	···	···	···
Ground cover	···	−3.3*	···	···	···	···
Native shrubs	···	···	−3.1	···	···	···
Intro. shrubs	X	···	···	···	···	···
Ground ferns	X	X	···	···	···	6.4*
Matted ferns	···	···	···	···	···	−2.8
Tree ferns	···	X	X	···	···	3.4*
Ieie	X	X	X	···	···	−5.6*
Passiflora	X	···	X	···	···	···
Native herbs	X	X	6.2*	···	···	···
Intro. herbs	X	X	−2.7	···	···	···
Native grasses	7.0*	3.6*	···	···	···	···
Intro. grasses	···	3.2	···	···	···	−3.3
Ohia flowers	X	X	X	X	X	···
Olapa fruit	X	X	X	X	X	3.4*

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

Hawaiian Goose densities are highest in dry subalpine ohia scrub and savanna on the island of Hawaii (Fig. 68). Occasional birds representing flyovers also occur in mesic and woodland habitat. A few pairs breed in the edges of mesic to wet forest kipukas surrounded by barren lava flows (N. Santos, R. Bachman, pers. comm.), but most nests are placed in areas of sparse vegetation (Elder and Woodside 1958). Hawaiian Geese have lower populations and densities on Maui than on Hawaii (Table 13), and occupy a narrower range of habitats. The regression models for habitat response (Table 14) indicate that Hawaiian Geese are most commonly associated with dry high elevation areas. Strong positive terms (i.e., t-statistics for the regression coefficients) for native herbs and native grasses in the three windward Hawaii models (Kau, Hamakua, Kipukas) reflect the diet of browse and seeds, suggesting that habitat response is partly determined by availability of suitable forage.

Stone et al. (1983) noted that all wild Hawaiian Goose populations require continual captive releases to sustain stable numbers. Some wild-hatched goslings continuously lost weight, suggesting insufficient quantity or quality of food (Banko 1982, Banko and Manuwal 1982). Habitat modification and predation are probable causes for the present failure to maintain self-sustaining populations. Suitable lowland habitat may also be critical to long-term survival (Stone et al. 1983).

←

FIGURE 68. Habitat response graphs of the Hawaiian Goose (Nene) differentiated along gradients of general vegetation type (horizontal axis) and forest development (vertical axis). (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

HAWAIIAN HAWK
Buteo solitarius

HAWAIIAN HAWK [IO] (*Buteo solitarius*)

Hawaiian Hawks, or Io, breed only on Hawaii, although vagrant birds have been recorded from Maui, Oahu, and Kauai (Banko 1980–1984). Recent fossil finds indicate that birds originally occurred on Molokai (Olson and James 1982b). This species is very adaptable and feeds on introduced and native birds, mammals, insects, and spiders (Perkins 1903, Tomich 1971a).

Perkins (1903) characterized Hawaiian Hawks as widely distributed and moderately common from sea level to at least 1500 m elevation. Munro (1944) stated that they were "well distributed over the island from about [600 to 1500 m] elevation," and that the numbers appeared to have declined from the 1890s. Morrison (1969) recorded 0.05 birds per observer hour in Hawaii Volcanoes National Park, leading Baldwin (1969a) to state that the numbers and range had increased in the national park from the 1940s.

TABLE 15
INCIDENTAL OBSERVATIONS OF THE HAWAIIAN HAWK

Study area	Dark phase	Light phase	Unidentified	Total
Kau	11	7	9	27
Hamakua	67	32	49	148
Kipukas	4	3	10	17
Kohala	0	0	2	2
Kona	29	14	37	80
Dark/light ratio				
Windward	1.95/1.00			
Leeward	2.07/1.00			
Total	111	56	107	274

Hawaiian Hawks occur in distinct light and dark color phases. We found that dark phase birds outnumber light phase birds 1.98:1, with no significant differences in this ratio between leeward and windward forests ($P = 0.88$, $X^2 = 0.02$, $df = 1$, Table 15). This contrasts with earlier statements that dark phase birds were relatively more common on the windward coast (Henshaw 1902).

Hawaiian Hawks occupy a broad range of habitats from papaya and macadamia orchards through virtually all types of forest including ohia rainforest and subalpine mamane-naio woodland (Fig. 69). They are virtually absent from areas with few or no trees. This species has probably adapted better than any other native bird to the introduced flora and fauna that dominate lowland areas. Illegal shooting and harassment of nest sites are probably the most significant factors affecting the species at present (Griffin 1984).

We found Hawaiian Hawks in all study areas on Hawaii. They are widely distributed outside

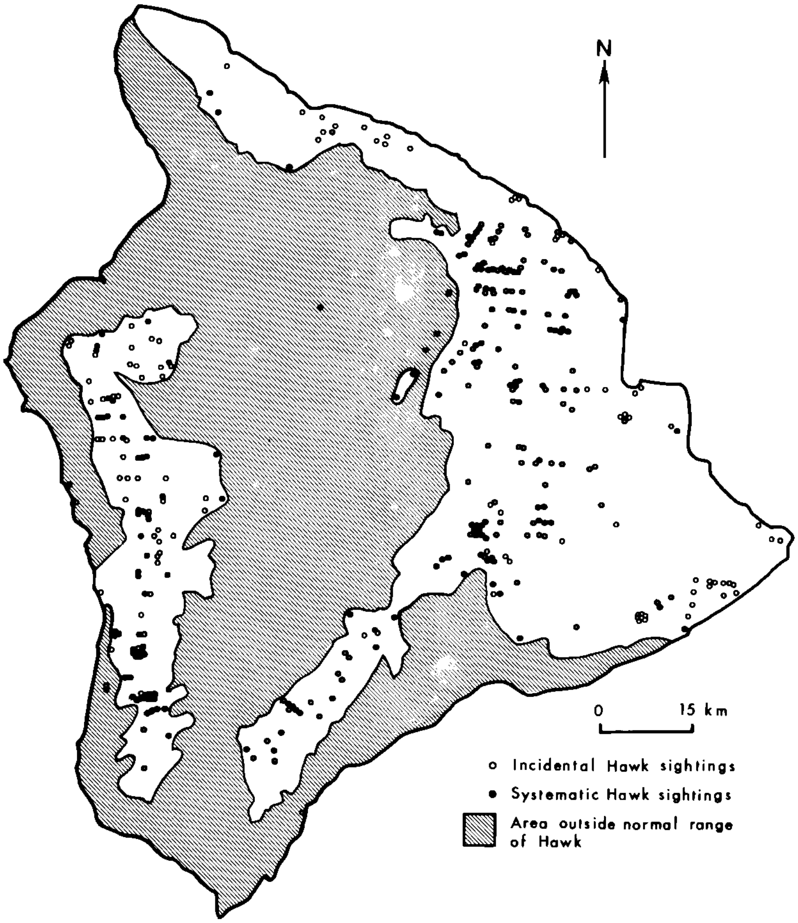


FIGURE 69. Distribution of the Hawaiian Hawk (Io) on the island of Hawaii.

our study areas, but are absent from the arid grasslands on the northwest side of the island, the Kau Desert, the dry scrublands of the Kapapala Tract, and the open savanna of the Kahuku tract. The species occurs from sea level to 2600 m elevation in favorable habitat. We did not estimate population size because the Hawaiian Hawk, like many other raptors, failed to meet many of the assumptions that underlie our density estimates. Griffin (1984) estimated the population to be 1400–2500 birds.

HAWAIIAN RAIL [MOHO] (*Porzana sandwichensis*)

The Hawaiian Rail, or Moho, was definitely known only from the island of Hawaii, but it or a similar species probably occurred on Molokai in historic times (Perkins 1903; Olson and James 1982a, 1982b). Last seen about 1884, Hawaiian Rails were reported to live in open scrub near continuous forest (Perkins 1903). Rats, dogs, and cats probably played a major role in their extinction (Berger 1981). Olson and James (1982b) found that at least eight flightless rail species originally occurred in the main Hawaiian Islands, with only one surviving into the 19th century. One of the fossil species, the very small Molokai rail, appears to be the smallest known rail.

Very little is known of the behavior of the Hawaiian Rail. Based on descriptions of the vocalizations and behavior of the closely related extinct Laysan Rail, we estimated the effective detection distance to be 30 m. Although the probability of detecting an extant population of 100 birds is among the lowest for all species (Table 12), we believe this value to be very conservative and the chance of this species still existing to be quite small.

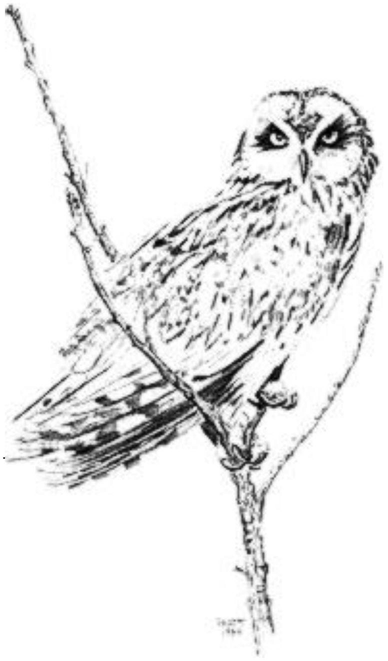
Small flightless black birds reported in 1977 by hunters in scrub ohia forest on Hawaii, upon investigation turned out to be juvenile Kalij Pheasants (J. M. Scott, pers. observ.).

LESSER GOLDEN-PLOVER
Pluvialis dominica

LESSER GOLDEN-PLOVER [KOLEA]
(*Pluvialis dominica*)

Lesser Golden-Plovers, or Kolea, occur as winter visitors in the Hawaiian Islands from sea level to over 3000 m elevation; a few birds stay through summer (Berger 1981). This species inhabits pastures, roadsides, golf courses, and other open areas. It is omnivorous, feeding extensively on insects, other invertebrates, and various plants (Okimoto 1975). Conversion of forest areas to pasturelands have probably resulted in a larger population than was present at Western contact.

We found birds in open areas, pasture lands, and bogs on Hawaii and Maui in several vegetation types (Tables 10, 11); they were most abundant in the bogs of West Maui. These birds were probably early arriving migrants. The occasional plovers found in other areas probably represent birds that failed to migrate to the Arctic breeding grounds.



SHORT-EARED OWL

Asio flammeus sandwichensis

SHORT-EARED OWL [PUEO]
(*Asio flammeus sandwichensis*)

The Short-eared Owl, or Pueo, is an endemic subspecies found on all the main islands, with records for many of the Northwestern Hawaiian Islands as well (Berger 1981). It is one of two extant raptors native to the Hawaiian Islands. Recent excavations have documented the occurrence of several other owls and hawks in the islands antedating Polynesian contact (Olson and James 1982b).

This species was widespread on all the main islands in the 1890s, although Perkins (1903) felt that numbers had declined since Western contact due to the increased area of land under cultivation (especially sugar cane) and possibly shooting. Their ground-nesting habit makes them vulnerable to cat and mongoose predation.

Short-eared Owls feed extensively on house mice (*Mus musculus*) and Polynesian rats (*Rattus exulans*) (Tomich 1971a). Fossil evidence suggests that they failed to become established in the Hawaiian Islands until Polynesians introduced *R. exulans* (Olson and James 1982b), but it is possible that flightless rails and other birds provide a sufficient prey base prior to rodent introductions.

We found Short-eared Owls on all the islands, more frequently as incidental observations than during count periods. Birds most often occur in grasslands, shrublands, and montane parklands. Less frequently they are seen quartering low over closed forest canopies. Short-eared Owls occur in almost all the study areas (Tables 10, 11) and are known from sea level to tree line outside these areas (Berger 1981). Because of the birds' behavior and our few observations, we did not estimate the population size or density. Because of the ubiquitous distribution, range maps were not constructed.

HAWAIIAN CROW
Corvus hawaiiensis

HAWAIIAN CROW [ALALA]
(*Corvus hawaiiensis*)

Hawaiian Crows, or Alala, are the largest passerines in the islands and feed primarily on fruit and to a lesser degree on arthropods, nestling birds, carrion, and nectar (Sakai and Ralph 1980, Giffin 1983). Olson and James (1982b) reported two fossil crow species from Oahu and Molokai, but found no evidence that Alala ever occurred on any island except Hawaii.

Hawaiian Crows have experienced a drastic decline in numbers and marked contraction in range since the early 1890s (Banko 1980–1984; J. G. Giffin, pers. comm.). Perkins (1893, 1903) found them common in wet forest and in koa and ohia parkland in Kona in 1892, but by 1894–1896 the population began to decline. Henshaw (1902) collected numerous specimens below 1000 m elevation in the Kau District from 1899 to 1902. A shooting campaign was waged against Hawaiian Crows by farmers in Kona in the early 1890s and by 1937 the numbers were greatly reduced in both Kau and Kona (Munro 1944). Unconfirmed reports of birds being shot continue to appear. Populations continued to decline from 1938 to 1949 (Baldwin 1969b). Banko (1980–1984) estimated that about 50 birds remained in 1976, occurring only in the North and South Kona Districts. Although Berger (1981) felt that the reasons for the great decline in numbers during the 20th century were inconclusive, J. G. Giffin (pers. comm.) suggested that loss and modification of suitable breeding habitat was one factor in the decline.

We recorded Hawaiian Crows during count periods only in the Kona study area (Fig. 70, Table 10), where they were rare within the 253 km^2 range. The average density was 0.35 birds/km^2 with significant differences between general vegetation types (Table 13). The population was estimated to be 76 ± 18 (95% CI) birds with 68% of those in koa-ohia forests and 30% in ohia.

The Hawaiian Crow appeared to have two major and two minor populations during our 1978 survey. One major population of about 24 birds occupied the north and west slopes of Hualalai;

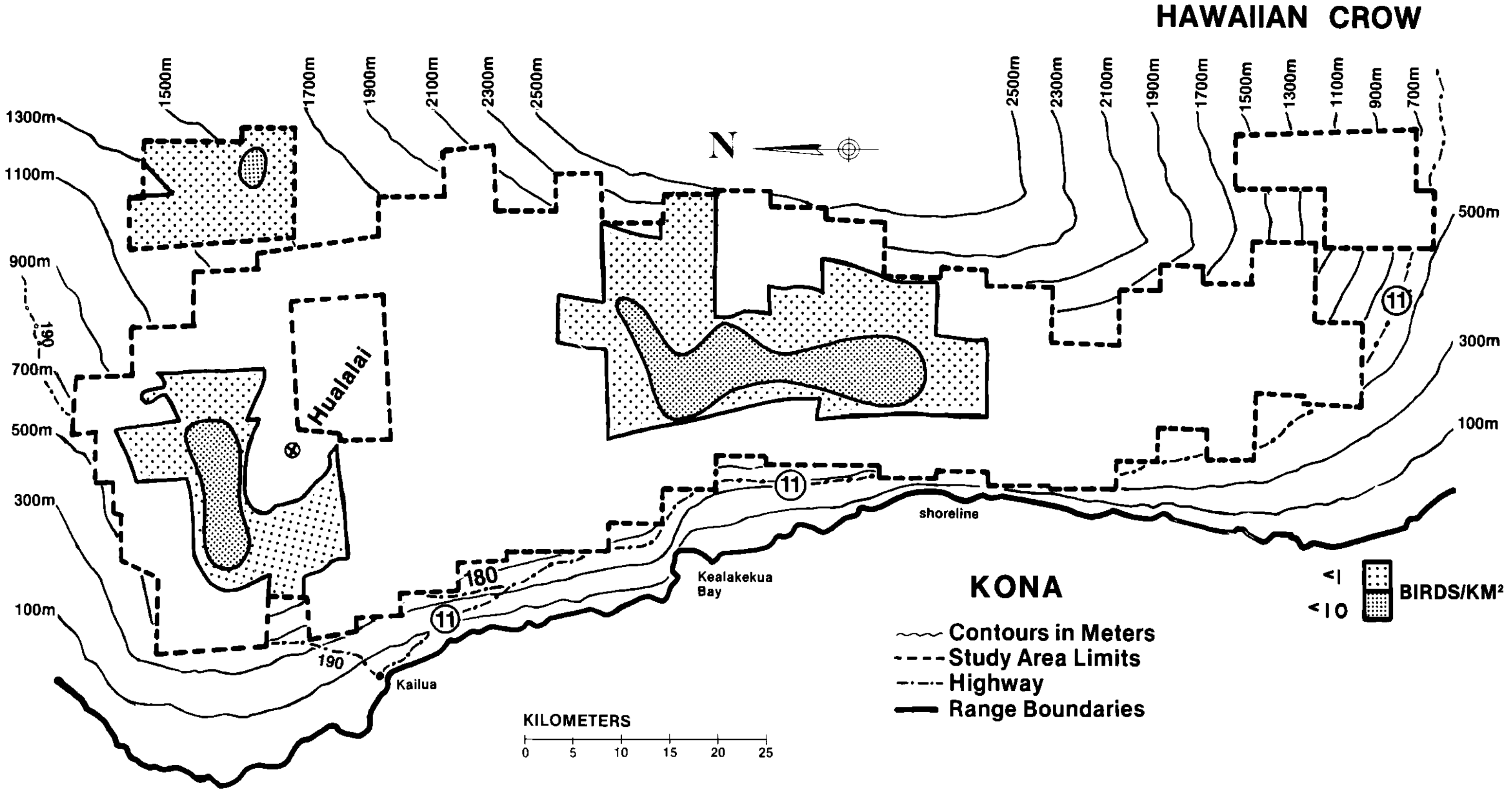


FIGURE 70. Distribution and abundance of the Hawaiian Crow (Alala) in the Kona study area.

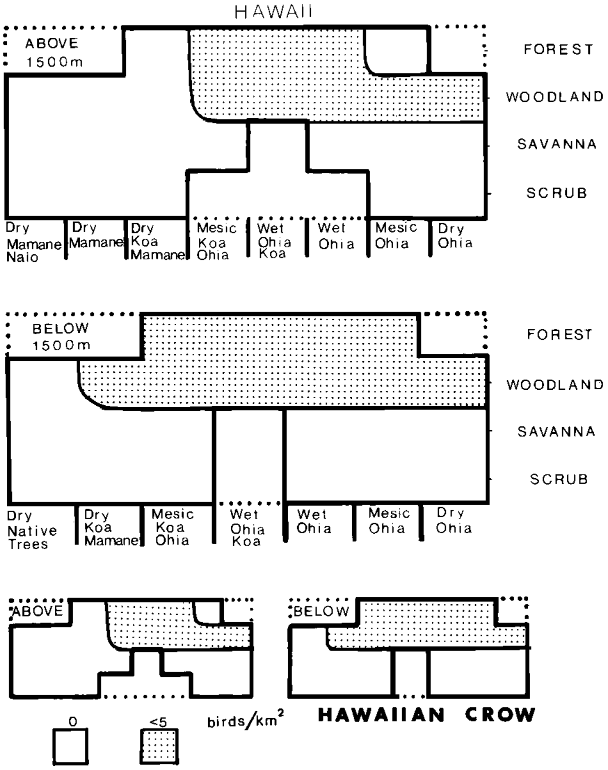


FIGURE 71. Habitat response graphs of the Hawaiian Crow (Alala). (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

the other of about 51 birds occupied the central Kona slopes of Mauna Loa above Kealakekua Bay. A 25-km gap of deforested ranchland and recent lava flows separates the two populations. Since our study, the Hualalai population has drastically declined to two birds, partly because of disturbance, unlawful logging, and illegal shooting, while the central Kona birds appear to have declined to probably fewer than 10 pairs on McCandless Ranch (J. G. Giffin, pers. comm.). The minor populations comprised one pair in south Kona on the Honomalino Tract that was not detected by us (the nest site was midway between transects and in 1984 only one bird remained [J. G. Giffin, pers. comm.]) and two detections northeast of Hualalai near Kipuka Alala. These latter observations were corroborated by ranchers who reported a few birds in this remote and rugged area.

We found three birds in the Kau study area, but none during a count period. Two were heard on 4 July 1976 at 1460 m elevation near transect 2 in an open-canopy ohia forest with a mixed native shrub understory. A single bird was heard on 6 June 1976 in a tall open ohia-koa forest with native shrub understory at 1340 m near transect 4.

Assuming an effective detection distance of 282 m, there is a 0.02 probability that 20 crows resided in the Kau study area without having been detected on a single station. Assuming clustered distributions of two (most likely), three, or four individuals, then the probabilities of no detection are 0.15, 0.28, and 0.38, respectively. In view of of the large amount of time we spent in Kau and our failure to locate the Kau birds earlier that year or since then, we suspect that they were postbreeding dispersants from the Kona populations.

The habitat response graphs for the Hawaiian Crow indicate a broad association with woodlands and forests; more habitat types are occupied below 1500 m than above (Fig. 71). The regression model (Table 14) shows that Hawaiian Crows are positively associated with mesic open to relatively closed forests. The habitat with highest breeding densities during the 1970–1982 period was relatively undisturbed koa-ohia forest (J. G. Giffin, pers. comm.); this is reflected in the regression model by the positive terms for koa and ground ferns, and negative terms for introduced grasses. J. G. Giffin (pers. comm.) found that Hawaiian Crows occupied virtually all of the undisturbed and none of the heavily disturbed koa-ohia forests in Kona, suggesting that habitat modification by cattle grazing and lumbering is a major limiting factor. The preference for undisturbed habitat is related to the diet, which consists chiefly of the fruit and nectar of subcanopy trees and understory shrubs sensitive to ungulate activity (Perkins 1903, Rock 1913, Munro 1944, Sakai and Ralph 1980, Giffin 1983). The positive term for olapa fruit in the regression model may also represent this. The diet changed to include carrion and fruit of introduced plants as the countryside was settled. Although the term for ieie in the regression model is negative, Hawaiian Crows feed on ieie in winter when they move to lower elevations where ieie is common.

Munro (1944) found that Hawaiian Crows occurred from 300 to 2400 m elevation; the range in 1978 was from 900 to 1900 m. We found the highest densities at 1300–1500 m near the lower elevational boundary of the range (Table 13; J. G. Giffin, pers. comm.). Only 20% of the present population occurs above 1500 m. In Kona the upper level of mosquitoes is usually 1400–1600 m elevation (HFBS data). Berger (1981) and D. Jenkins (in Giffin 1983) reported several cases of avian malaria and pox infections in Hawaiian Crows. The wide-cruising range and seasonal movement of Hawaiian Crows (Giffin 1983) may increase their vulnerability to disease by increasing the frequency with which individual birds enter disease-infested areas. Although habitat quality has dramatically improved in the Honaunau Forest Reserve due to natural reforestation since 1960 (R. Bachman, pers. comm.) and Hawaiian Crows were once common there, few birds have been seen there since 1982 (J. G. Giffin, pers. comm.). The parallel near-absence of Akiapolaau, Hawaii Creeper, and Akepa there and elsewhere in central Kona where the habitat appears to be suitable, is significant because avian disease is suspected to be a limiting factor for these species.

In some areas fire has destroyed Hawaiian Crow habitat. Tomich (1971b) pointed out the threat of fountain grass to dry native forest where Hawaiian Crows formerly nested. This aggressive and fire-adapted African tussock grass dies back annually and survives wildfires that result from the accumulation of dead material. In 1960 and 1969 fires decimated areas of mature dry forests north of Puu Waawaa where Hawaiian Crows nested because fountain grass had invaded the understory (Tomich 1971b).

Unlike most passerines, fledgling Hawaiian Crows are unable to fly when they leave the nest (Giffin 1983). Mongoose predation on fledglings has been documented (Giffin 1983), and feral cats are presumably another problem.

Intensive management of the Hawaiian Crow has begun through the Hawaii Division of Forestry and Wildlife. At the Pohakuloa Endangered Species Breeding Facility on Hawaii, a small captive flock has bred successfully and it is hoped that the flock will produce birds that can be used in restocking wild populations. In 1984 the Hawaii Board of Land and Natural Resources established a wildlife sanctuary in the koa-ohia forest on the north slopes of Hualalai to protect the remnant populations of Hawaiian Crows, Hawaii Creepers, and Akepa.

The distributional pattern of the Hawaiian Crow (Fig. 70) suggests a relict population contracting to the best remaining habitat (Diamond 1975). We suspect that because of avian disease these areas lie at higher elevations than the optimum historical habitats, which may have centered on mature dry and mesic forests (Tomich 1971b), such as those characterized by the remnant woodlands at Puu Waawaa (see Table 2). At present a viable wild population may survive only in central Kona (transects 60–65). Clearly the Hawaiian Crow is on the verge of extinction. Management actions needed to restore this species have been discussed in the recovery and restoration plans (Burr et al. 1982, Burr 1984). Without prompt action, the outlook for the Hawaiian Crow is not optimistic.

ELEPAIO
Chasiempis sandwichensis

ELEPAIO (*Chasiempis sandwichensis*)

The Elepaio, a monarchine flycatcher endemic to the islands, feeds on insects and other invertebrates, often capturing them in the air by sallying from a perch (Conant 1977). Separate subspecies occur on Hawaii, Oahu, and Kauai. There is no fossil evidence that Elepaio ever occurred on Maui, Molokai, or Lanai (Olson and James 1982b).

Local plumage variation between habitats led Pratt (1980) to recognize three subspecies on Hawaii: *ridgwayi* on the wet windward slopes, *bryani* in the arid mamane-naio woodland on Mauna Kea, and *sandwichensis* on the mesic Kona slopes. The sedentary nature of the species and local difference in rainfall probably facilitated this phenomenon (Pratt 1980). Intra-island subspecific differentiation may also indicate substantial ability of Elepaio to adapt genetically to prevailing local conditions, and help explain how the bird came to occupy a wide variety of habitats.

In the 19th century, Elepaio were described as extremely common to abundant and widely distributed on Oahu, Kauai, and Hawaii (Wilson and Evans 1890–1899, Perkins 1903). Munro (1944) indicated that birds were holding their own on all three islands. On Kauai, Richardson and Bowles (1964) considered them to be common and widespread chiefly in native forests.

We found Elepaio widespread on Hawaii (Tables 10, 11, Figs. 72–76), occurring in every study area, frequently at high densities and low elevations (Table 16). Highest Elepaio densities were recorded on Kohala Mountain and the koa-ohia forests of Kau. The distributional patterns and numbers of Elepaio on Hawaii and Kauai indicate a healthy population at the species level.

The Mauna Kea subspecies *bryani* may have a precarious future. Isolated from the other subspecies, it occupies only a fraction of the potential range (Pratt 1980), and has a population of 2500 ± 900 (95% CI) birds centered in a dry woodland that is highly susceptible to wildfire. On Mauna Kea, populations of Elepaio, Palila, Common Amakihi, and Akiapolaau are most common at Puu Laau. A 7-km gap of apparently unsuitable habitat (disturbed scrub and grassland) separates the Mauna Kea and Kona subspecies of Elepaio.

The leeward Hawaii subspecies *sandwichensis* has a population of 63,000 ± 3000 (95% CI) birds in the Kona study area. Elepaio drop out at low elevations north of Hualalai at the beginning of the Keamuku flow. Low densities south of Hualalai correspond to deforested ranchland. The Kona population is tenuously connected to Kau across the open pastures, residential subdivisions, and recent flows of the Kahuku Tract.

The subspecies *ridgwayi* is divided into three populations. The 12,000 ± 1500 (95% CI) birds in Kau reach highest densities in koa-ohia forest. Few birds occupy the lower elevations of the south corner of the study area or the very wet central forest. The Kau population drops out sharply in the deforested rangeland of the Kapapala Tract. The windward Hawaii population of 124,000 ± 6000 (95% CI) birds also shows marked avoidance of disturbed understories in the upper northwest corner of the Hamakua study area, and in the dry scrubland of Puna and Kapapala. In Hawaii Volcanoes National Park, population studies by Baldwin (1953), Conant (1975), and Banko and Banko (1980) suggest that Elepaio abundance changed little in most habitats in the 1940–1975 period, except for greater abundance in koa-ohia parkland at 1800 m elevation along the Mauna Loa Strip Road, where habitat regeneration is probably a factor. The third population of *ridgwayi* comprises 14,000 ± 2000 birds in the Kohala study area. Low densities occur in the northeast and at the edges of

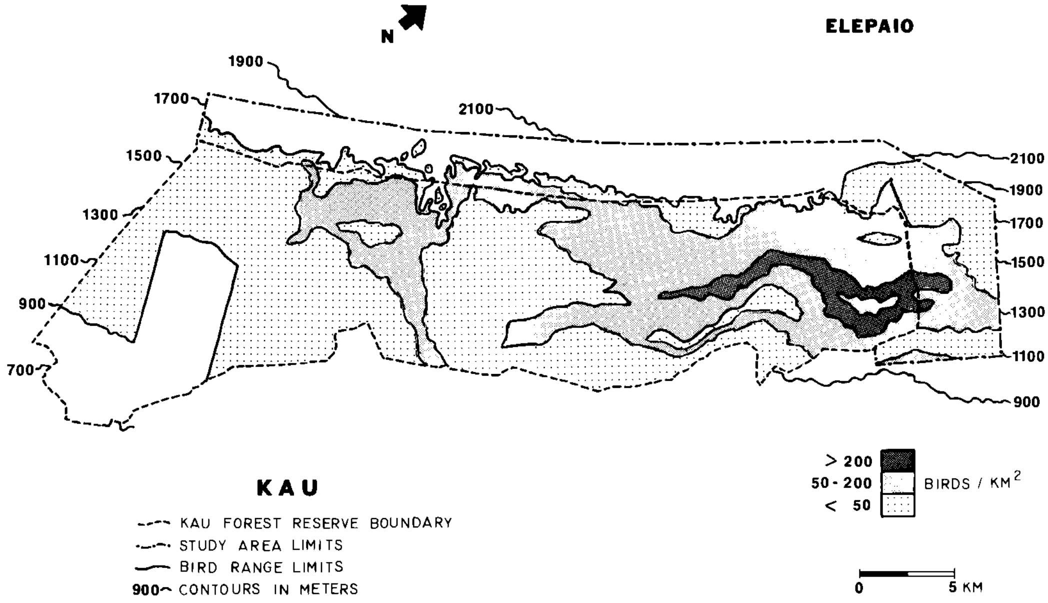


FIGURE 72. Distribution and abundance of the Elepaio in the Kau study area.

TABLE 16

DENSITY [MEAN (SE)] OF THE ELEPAIO BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Kauai
Elevation								
100–300 m	···	···	···	···	···	···	···	···
300–500 m	···	23 (11)	22 (4)	···	78 (23)	···	0	···
500–700 m	0	32 (5)	52 (7)	···	85 (11)	···	0	···
700–900 m	24 (13)	46 (5)	87 (11)	···	57 (6)	···	0	···
900–1100 m	47 (9)	91 (8)	10 (4)	···	61 (5)	···	78 (21)	···
1100–1300 m	47 (8)	107 (7)	9 (6)	88 (18)	55 (5)	···	183 (28)	···
1300–1500 m	73 (9)	196 (10)	···	32 (10)	47 (4)	···	254 (23)	267 (14)
1500–1700 m	67 (8)	226 (14)	···	63 (11)	98 (5)	···	241 (37)	230 (13)
1700–1900 m	55 (8)	160 (13)	···	16 (6)	96 (7)	···	···	···
1900–2100 m	42 (14)	30 (8)	···	8 (6)	59 (6)	47 (17)	···	···
2100–2300 m	0	47 (21)	···	0	38 (6)	39 (10)	···	···
2300–2500 m	···	···	···	···	17 (7)	32 (9)	···	···
2500–2700 m	···	···	···	···	···	17 (10)	···	···
2700–2900 m	···	···	···	···	···	+ (+)	···	···
2900–3100 m	···	···	···	···	···	+ (+)	···	···
Habitat								
Ohia	29 (3)	124 (5)	47 (4)	9 (3)	48 (2)	···	198 (16)	249 (9)
Koa-ohia	104 (7)	132 (6)	···	83 (14)	101 (5)	···	···	···
Koa-mamane	···	47 (12)	···	27 (6)	99 (6)	···	···	···
Mamane-naio	···	···	···	···	12 (7)	26 (5)	···	···
Mamane	···	···	···	···	101 (8)	25 (9)	···	···
Other natives	···	48 (13)	···	56 (31)	12 (5)	···	···	···
Intro. trees	···	13 (4)	···	···	38 (10)	···	153 (54)	···
Treeless	0		0	26 (26)	14 (7)	···	···	13 (13)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

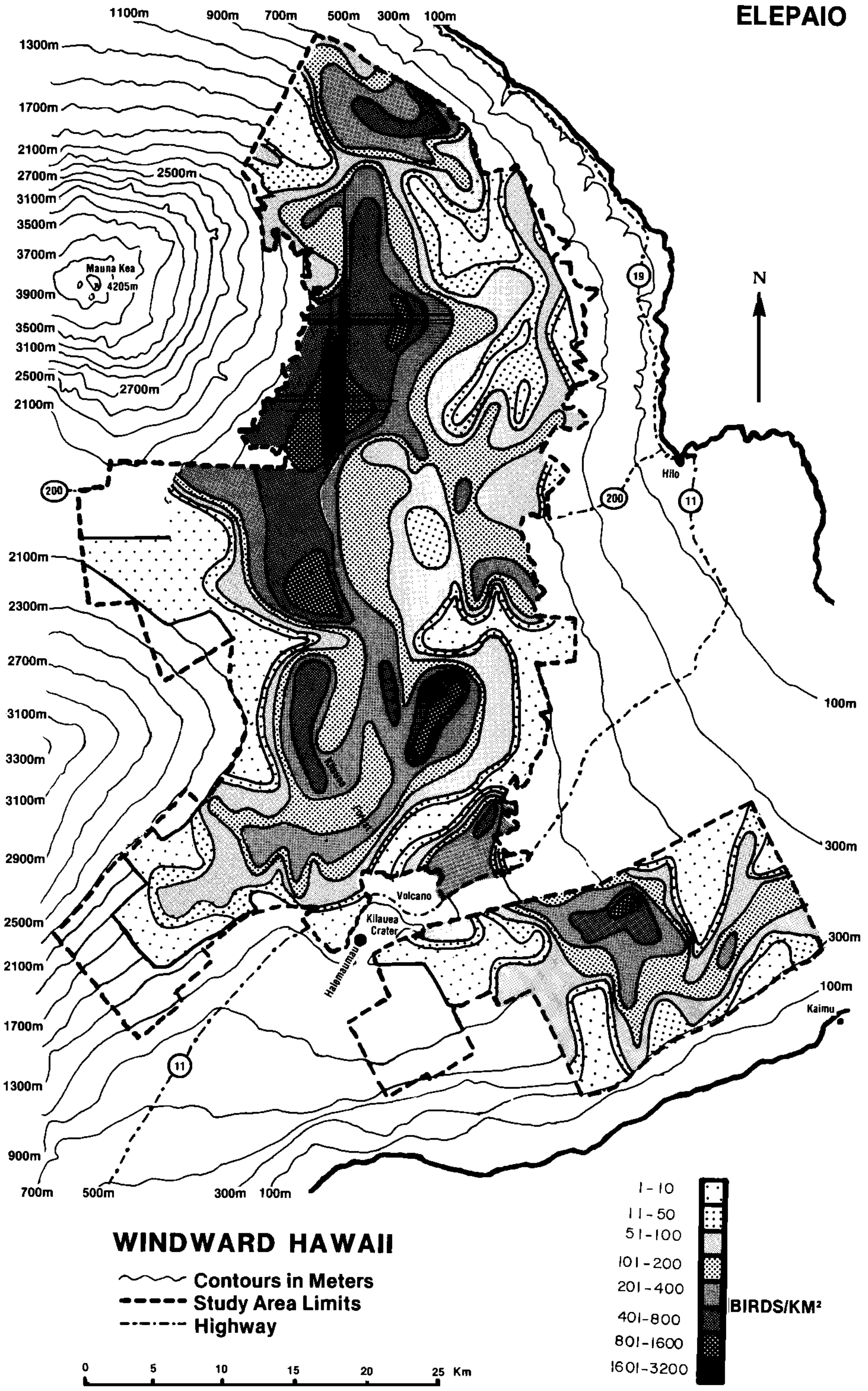


FIGURE 73. Distribution and abundance of the Elepaio in the windward Hawaii study areas.

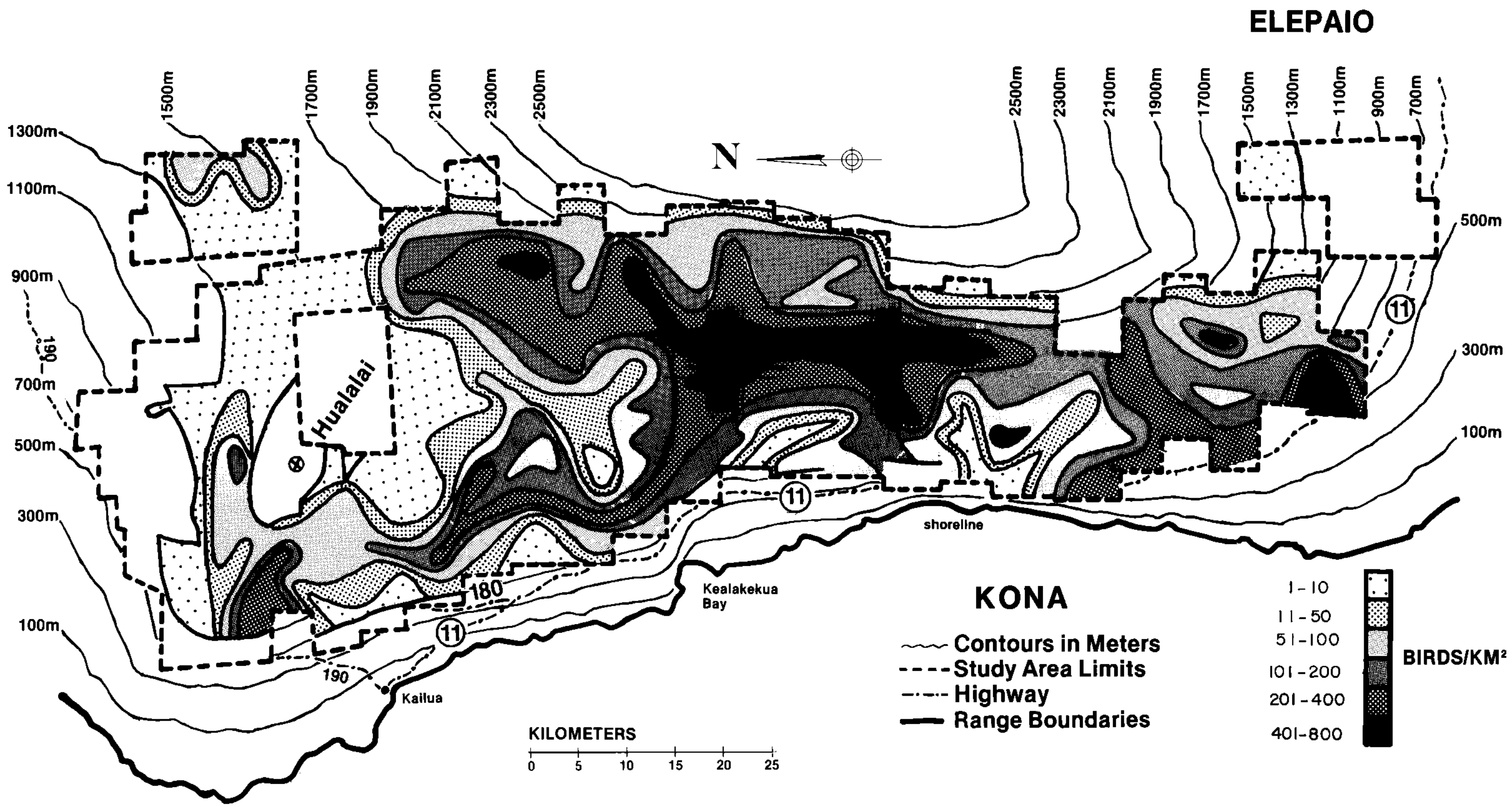


FIGURE 74. Distribution and abundance of the Elepaio in the Kona study area.

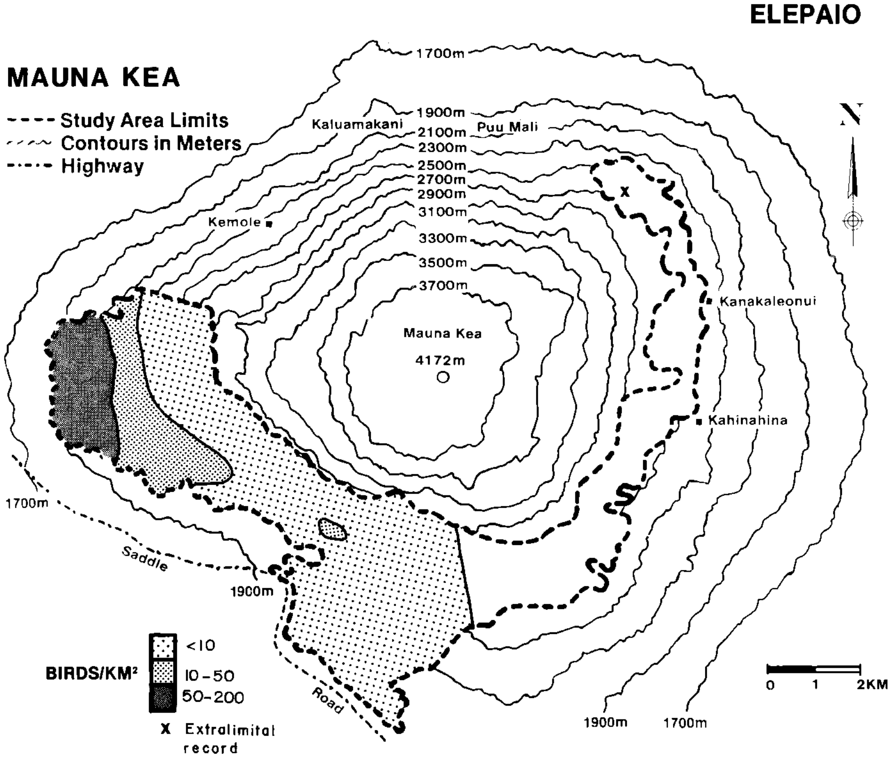


FIGURE 75. Distribution and abundance of the Elepaio in the Mauna Kea study area.

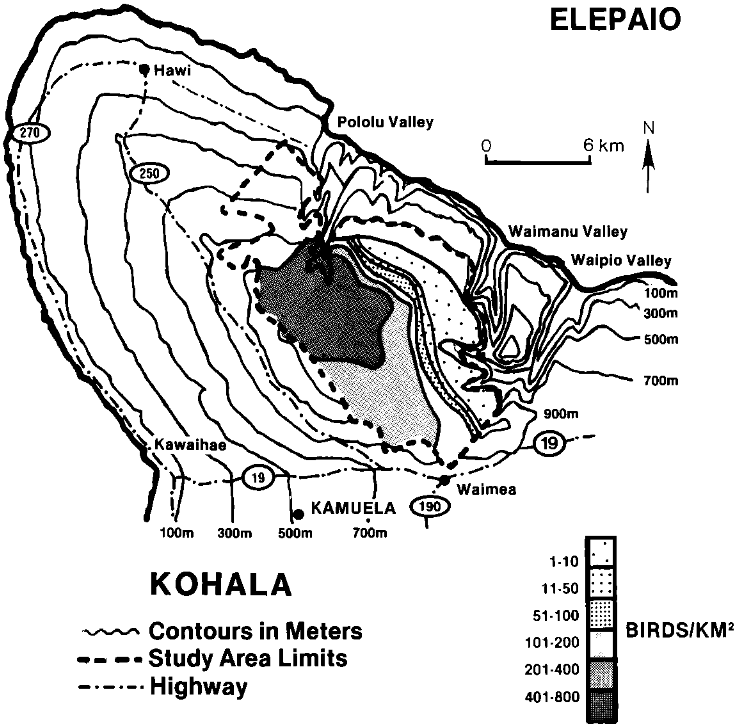


FIGURE 76. Distribution and abundance of the Elepaio in the Kohala study area of Hawaii.

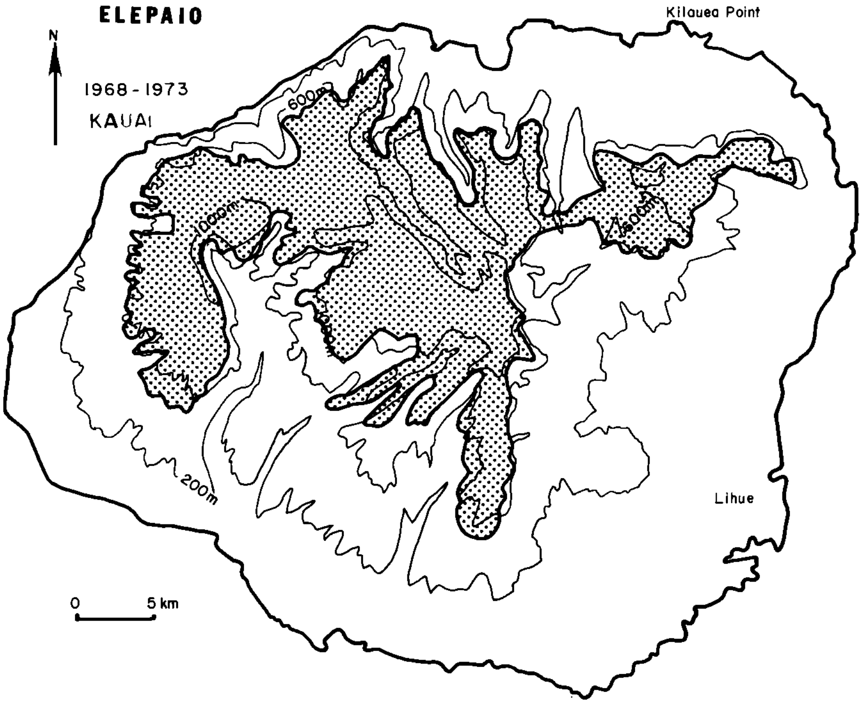


FIGURE 77. Range of the Elepaio on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

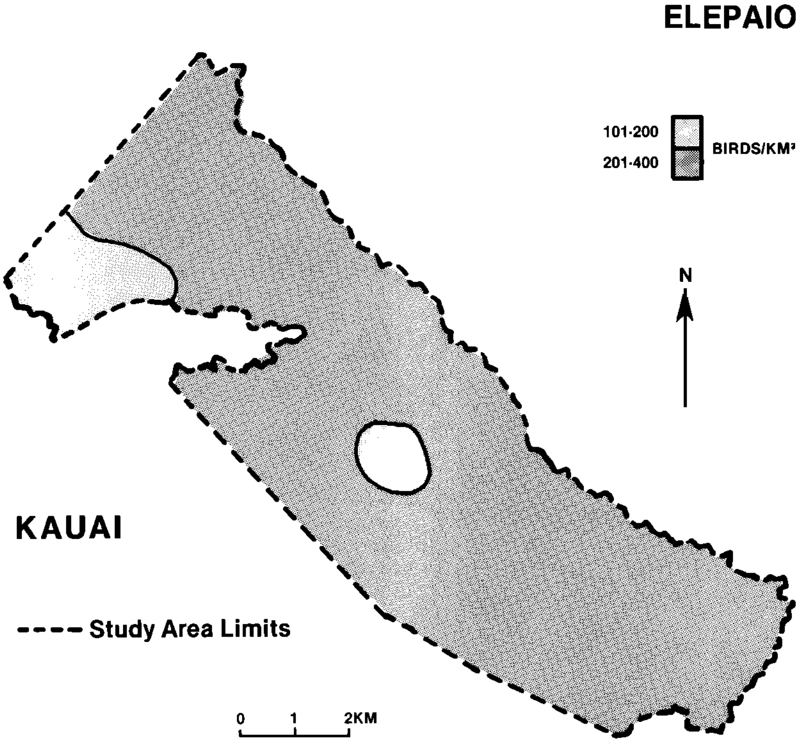


FIGURE 78. Distribution and abundance of the Elepaio in the Kauai study area.

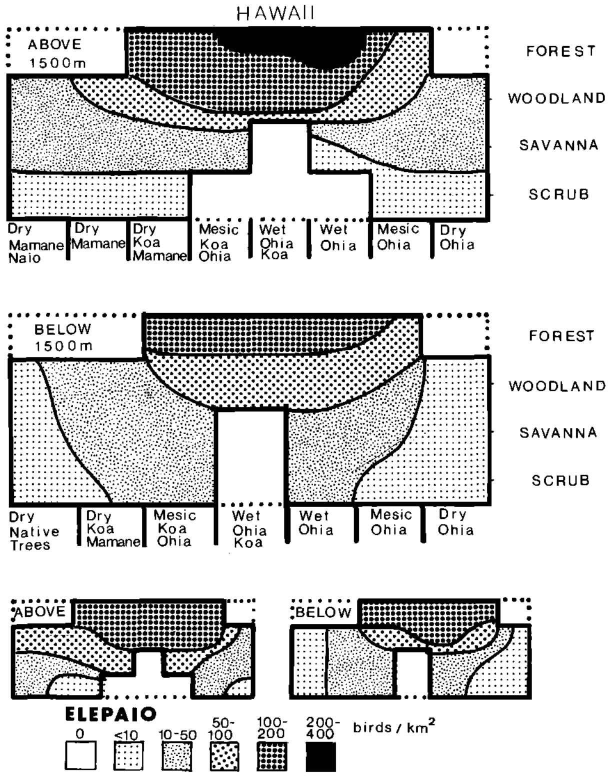


FIGURE 79. Habitat response graphs of the Elepaio. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

the study area where understories were opened by cattle.

Elepaio are widely distributed in the native forests of Kauai, inhabiting the west rim and slopes of Waimea Canyon, the Na Pali plateaux, Kokee State Park, the Alakai Swamp, Kahili Peak and the Kapalaoa Ridge, Laau Ridge, Namolokama Mountain, the Makaleha Mountains, and Anahola Mountain (Sincock et al. 1984, Fig. 77). Sincock et al. (1984) estimated a total population of 40,000 ± 7000 birds for all of Kauai. In the Kauai study area, Elepaio have a wide distribution (Fig. 78, Table 11) and a population of 5900 ± 500 (95% CI). The 1968–1973 survey by J. L. Sincock (pers. comm.) showed 5000 ± 1000 birds for the same area. The difference in results between his survey and ours is statistically insignificant, well within expected annual variation for a passerine population, and suggests a stable population in that area.

The habitat response graph (Fig. 79) shows that Elepaio occupy virtually every major habitat type above and below 1500 m elevation. Like many native passerines, Elepaio attain highest densities in wet to mesic forests above 1500 m (Fig. 79). Densities are lower in woodland, savanna, scrub, and drier habitats. The regression models (Table 17) show that they are most common in wet forests at higher elevations. The weak response of Elepaio to flower or fruit variables in the models may reflect the insectivorous diet.

Little response is seen in the regression models toward total shrub or ground cover; however, there are strong responses to individual understory components. Elepaio are negatively associated with matted ferns in five models and with passiflora and grasses in two models. Little response to native shrubs and conflicting response to introduced shrubs is seen in Hamakua and Puna. This may represent a bell-shaped response to introduced shrubs, since Puna has the highest introduced shrub cover of the eight study areas occupied by Elepaio. Elepaio may also respond negatively to fire tree, which frequently dominates the understory in Puna but not elsewhere.

Elepaio appear to be the most successful native passerine in adapting to introduced vegetation, although highest densities occur in native forests.

TABLE 17
REGRESSION MODELS FOR HABITAT RESPONSE OF THE ELEPAIO[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Kauai
R^2	0.23*	0.30*	0.26*	0.43*	0.37*	0.31*	0.60*	0.21*
Moisture	···	···	5.0*	···	8.3*	X	X	X
Elevation	2.6	12.2*	···	3.3	−3.7*	···	13.0*	2.6
$(\text{Elevation})^2$	−2.2	−8.9*	···	−3.5*	6.7*	−3.5*	···	···
Tree biomass	···	−4.0*	−4.3*	5.6*	−8.5*	5.8*	3.4*	3.5*
$(\text{Tree biomass})^2$	5.0*	7.6*	···	···	12.8*	···	···	−3.0
Crown cover	···	···	5.1*	···	···	···	···	···
Canopy height	···	···	2.7	···	···	···	2.7	···
Koa	9.8*	···	X	···	7.2*	X	X	X
Ohia	···	4.9*	···	−5.4*	···	X	···	X
Naio	X	X	X	4.3*	4.3*	···	X	X
Mamane	X	···	···	2.1	8.6*	−4.8*	X	X
Intro. trees	X	−3.8*	···	X	···	X	···	X
Shrub cover	···	···	···	···	···	−10.3*	···	···
Ground cover	···	···	···	···	···	···	···	···
Native shrubs	···	···	···	−5.3*	···	X	···	···
Intro. shrubs	X	7.4*	−4.9*	···	···	X	···	···
Ground ferns	X	X	···	···	7.0*	X	···	···
Matted ferns	···	−2.5	−5.9*	···	−4.1*	X	−2.6	−2.5
Tree ferns	···	X	···	X	···	X	···	···
Ieie	X	X	···	X	···	X	X	···
Passiflora	X	−11.9*	X	X	−10.1*	X	···	X
Native herbs	X	X	···	···	−2.8	X	···	···
Intro. herbs	X	X	···	···	···	···	−4.7*	···
Native grasses	···	···	−4.1*	···	−8.1*	···	···	···
Intro. grasses	···	···	−4.4*	···	···	···	···	···
Ohia flowers	···	···	−2.3	···	−2.6	X	···	···
Olapa fruit	···	−3.8*	···	−5.4*	···	X	···	···
Mamane flowers	X	X	X	···	X	···	X	X
Mamane fruit	X	X	X	X	X	···	X	X
Naio fruit	X	X	X	X	X	···	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.01$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

On Oahu, Elepaio occupy a wide variety of native and introduced forests (Berger 1981), and nest in dense introduced shrub understory (Conant 1977). On Kauai, Elepaio frequent lowland forests of introduced trees (Richardson and Bowles 1964).

KAMAO (*Myadestes myadestinus*)

Pratt (1982) offered convincing evidence that *Phaeornis* should be merged with the solitaire genus *Myadestes,* and that some Hawaiian thrushes formerly treated as subspecies are sufficiently distinct to merit full species status. Pratt recognized the Kauai race as *M. myadestina,* the Lanai, Molokai, and presumably Maui races as *M. lanaiensis,* and the Hawaii race as *M. obscurus.* Our field experience with the Hawaiian thrushes corroborates Pratt's conclusions that these appear to be biologically distinct species.

The Kamao is sometimes referred to as the Large Kauai Thrush. Kamao feed opportunistically on fruit and to a lesser extent on insects and land snails (Henshaw 1902, Perkins 1903).

Kamao were the most common forest birds in 1891 on Kauai, but by 1928 they were gone from the lower forests (Munro 1944). Richardson and Bowles (1964) found them mostly restricted to the Alakai, and guessed the population was "some hundreds, if not a few thousands." For 1968–1973 Sincock et al. (1984) estimated a population of 337 ± 243 (95% CI) birds with 173 ± 116 in our study area. During the 1981 survey, only 24 ± 20 birds remained, located at the remote south portion of the Alakai (Table 18, Fig. 80). Sincock et al. (1984) found the species primarily distributed in the upper (south) Alakai Swamp, with one isolated occurrence in Kokee State Park (Fig. 81). This pattern is also reflected by the positive term for elevation in the regression model for habitat response (Table 19). Abundant suit-

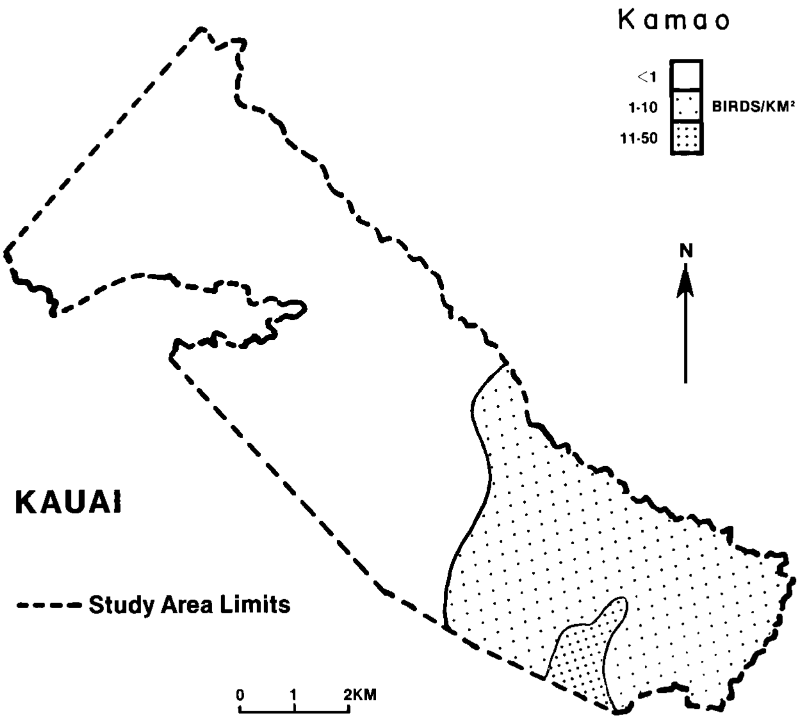


FIGURE 80. Distribution and abundance of the Kamao in the Kauai study area.

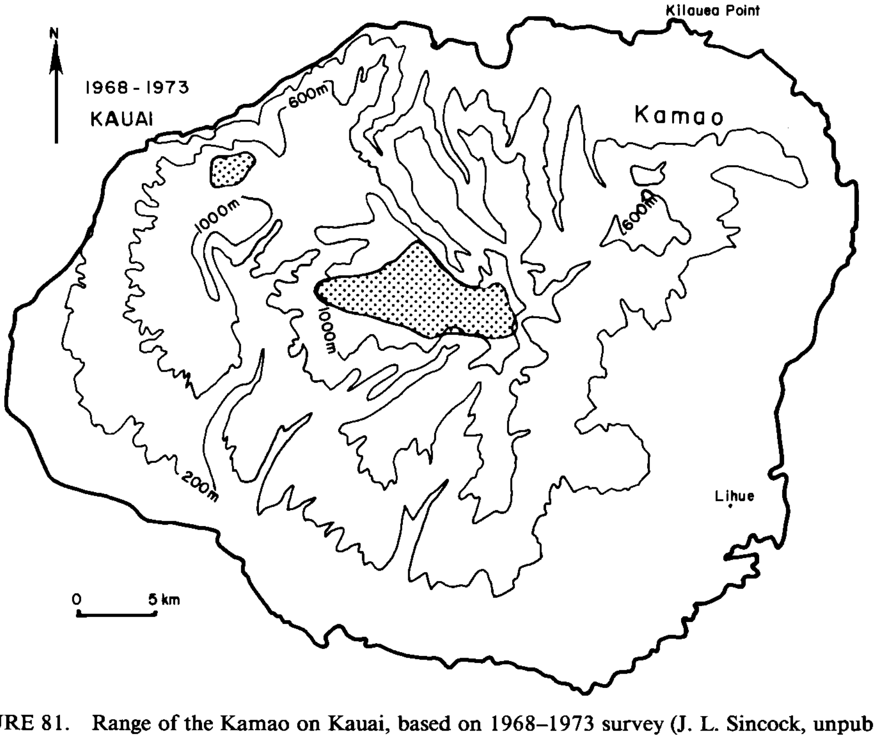


FIGURE 81. Range of the Kamao on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

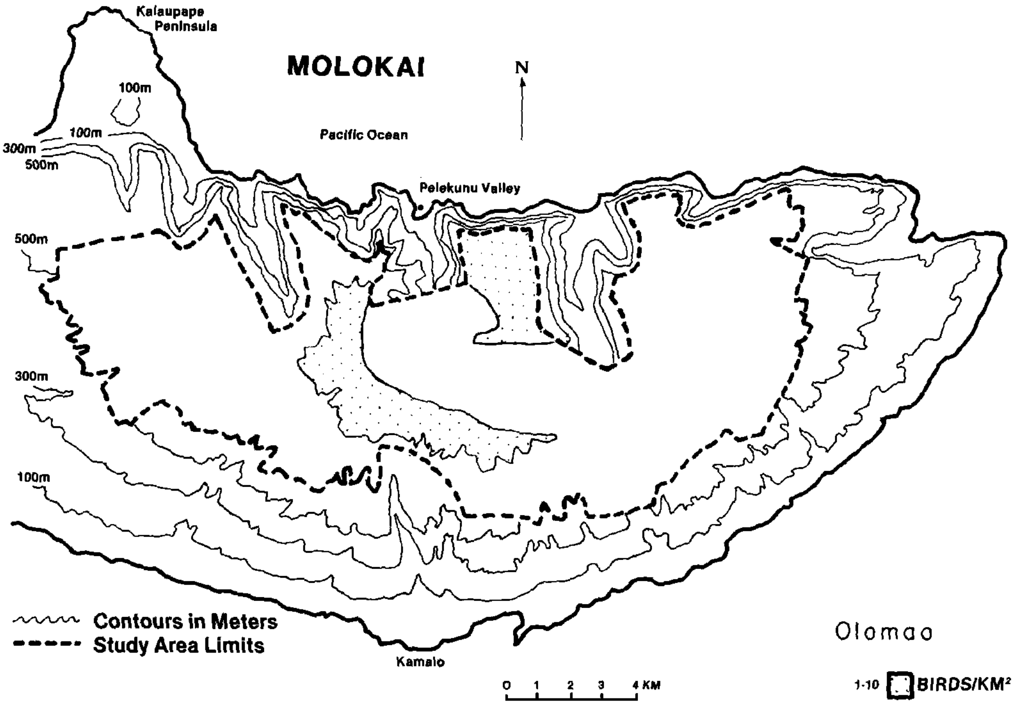


FIGURE 82. Distribution and abundance of the Olomao in the Molokai study area.

TABLE 18
DENSITY [MEAN (SE)] OF THE KAMAO, OLOMAO, OMAO, AND PUAIOHI BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kamao	Olomao	Omao					Puaiohi
	Kauai	Molokai	Kau	Hamakua	Puna	Kipukas	Kona	Kauai
Elevation								
100–300 m	···	0	···	···	···	···	···	···
300–500 m	···	0	···	24 (24)	20 (3)	···	0	···
500–700 m	···	0	0	17 (4)	84 (5)	···	0	···
700–900 m	···	0	174 (18)	47 (4)	117 (6)	···	0	···
900–1100 m	···	3 (3)	191 (13)	90 (5)	173 (14)	···	0	···
1100–1300 m	+ (+)	+ (+)	211 (11)	96 (3)	56 (10)	1 (1)	15 (8)	1 (1)
1300–1500 m	4 (2)	+ (+)	236 (9)	149 (5)	···	5 (2)	81 (7)	+ (+)
1500–1700 m	···	···	202 (12)	153 (6)	···	14 (3)	52 (10)	···
1700–1900 m	···	···	185 (13)	129 (7)	···	44 (4)	3 (2)	···
1900–2100 m	···	···	44 (8)	52 (7)	···	4 (1)	0	···
2100–2300 m	···	···	0	0	···	9 (3)	1 (1)	···
2300–2500 m	···	···	···	···	···	···	0	···
2500–2700 m	···	···	···	···	···	···	···	···
2700–2900 m	···	···	···	···	···	···	···	···
2900–3100 m	···	···	···	···	···	···	···	···
Habitat								
Ohia	2 (1)	1 (1)	178 (6)	118 (3)	88 (4)	15 (2)	10 (4)	1 (+)
Koa-ohia	···	···	222 (8)	92 (3)	···	34 (6)	51 (7)	···
Koa-mamane	···	···	···	28 (13)	···	8 (3)	0	···
Mamane-naio	···	···	···	···	···	···	0	···
Mamane	···	···	···	···	···	···	0	···
Other natives	···	0	···	38 (6)	···	39 (20)	0	···
Intro. trees	···	0	···	41 (7)	···	···	0	···
Treeless	0	0	40 (28)	35 (4)	12 (12)	14 (11)	0	0

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

able habitat appears to occur outside the present range. The contraction of the range of the Kamao into the Alakai occurred approximately simultaneously with similar contractions by several other native species.

OLOMAO (*Myadestes lanaiensis*)

Olomao were almost ubiquitous in the forests of Molokai and Lanai in the 1890s (Perkins 1903), but the decline in numbers and reduction in range occurred before the 1930s (Munro 1944). Aside from a secondhand report for West Maui (Perkins 1903), there was no evidence that this species ever occurred on Maui until S. L. Olson and H. F. James (pers. comm.) unearthed fossils at Ulupalakua in 1982. The chances of our having missed a population of 100 birds in the Maui study areas are quite low (Table 12). Olomao feed opportunistically on fruit and to a lesser extent on insects and land snails (Henshaw 1902, Perkins 1903).

The population on Molokai (Fig. 82), estimated at 19 ± 38 (95% CI), is a small remnant and appears to have a low probability of long-term survival. Suitable habitat appears to be abundant. We found birds on Olokui Plateau (3 HFBS sightings), and in Kamakou Preserve and adjacent areas (2 sightings by Scott et al. [1977] and 3 HFBS sightings). Olomao generally occur above 1000 m elevation (Table 18).

OMAO
Myadestes obscurus

OMAO (*Myadestes obscurus*)

Omao were abundant and widespread in the denser forests on Hawaii above 300 m elevation (Henshaw 1902, Perkins 1903). They now occupy only about 30% of their former range on Hawaii (van Riper and Scott 1979). Omao feed opportunistically on fruit and to a lesser extent on insects and land snails (Henshaw 1902, Perkins 1903, van Riper and Scott 1979, Berger 1981). Perkins (1903) reported that birds migrated in the forests to caterpillar outbreaks, although we have noted only relatively localized movement. Most Omao nests have been found in cavities and on protected platforms (van Riper and Scott 1979). This may be a bioenergetic adaptation for the cold wet environment of montane rainforests, reflecting the close relationship with other *Myadestes* solitaires.

Omao are widespread and common in the forests of windward Hawaii, but are absent from Kohala and most of Kona (Tables 10, 18, Figs. 83–85). Two well-established populations

TABLE 19

Regression Models for Habitat Response of the Kamao, Omao, and Puaiohi[a]

	Kamao	Omao				Puaiohi
	Kauai	Kau	Hamakua	Puna	Kipukas	Kauai
R^2	0.12*	0.36*	0.57*	0.64*	0.32*	0.04
Moisture	X	3.6*	···	7.4*	···	X
Elevation	3.9*	6.4*	20.7*	5.9*	3.2	···
(Elevation)^2	···	−5.8*	−16.4*	−4.8*	−3.6*	···
Tree biomass	2.2	−2.0	···	···	···	···
(Tree biomass)^2	···	4.5*	3.1	−2.4	5.6*	···
Crown cover	···	···	−5.9*	3.8*	···	···
Canopy height	···	···	···	···	···	···
Koa	X	···	−7.8*	X	···	X
Ohia	X	···	7.4*	···	···	X
Naio	X	X	X	X	···	X
Mamane	X	X	···	···	···	X
Intro. trees	X	X	−3.9*	···	X	X
Shrub cover	···	3.1	3.2	···	···	···
Ground cover	···	···	−7.5*	···	···	···
Native shrubs	···	···	2.3	···	···	···
Intro. shrubs	···	X	9.4*	−2.9	···	···
Ground ferns	···	X	X	···	2.4	···
Matted ferns	···	···	···	···	···	···
Tree ferns	···	···	X	6.0*	X	···
Ieie	···	X	X	···	X	···
Passiflora	X	X	−8.3*	X	X	X
Native herbs	···	X	X	···	2.3	···
Intro. herbs	···	X	X	−6.3*	−4.0*	···
Native grasses	···	···	6.7*	4.8*	···	···
Intro. grasses	···	···	7.5*	−3.8*	−3.8*	···
Ohia flowers	···	···	4.1*	···	−5.1*	···
Olapa fruit	···	···	···	···	···	2.5
Mamane flowers	X	X	X	X	···	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

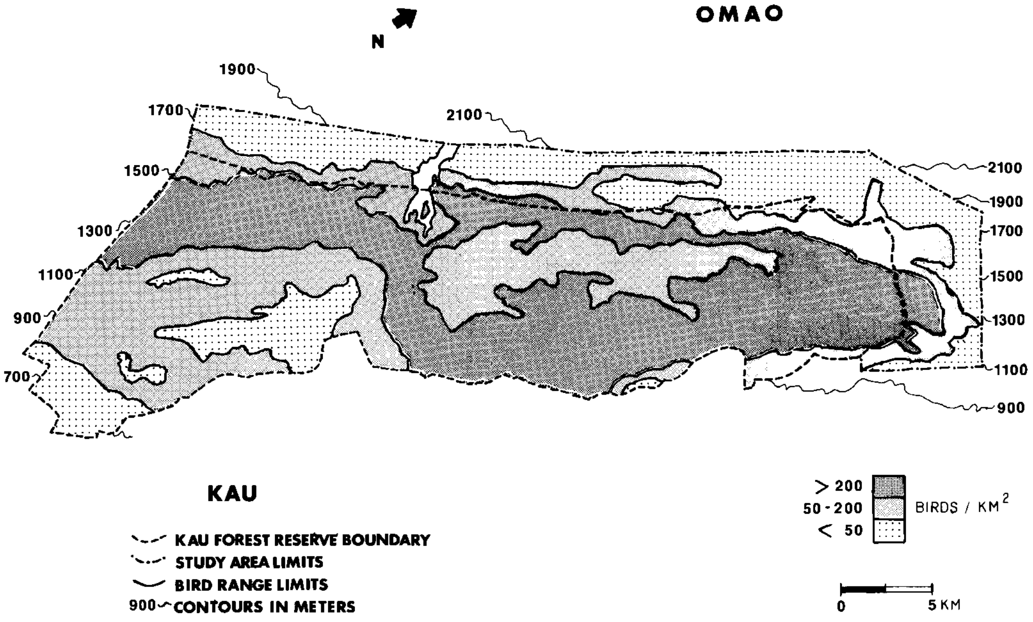


FIGURE 83. Distribution and abundance of the Omao in the Kau study area.

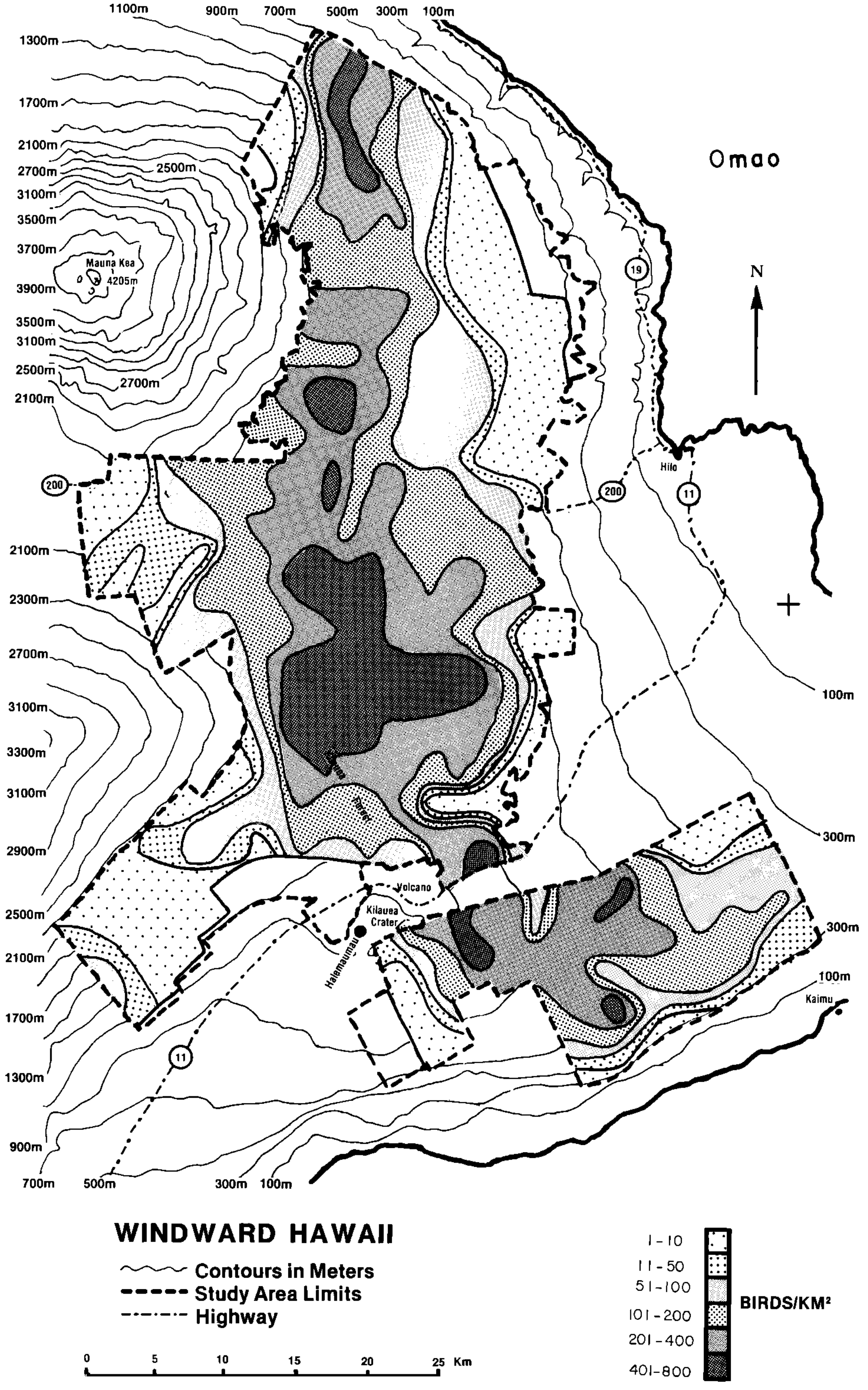


FIGURE 84. Distribution and abundance of the Omao in the windward Hawaii study areas.

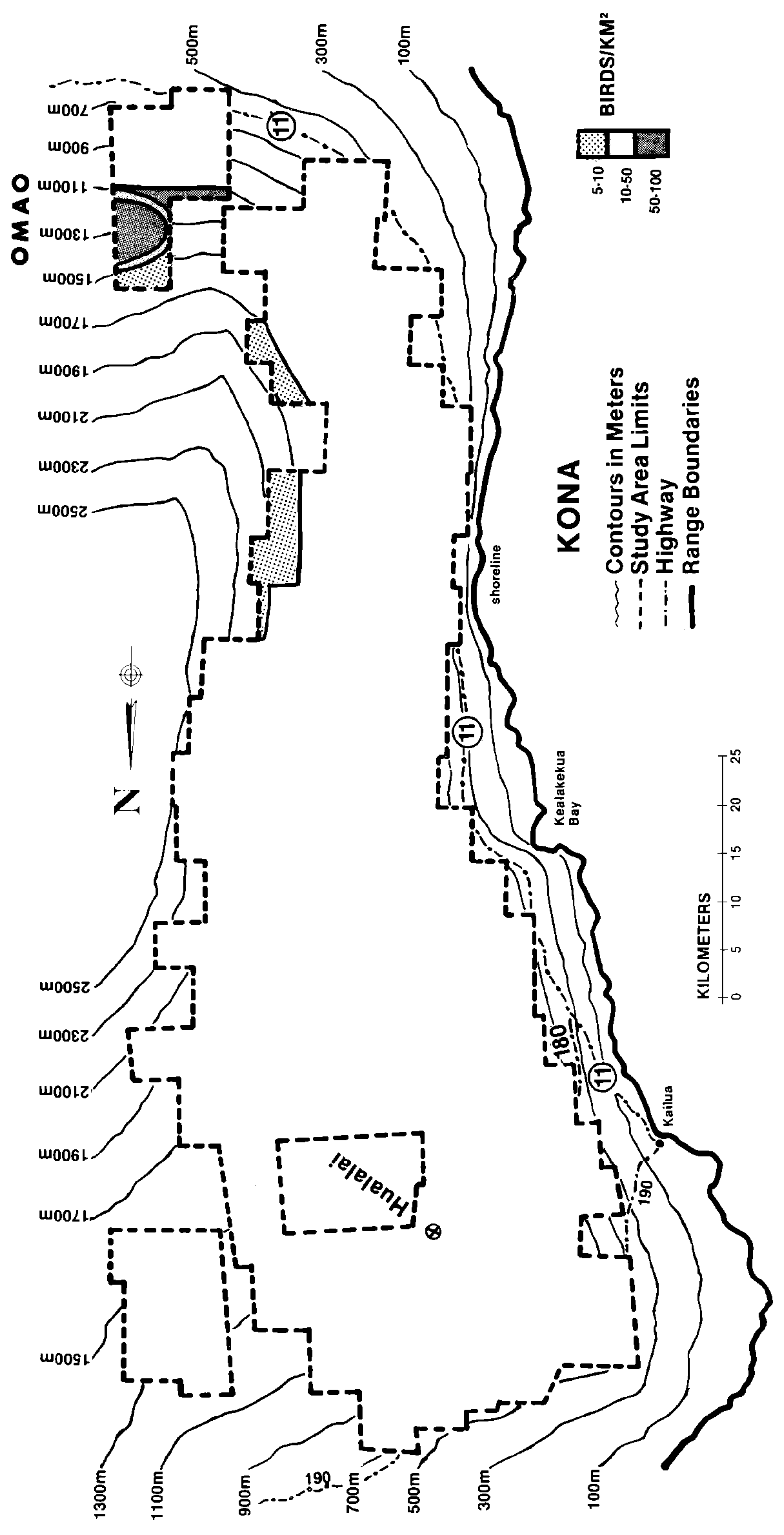


FIGURE 85. Distribution and abundance of the Omao in the Kona study area.

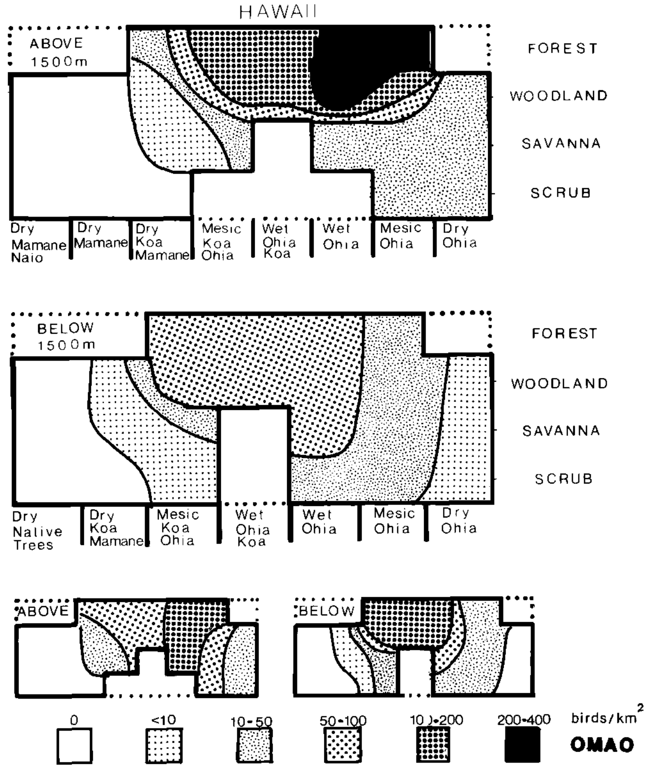


FIGURE 86. Habitat response graphs of the Omao. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

occur on Hawaii, the 56,000 ± 3000 (95% CI) Kau birds weakly separated from the 113,000 ± 3000 Hamakua and Puna birds by deforested rangeland on the Kapapala Tract. A third population may exist above the areas we sampled in the alpine scrub on Mauna Loa from 2000 to 3000 m elevation (Dunmire 1961, van Riper and Scott 1979, Conant 1981). The few birds observed in Kona seemed to represent birds from the margins of the Kau and alpine populations, and not remnants of the original Kona forest population.

Highest observed densities of Omao occur in the Kau study area. Fairly high numbers at lower elevations in Kau and Puna indicate a robust population not threatened by extinction. The absence from low elevations in north Hamakua appears to be a distributional anomaly of unknown origin. Population studies in Hawaii Volcanoes National Park suggest that bird densities increased during 1940–1975 in ohia rainforest near Kilauea Crater and in koa-ohia parkland along the Mauna Loa Strip Road (Baldwin 1953, Conant 1975, Banko and Banko 1980).

The habitat response graph (Fig. 86) shows that Omao are common in mesic and wet ohia forests above 1500 m elevation. Omao are much less common in shrub and savanna, and do not occur in low rainfall habitats (left end of response graphs). A strong negative response to passiflora (banana poka in this case) is seen in the regression model for the Hamakua area (Table 19). Habitat response to introduced shrubs and introduced grasses appears to differ between the Hamakua and Puna areas.

If reported correctly, the habit of migrating to local areas of food abundance would have made birds especially likely to contract avian disease. Malaria or pox susceptibility combined with seasonal movement may explain the early extinction over most of Kona.

PUAIOHI
Myadestes palmeri

PUAIOHI [SMALL KAUAI THRUSH]
(*Myadestes palmeri*)

Puaiohi are very rare birds of the high-elevation ohia forests in the Alakai Swamp (Richardson and Bowles 1964, Sincock et al. 1984). They were always rare historically (Perkins 1903), and their biology is little known. Puaiohi feed primarily on fruit and insects (Richardson and Bowles 1964, Sincock et al. 1984).

The first known nest was found during the HFBS (Kepler and Kepler 1983); it was constructed on a shelf in a cliff face adjacent to a stream and was similar in appearance, construction, and placement to nests of Townsend's Solitaire (*Myadestes townsendi*). The similarity of the nests of these two species supports the placement of *Phaeornis* in *Myadestes* (Pratt 1982). A second nest similar to the first was found in 1983 (Ashman et al. 1984). Like Omao (van Riper and Scott 1979), Puaiohi seem to be cavity and platform nesters. Although this behavior may be bioenergetically adaptive to the cold wet environment of montane rainforests, it is probably retained from the putative mainland ancestors; Townsend's Solitaire was suggested as the closest living relative (Pratt 1982).

We detected 13 Puaiohi during our intensive surveys of the Alakai Swamp (Table 11, Fig. 87). Five more were recorded outside the count periods. We estimated the population at 20 ± 34 (95% CI) birds (Tables 11 and 18). This compares with an estimate of 176 ± 192 birds for all of Kauai in 1968–1973 and 97 ± 129 for our study area by Sincock et al. (1984). Sincock et al. (1984) found that this species occurred through all but the southwest portion of the Alakai Swamp, and on Laau Ridge, with an isolated occurrence at Kokee State park (Fig. 88).

In the 1890s Kamao were 100 times more numerous than Puaiohi (Perkins 1903). They are now about equally common on Kauai, and both taxa apparently experienced a tenfold drop in populations during the 1970s. Both our data and Sincock's indicate that Puaiohi are more common than Kamao in the north half of the Alakai, and that Kamao are more common in the south Alakai. Sincock et al. (1984) found that Puaiohi had retreated from the Kokee State Park area, along with the other endangered passerines. Puaiohi are most frequently encountered near stream banks covered with ferns, sedges, and mosses (Sincock et al. 1984). Future efforts to determine population size should consider this in allocating sampling effort.

The regression model (Table 19) shows that Puaiohi are associated with olapa fruit. Although small sample sizes are involved, this result is probably accurate, because olapa fruit constitute a chief dietary item (Richardson and Bowles 1964).

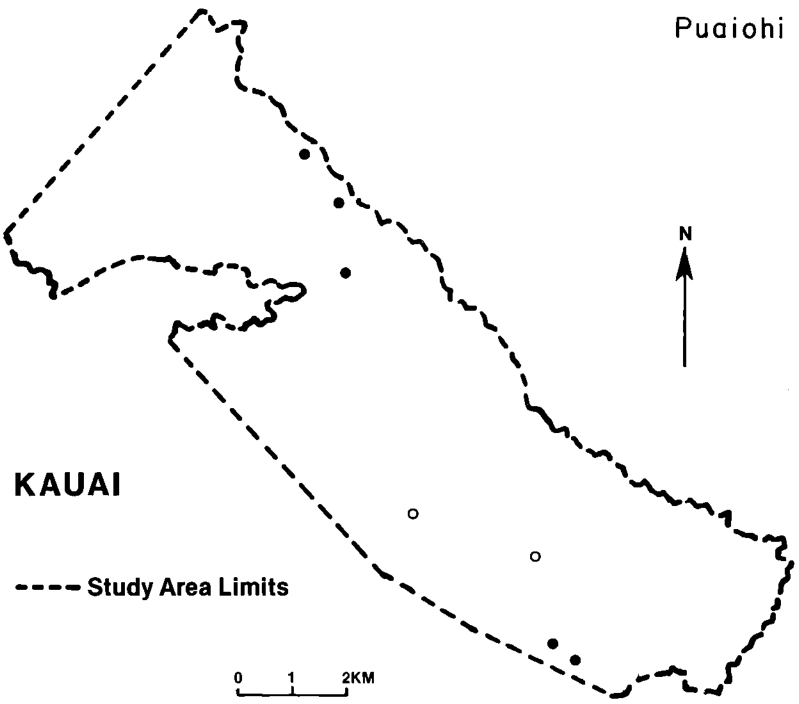


FIGURE 87. Distribution and abundance of the Puaiohi (Small Kauai Thrush) in the Kauai study area. (Solid circles mark count records; open circles mark incidental observations during the survey period.)

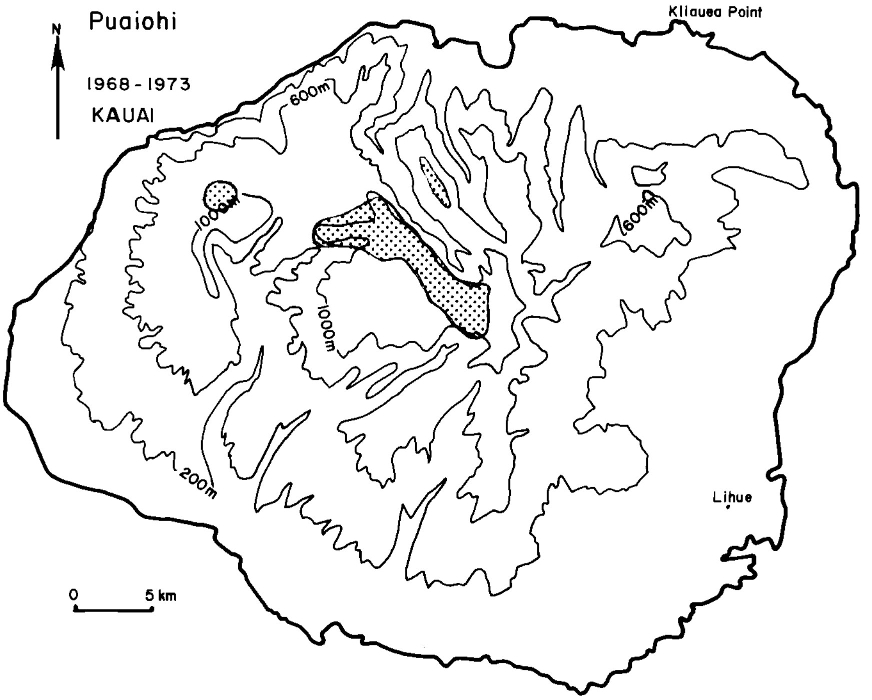


FIGURE 88. Range of the Puaiohi (Small Kauai Thrush) on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

KAUAI OO
Moho braccatus

Kauai Oo [Ooaa] (*Moho braccatus*)

Also known as the Ooaa, the Kauai Oo is the smallest of the four oo species found in the Hawaiian Islands, and is endemic to Kauai. In the 1890s, they were common forest birds from near sea level to the highest elevations (Munro 1944). Fossils have been found in former dry lowland forest areas (Olson and James 1982b). Kauai Oo apparently suffered a drastic decline in numbers shortly after 1900, as Munro (1944) was unable to locate them in the 1920s and 1930s. They were sighted in 1936 and 1940 (Donaghho 1941), rediscovered in 1960 (Richardson and Bowles 1961), and have been recorded regularly since (Sincock et al. 1984). Sincock located the first nest in 1971 in a tree cavity and found similar nests in 1972 and 1973. Kauai Oo feed primarily on invertebrates but also take olapa fruit and nectar from ohia and other plants (Perkins 1903, Richardson and Bowles 1964).

We estimated a total population of only 2 ± 2 (95% CI) Kauai Oo; we found one pair, recorded six times during our 1981 survey (Tables 11, 20, Fig. 89). They were carrying nesting material and giving the "beep beep" call of nesting birds. There may be little hope for the continued survival of this species. Because of the loud, easily identified call during the breeding season, it seems unlikely that we missed any breeding pairs in the study area, although possibly a few nonbreeding birds were overlooked, and additional birds may occur outside the area. The pair we found was in a stream valley in the south Alakai Swamp in dense, closed ohia-olapa forest with a closed, native understory typical of that region. Richardson and Bowles (1964) described the habitat of the species as thick forest, with the birds preferring high elevation canyons instead of forested ridges.

In 1960 Richardson and Bowles (1964) found a small population near the head of Koaie Stream. Sincock et al. (1984) estimated a total of 36 ± 29 (95% CI) birds for 1968–1973, with only 12 ± 17 occurring in our study area. Sincock found the species only within the southeast and southwest areas of the Alakai Swamp (Fig. 90), except possibly for one unidentified large dark bird fleetingly sighted on Namolokama Mountain in 1968. This species has steadily declined in numbers since 1968 and retreated from the Koaie Stream area; the last known birds are located in a very remote area of the Alakai (Sincock et al. 1984). Because this area has torrential rainfall and Richardson and Bowles (1964) found no Kauai Oo in this area, the habitat may be marginal. In 1983 J. L. Sincock and P. W. Sykes, Jr., found one remaining bird at a nest site in the central Alakai Swamp; no evidence of its mate was found over a three-day period. In 1984 U.S.F.W.S. biologists saw one bird and heard a possible second in the same area in May, and saw a single bird in September.

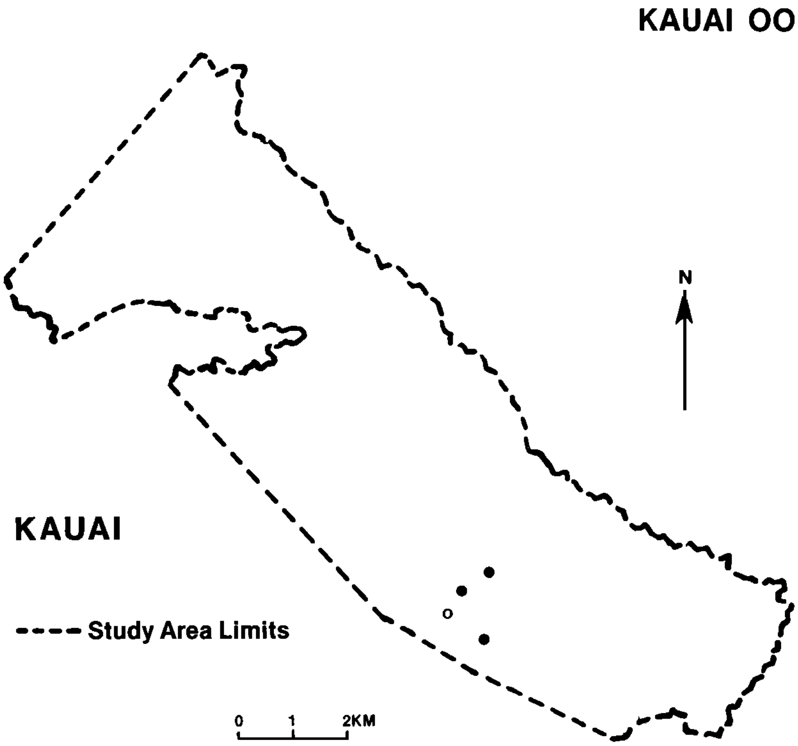


FIGURE 89. Distribution and abundance of the Kauai Oo (Ooaa) in the Kauai study area. (Circles mark count records.)

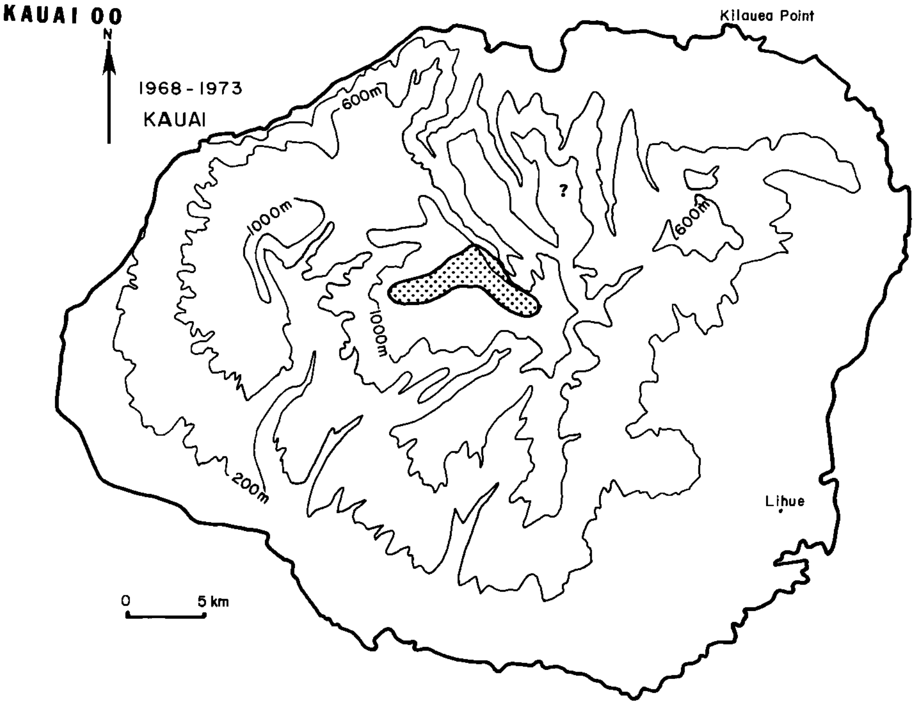


FIGURE 90. Range of the Kauai Oo (Ooaa) on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

TABLE 20

DENSITY [MEAN (SE)] OF THE KAUAI OO, OU, PALILA, MAUI PARROTBILL, ANIANIAU, AND NUKUPUU BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kauai Oo	Ou			Palila	Maui Parrotbill	Anianiau	Nukupuu
	Kauai	Hamakua	Puna	Kauai	Mauna Kea	E. Maui	Kauai	E. Maui
Elevation								
100–300 m	···	···	···	···	···	···	···	···
300–500 m	···	0	0	···	···	0	···	0
500–700 m	···	0	0	···	···	0	···	0
700–900 m	···	0	+ (+)	···	···	0	···	0
900–1100 m	···	+ (+)	0	···	···	0	···	0
1100–1300 m	+ (+)	1 (1)	0	···	···	3 (3)	235 (14)	0
1300–1500 m	+ (+)	8 (3)	···	0	···	9 (5)	276 (18)	7 (7)
1500–1700 m	···	+ (+)	···	+ (+)	···	7 (3)	···	+ (+)
1700–1900 m	···	+ (+)	···	···	···	15 (5)	···	+ (+)
1900–2100 m	···	0	···	···	10 (5)	21 (17)	···	+ (+)
2100–2300 m	···	0	···	···	37 (12)	+ (+)	···	+ (+)
2300–2500 m	···	···	···	···	18 (4)	0	···	0
2500–2700 m	···	···	···	···	18 (5)	0	···	0
2700–2900 m	···	···	···	···	9 (5)	0	···	0
2900–3100 m	···	···	···	···	+ (+)	···	···	···
Habitat								
Ohia	+ (+)	4 (2)	+ (+)	+ (+)	···	12 (3)	255 (11)	4 (4)
Koa-ohia	···	0	···	···	···	+ (+)	···	+ (+)
Koa-mamane	···	0	···	···	···	···	···	···
Mamane-naio	···	···	···	···	24 (4)	···	···	···
Mamane	···	···	···	···	9 (3)	0	···	0
Other natives	···	0	···	···	···	0	···	0
Intro. trees	···	0	···	···	···	0	···	0
Treeless	0	0	0	0	···	0	44 (44)	0

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

BISHOP'S OO
Moho bishopi

BISHOP'S OO (*Moho bishopi*)

This species has been collected only from Molokai where birds were last seen in 1904 (Munro 1944), and where more recent searches have failed to find them (Richardson 1949; Pekelo 1963a, 1963b, 1967; Pratt 1974; Scott et al. 1977; HFBS data).

Munro (1944:86) described Bishop's Oo as "active birds in the low trees on the gulch wall. They were inquisitive and though they approached me closely, they were timid and continually on the alert; never still an instant, chattering continuously. They stayed for some time before taking fright and leaving." Perkins (1903: 442) stated that they were "easily called by imitating [the] cry, though [they] will not infrequently come and inspect the intruder uncalled . . . [they] rarely expose [themselves] to more than a momentary view, diving beneath the foliage of the bushes at the slightest alarm." Perkins noted that the call was sometimes audible at a distance of 1000 m.

Based on these descriptions, we used an effective detection distance of 75 m in determining the probability of our finding Bishop's Oo or a similar species on Molokai and Maui (Table 12). We estimated the probability of detecting an extant population of 10, 50, and 100 birds on Maui at 0.49, 0.97, and 0.99, respectively. Probabilites are lower for Molokai.

Oo have been reported from Maui since 1828 (Banko 1980–1984), the most notable sightings being by Henshaw (1902) and Sabo (1982). In these two sightings the observers were convinced that the bird was an adult oo, possibly Bishop's Oo from the field marks; these records have been accepted by Pyle and Ralph (1982) and the A.O.U. (1983). Until a specimen or photograph is obtained, however, the specific identity of the "Maui Oo" remains debatable. The most recent sightings were from ohia rainforests on the northeast slopes of Haleakala, in the Hanawi watershed at 1600–2000 m elevation. There was one incidental sighting of an unidentified black bird with an oo silhouette from that area during the 1980 HFBS and another by D. Boynton (pers. comm.) in 1983. Fossils of *Moho* sp. occur on Maui (S. L. Olson, pers. comm.).

Bishop's Oo are primarily nectarivorous and were said to especially prefer lobeliad nectar (Perkins 1903). Lobeliads are particularly sensitive to habitat degradation by pigs, indicating that pigs posed an indirect threat to the species.

HAWAII OO (*Moho nobilis*)

Hawaii Oo were one of the most spectacular native birds. They were aggressive birds at the top of the dominance hierarchy of nectarivores and displaced Iiwi, Hawaii Mamo, and Apapane from nectar sources (Perkins 1903).

Once widely distributed throughout the forests on Hawaii, Hawaii Oo were commonly found from 400 to 1200 m elevation (Wilson and Evans 1890–1899), with seasonal movements to 1800 m (Rothschild 1893–1900). Perkins (1893) noted that they occurred mostly from 500 to 900 m elevation, inhabited ohia and koa-ohia forests, but deserted forests opened up by cattle. Hawaii Oo had disappeared by 1896 from the Puu Lehua area in Kona (Banko 1980–1984).

Records of this species occurring seasonally in the mamane forests of the Mauna Kea-Mauna

Loa saddle (Wilson and Evans 1890–1899) suggest that they may have exploited the rich nectar sources in that forest by daily movements up the mountain, similar to the mass movements still seen for Iiwi and Apapane (Baldwin 1953; MacMillen and Carpenter 1980; C. B. Kepler and J. M. Scott, pers. observ.).

Hawaii Oo were very common during the 1800s, and as late as 1898 more than 1000 were collected for the feather trade above Hilo (Henshaw 1902). By the turn of the century, they had decreased drastically (Perkins 1903). There have been numerous unverified records during the 1900s with several reports even into the 1970s on windward Mauna Kea, but none by trained biologists (Banko 1980–1984). We failed to sight Hawaii Oo or other unidentified black birds on Hawaii.

Hawaii Oo apparently seldom sang (Perkins 1903) but had a very loud and distinctive call uttered frequently before 09:00 that could be heard at great distances. Perkins (1903) heard the call from 800 m away and described it as "unlike that of any native bird and no one who has once heard it and identified it can ever again be in doubt as to the bird." This species was very active, "constantly on the move from tree to tree, hardly ever at a less height than [30 m] from the ground" (Wilson and Evans 1890–1899).

These descriptions of the behavior contrast with others that these were the most timid and wary of forest birds and flew off as soon as a human was sighted (Munro 1944:87). Based on the descriptions in the literature and our experience with Kauai Oo, we estimated the effective detection distance for Hawaii Oo to be 75 m. The chances of our having overlooked a population of 100 birds in the study areas on Hawaii are small (Table 12).

KIOEA (*Chaetoptila angustipluma*)

Kioea were the largest historically known Hawaiian meliphagids, and were lively nectarivores (Munro 1944). Only four specimens of this poorly known species were collected, all in the 19th century from the island of Hawaii (Banko 1979). The areas mentioned in discussions of the range were the eastern slopes of Mauna Loa northwest of Kilauea Crater and the saddle area between Mauna Loa and Mauna Kea, corresponding to our Hamakua and Kipukas study areas. Recent findings of Olson and James (1982b, pers. comm.) indicate that similar species occurred on Oahu and East Maui. From the fossil records and fragmentary natural history notes, it appears that Kioea occurred primarily in dry woodlands or scrublands below 1500 m elevation.

The only descriptions of Kioea vocalizations were by Peale (1848) who found them "disposed to be musical," and Pickering (in Cassin 1858) who saw them land in the tops of trees and utter a loud "chuck." We thus have little information on which to base our estimates of area surveyed for this species. Based on the limited data, we assumed they would be about as detectable as Hawaii Oo. The chances of this species still existing are remote (Table 12). We know of no records since Mills collected specimens about 1859.

OU
Psittirostra psittacea

OU (*Psittirostra psittacea*)

Ou feed principally on fruit and, to a lesser degree, on insects and nectar (Perkins 1903, Munro 1944). Perkins (1903) observed that the fruit and flowers of ieie were a chief food of Ou, and suggested that their peculiar bill may have

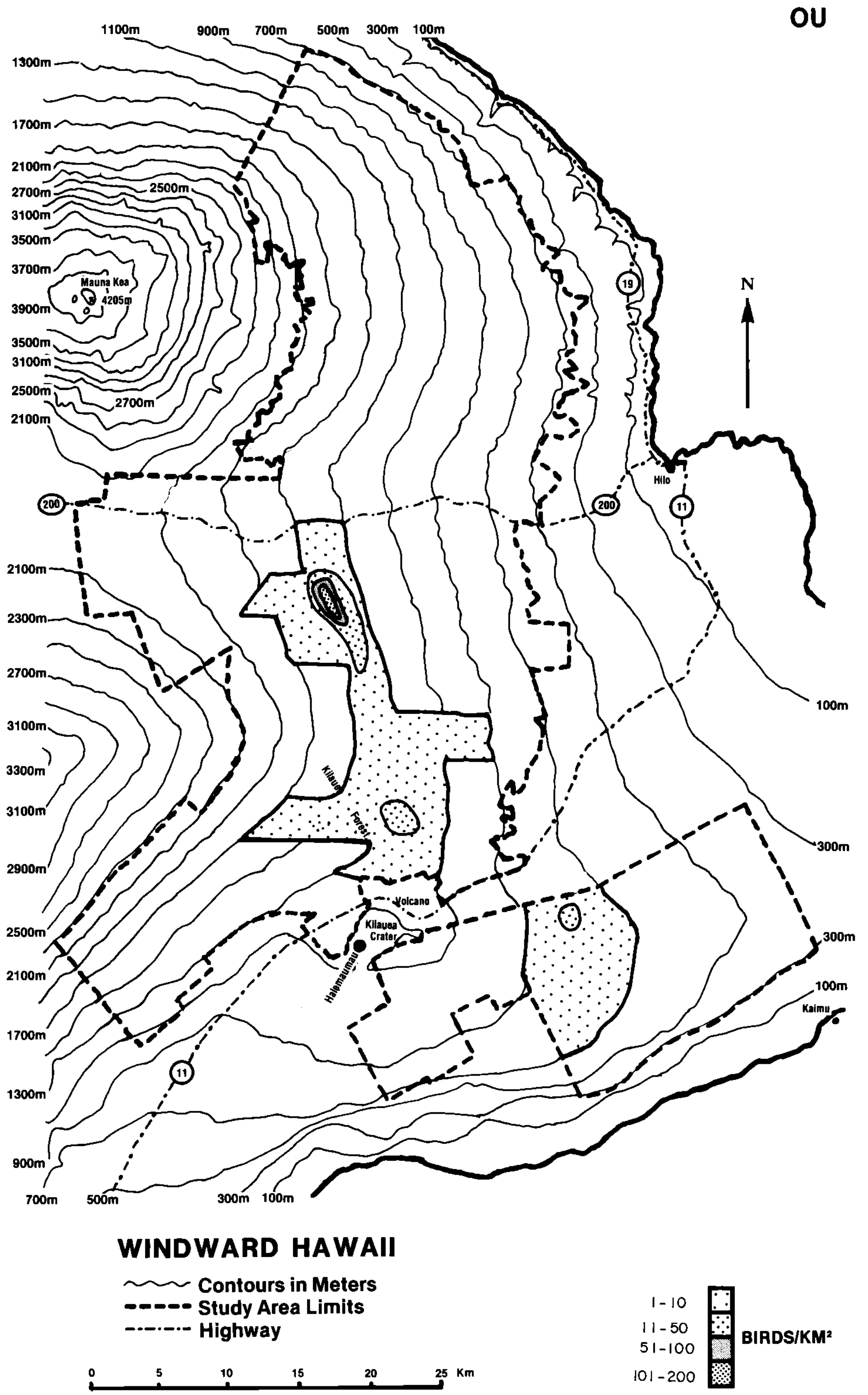


FIGURE 91. Distribution and abundance of the Ou in windward Hawaii study areas.

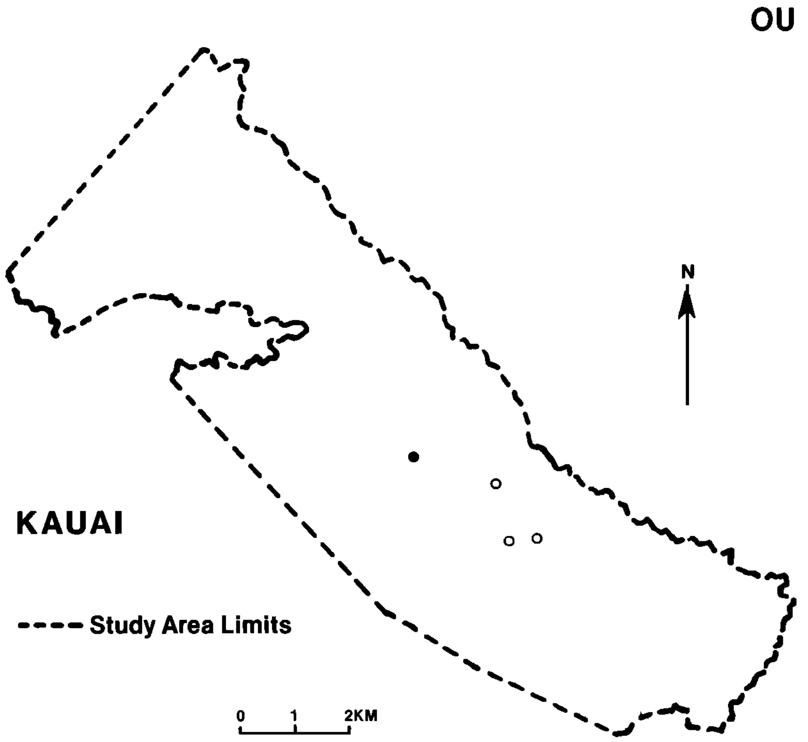


FIGURE 92. Distribution and abundance of the Ou in the Kauai study area. (Open circle marks count record; closed circles mark incidental observations during study period.)

been adapted originally for feeding on ieie. Ou also feed on other fruit, including lobliads, *Ilex, Pelea, Pipturus,* the introduced mountain apple (*Eugenia malaccensis*), guavas, and formerly banana and peach (Henshaw 1902, Perkins 1903). Ou used to wander down to lower elevations (Perkins 1893), particularly to feed on guava, and Munro (1944) suggested that this habit rendered them vulnerable to mosquito-borne diseases. The early disappearance of Ou from Kona may have been due to this habit and to the high elevational range of mosquitoes in that area.

Ou were extremely rare and localized on Hawaii and Kauai (Table 20, Figs. 91 and 92) during our survey. They were limited to two small populations, one of 400 ± 300 (95% CI) birds in the Hamakua and Puna study areas on Hawaii, the other of 3 ± 6 birds in the Alakai Swamp on Kauai.

Ou were formerly common on Hawaii, Maui, Molokai, Lanai, Oahu, and Kauai (Perkins 1903, Wilson and Evans 1890–1899). In the 1890s Ou were abundant at certain times of the year at Kilauea Crater (Perkins *in* Banko and Banko 1980). During 1936–1951, Ou appeared to be uncommon in Hawaii Volcanoes National Park from 800 to 1200 m elevation (Richards and Baldwin 1953), although areas in range from 1200 to 1500 m may have been rarely visited. Baldwin (1953) recorded Ou on 5 of 23 plot counts at Napau Crater (870 m elevation), with as many as six in one day; Richards found 15 in one day on the Olaa Tract. Location concentrations were found during our survey on the Olaa Tract and in the kipukas below Powerline Road in Upper Waiakea Forest Reserve, where as many as 12 birds were counted on one station. Ou have been infrequently seen in ohia rainforest near Kilauea Crater (van Riper 1978a) and east of Napau Crater (D. Reeser, pers. comm.), in mesic ohia woodland near Kilauea Iki, and mixed mesophytic forest at Kipuka Puaulu (S. Mountainspring, pers. observ.). One incidental record was made during our survey north of Saddle Road in the Mauna Kea forests of the Hamakua study area, but the historical record for Ou in this area is poor. A resurvey of the Ou's range in 1984 suggested that populations had declined in the Hamakua study area since 1977 (U.S.F.W.S. data).

Sincock et al. (1984) estimated a population of 62 ± 82 (95% CI) Ou on Kauai for the 1968–

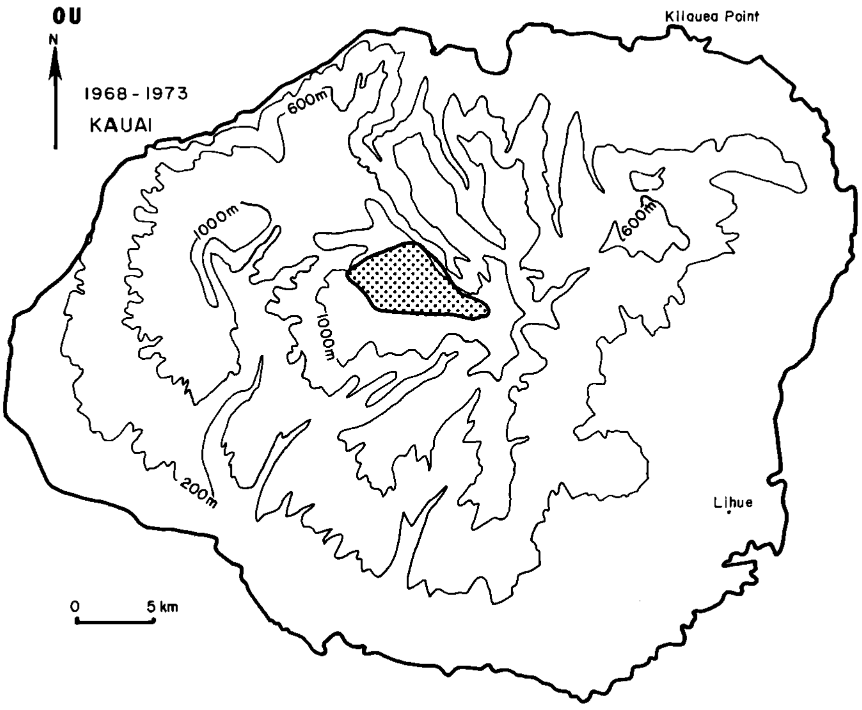


FIGURE 93. Range of the Ou on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

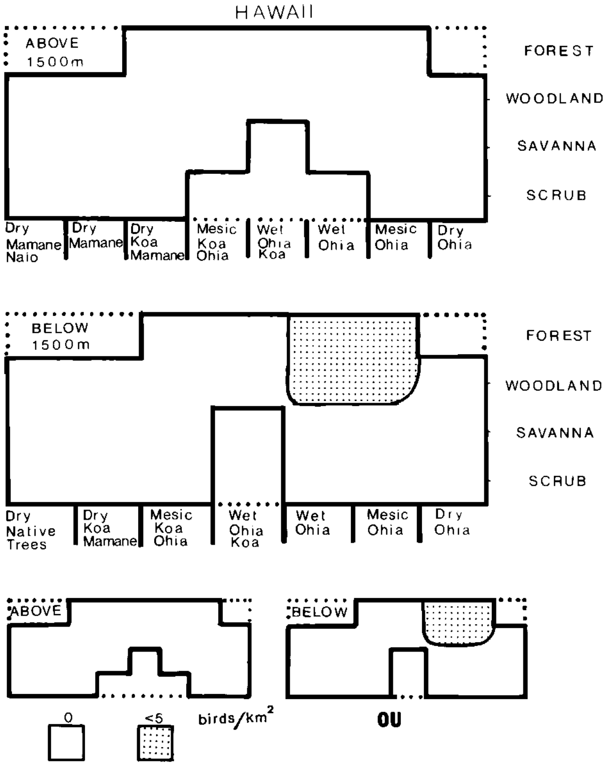


FIGURE 94. Habitat response graphs of the Ou. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

1973 period, including 34 ± 40 in our study area. His incidental observations suggest that the population increased in the mid 1970s, but by 1981 had grown quite scarce. Our data suggest a population of fewer than ten birds. A small number of birds may have occurred outside our study area. Five birds were seen flying in the same direction over a five-minute period in an incidental observation during the 1981 survey, but some of these possibly were duplicate sightings. In 1968–1973 Ou occurred chiefly in the central and southeast areas of the Alakai Swamp (Fig. 93). Like other endangered Kauai passerines, Ou are retreating to the core of the Alakai Swamp.

During our survey Ou were most abundant on Hawaii from 1300 to 1500 m elevation and were recorded as low as 900 m in Puna. The habitat response graphs show that Ou occupy mesic to wet ohia forests and woodlands, but are absent from koa forests and parkland (Fig. 94). The absence in koa is also reflected in the regression model for habitat response (Table 21). Ou appear to occupy a restricted range of habitats compared to the range recorded in historical accounts; Perkins (1903), for example, noted seasonal occurrences in koa forests and dry montane woodlands on Hawaii. Baldwin (1953) found Ou in tree ferns and the upper parts of trees; our survey found them in similar areas, often in the vicinity of *Tetraplasandra* trees, whose fruit they probably feed upon (see also Mull and Mull 1971).

Because of the Ou's vocal nature, the probability is low that we failed to detect a population as large as 100 birds in those areas where they are widely regarded as extinct (Table 12).

The absence of Ou in the Kau study area may reflect the lack of extensive tracts of wet forest at low elevations in this area. Low elevation forests may have provided food or shelter during seasonal periods of resource shortage or inclement weather at higher elevations. In Kona we speculate that Ou became extinct because of (1) extensive conversion of low elevation forest to agriculture by 1900, (2) habitat fragmentation at mid and upper elevations, and (3) early spread of disease in leeward Hawaii. That Ou were much more common at lower elevations on Hawaii as recently as the 1940s (Richards and Baldwin 1953) suggests that additional limiting factors may have come into play.

PALILA
Loxioides bailleui

PALILA (*Loxioides bailleui*)

Palila occurred historically in the mamane-naio forests on west and southwest Mauna Loa and on Mauna Kea. They presently occur only on the upper slopes of Mauna Kea. The population has fluctuated between 1600 and 6400 birds since 1975, and has been studied to a greater extent than most other endangered species (Berger 1970, van Riper et al. 1978, van Riper 1980, Scott et al. 1984). Fossil records reveal that Palila

PALILA

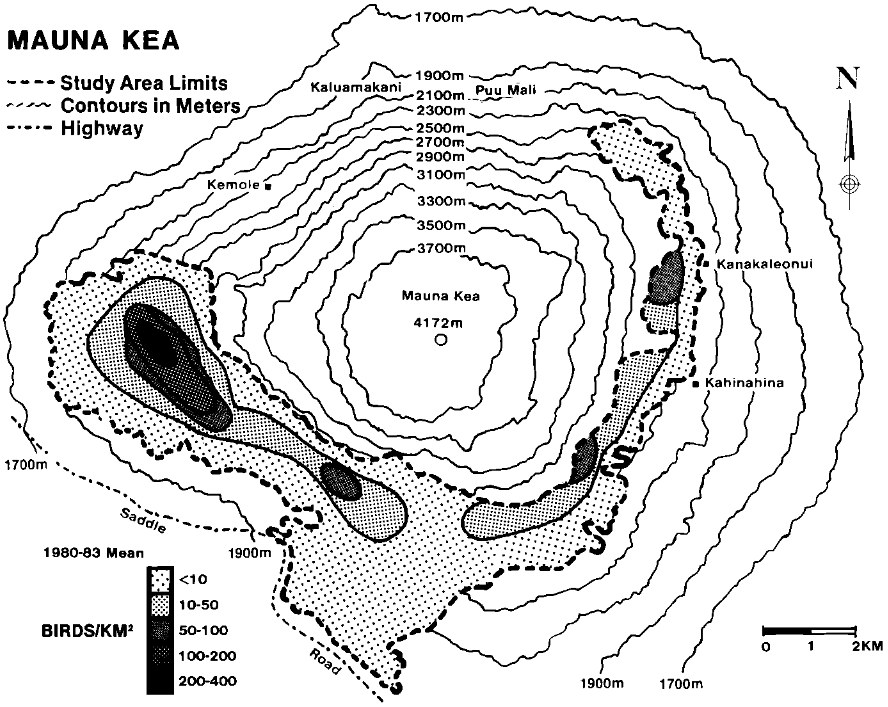


FIGURE 95. Distribution and abundance of the Palila in the Mauna Kea study area.

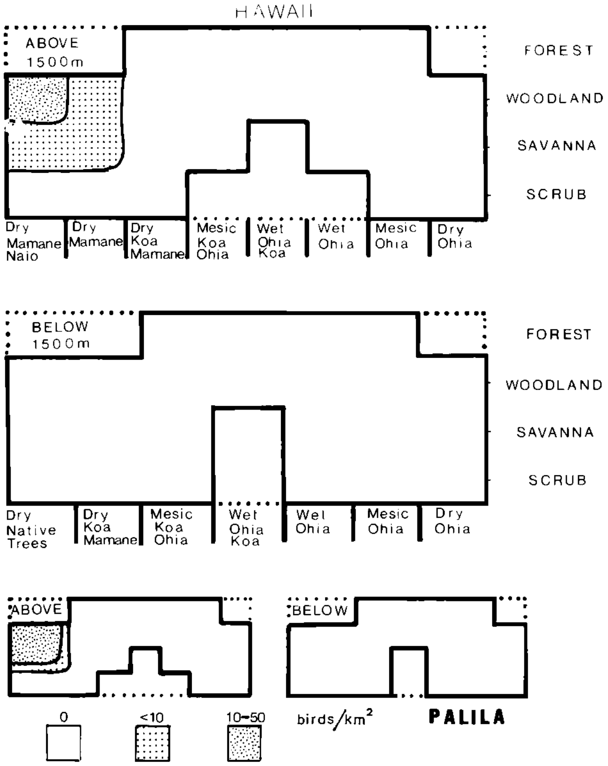


TABLE 21

Regression Models for Habitat Response of the Ou, Palila, Maui Parrotbill, Anianiau, and Akiapolaau[a]

	Ou	Palila	Maui Parrotbill	Anianiau	Akiapolaau			
	Hamakua	Mauna Kea	Maui	Kauai	Kau	Hamakua	Kona	Mauna Kea
R^2	0.01	0.12*	0.06*	0.20*	0.06*	0.09*	0.01*	0.01
Moisture	...	X	4.7*	X	...	...	...	X
Elevation	...	...	4.9*	...	...	10.3*	...	...
(Elevation)^2	...	...	...	...	...	...	...	...
Tree biomass	...	4.3*	2.8	...	...	...	...	...
(Tree biomass)^2	...	...	...	...	...	...	...	...
Crown cover	...	...	...	...	...	...	...	...
Canopy height	...	...	...	...	...	...	...	...
Koa	−2.4	X	...	X	6.3*	8.6*	3.9*	X
Ohia	...	X	...	X	...	...	...	X
Naio	X	...	X	X	X	X	...	...
Mamane	...	−3.2	...	X	X	−3.9*	...	2.1
Intro. trees	...	X	...	X	X	...	...	X
Shrub cover	...	...	...	...	...	...	...	...
Ground cover	...	...	...	...	...	4.0*	...	...
Native shrubs	...	X	...	...	...	6.2*	...	X
Intro. shrubs	...	X	...	−5.7*	X	3.0	...	X
Ground ferns	X	X	...	2.3	X	X	...	X
Matted ferns	...	X	...	...	...	...	...	X
Tree ferns	X	X	...	...	...	X	...	X
Ieie	X	X	...	...	X	X	...	X
Passiflora	...	X	...	X	X	−4.5*	...	X
Native herbs	X	X	...	...	X	X	...	X
Intro. herbs	X	...	...	...	X	X	...	...
Native grasses	...	...	2.6	...	3.6*	−4.3*	...	...
Intro. grasses	...	...	...	...	...	−4.0*	...	...
Ohia flowers	...	X	...	...	...	−3.1	...	X
Olapa fruit	...	X	−2.4	...	...	...	...	X
Mamane flowers	X	−2.6	...	X	X	X	X	...
Mamane fruit	X	3.5*	X	X	X	X	X	...
Naio fruit	X	...	X	X	X	X	X	...

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

originally occurred down to sea level on Oahu, thus providing "a striking example of how the distribution of native birds has been artificially modified in the Hawaiian archipelago" (Olson and James 1982b:39). Palila feed chiefly on the green pods of the mamane tree but also take naio berries and insects, especially caterpillars.

We found this species only on Mauna Kea in dry mamane and mamane-naio savanna and woodlands (Tables 10, 20, Fig. 95). Palila reach highest densities in mixed woodland near Puu Laau. Secondary population centers are located northeast of Mauna Kea State Park (Pohakuloa Gulch area) in well-developed mamane-naio woodland, on the southeast slope at timberline, and near Kanakaleonui on the east slope in a relict stand of mamane. The overall Palila distribution suggests a very tenuous connection between the eastern and western halves of the population in the vicinity of the Hale Pohaku development.

Palila range from 2000 to 3000 m elevation, reaching highest densities at 2100–2300 m (Table 20). These bounds are much higher than its 1200 to 1800 m range in Kona in 1892 (Perkins 1903). Scott et al. (1984) showed that the dis-

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FIGURE 96. Habitat response graphs of the Palila. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

tance from the upper to the lower elevational limit of mamane-naio woodland is the most important variable in determining habitat response. Palila are more common in areas with greater crown cover, taller trees, and higher proportion of native plants in the understory. Annual variation of Palila density within a habitat type is related to the levels of their staple food, mamane pods. Scott et al. (1984) suggested that the population is limited by the width of the mamane-naio zone and the abundance of mamane pods.

The habitat response graph (Fig. 96) underscores the dependence on mamane and mamane-naio woodlands, and shows lower densities in deforested areas. In some years Palila were more common in mamane than in mamane-naio. The regression model (Table 21) emphasizes tree biomass and mamane fruit; the negative mamane term reflects the low levels of mamane fruit in pure mamane areas in 1983 (Scott et al. 1984).

The probability of our having missed a population of 100 birds of this species in Kona is low (Table 12). Extensive searches of the mamane forests on Hualalai and Mauna Loa subsequent to our survey also failed to locate this species (J. L. Giffin, pers. comm.). The extinction in Kona was probably related to the contemporaneous disappearance of the other finch-billed honeycreepers, but is puzzling because of the well-developed mamane forests extant on Mauna Loa.

LESSER KOA-FINCH (*Rhodacanthis flaviceps*)

One of five large finch-billed species extant on Hawaii when Cook arrived in 1778, Lesser Koa-Finches were known only from the koa forests of the upper leeward slopes of Mauna Loa (Munro 1944). They fed on koa pods in flocks with Greater Koa-Finches, and nothing else is known of their behavior. The range was restricted to the environs of Puu Lehua, about 15 km SSE of Hualalai (Rothschild 1893–1900), and the species was probably on the verge of extinction when discovered. Originally, birds were apparently widespread in dry lowland habitat, as fossils have been found at Barber's Point on Oahu (Olson and James 1982b).

Our assumptions of effective detection distance (30 m) were based on descriptions of the very similar Greater Koa-Finch and our knowledge of Palila behavior. In assessing the possible distribution pattern, we assumed that they most likely inhabited upper elevation koa forests. There have been no records of this species since Munro and Palmer collected their specimens in 1891, and it is generally regarded as extinct (Table 12, Berger 1981).

GREATER KOA-FINCH (*Rhodacanthis palmeri*)

The largest of the historically known Hawaiian honeycreepers was the Greater Koa-Finch. These birds sometimes flocked with Lesser Koa-Finches, and like them fed extensively on the seeds of the koa tree, also taking other seeds and lepidoptera larvae (Perkins 1903). Greater Koa-Finches were most numerous in koa forests at 1200 m elevation and occurred from 900 m probably to 1800 m (based on vegetation and H. Palmer's diary in Rothschild 1893–1900); they ranged in Kona from Puu Lehua (15 km SSE of Hualalai) south at least to the Honaunau Tract, and also occurred in the koa forests north of Kilauea Crater (Rothschild 1893–1900, Perkins 1903).

Munro (1944) described the song or call as "several whistled flute-like notes, the last ones prolonged" and found birds by their whistles "loud from the tops of the koas." We assumed that the calls of this species would be detectable at least to the distances (30 m) we have documented for Palila (Scott et al. 1984). In assessing the distribution, we assumed that birds would be found throughout the koa forests of Kona and Kau above 1500 m elevation.

Munro (1944) reported two unverified records for Greater Koa-Finches, one as late as 1937 at Kipuka Puaulu in Hawaii Volcanoes National Park by Donaghho (1951). We know of no substantiated recent records and there appears to be little chance that this species survives (Table 12).

KONA GROSBEAK (*Chloridops kona*)

Kona Grosbeaks, also known as Grosbeak Finches, fed almost exclusively on the hard dried fruit of naio, which their powerful jaws were well adapted to crack (Perkins 1903). Until recently, Kona Grosbeaks stood as an extreme example of adaptive radiation in the Hawaiian honeycreepers. At least eight additional species of finch-billed honeycreepers are now known to have formerly inhabited Hawaiian forests, however, including the giant Oahu grosbeak finch, whose "massive mandible rivals in size that [of] the largest finchlike bills in the world" (Olson and James 1982b:40).

Kona Grosbeaks frequented naio stands on rough aa flows from 1050 to 1650 m elevation in a small area in Kona from Puu Lehua south to the Honaunau Tract (Rothschild 1893–1900). Kona Grosbeaks were apparently rare when Wilson (1888) first collected them. Perkins (1903) also collected in the same area and described them as rare and patchy in distribution over a 10-km^2 area, although Palmer found them over a distance of 20–30 km (Rothschild 1893–1900).

Kona Grosbeaks were apparently silent for longer intervals than the other finches, and their call was weak (Perkins 1903). The birds were also sluggish, solitary, and inconspicuous (Perkins 1903). Thus we assumed an effective detection distance of 30 m. In determining the probability of overlooking this species, we considered all dry and mesic forests above 1500 m elevation with naio to have been within the range (Table 12).

MAUI PARROTBILL
Pseudonestor xanthophrys

MAUI PARROTBILL
(*Pseudonestor xanthophrys*)

Maui Parrotbills, or Pseudonestor, are relatively rare birds of the upper montane rainforest of East Maui. They were considered rare in the 1890s, and Munro (1944) failed to find them in 1928. Early workers thought the birds were restricted "to a small portion of the forest on the northwest slope of Haleakala, at an elevation of [1200–1500 m]" (Perkins 1903).

Perkins (1903) and Henshaw (1902) associated Maui Parrotbills with koa forests, where they feed chiefly on the boring larvae and pupae of native longhorn beetles (Cerambycidae). Most koa forests above 1300 m elevation have been destroyed since the 1890s, and the distribution has mostly contracted to areas of ohia rainforest (Richards and Baldwin 1953, Banko 1968, Scott and Sincock 1977, Conant 1981). In rainforests the birds excavate for borers as observed on koa, the prey also including the larvae and pupae of microlepidopteran moths (S. Mountainspring, pers. observ.).

Maui Parrotbills have an apparently continuous distribution from the upper Waikamoi watershed southeast to upper Kipahulu Valley. Highest densities are reached in the Hanawi watershed area. Although we did not find birds between Kipahulu Valley and Kaupo Gap (Fig. 97), a likely place for them would be the koa-ohia forest at 1500–1900 m elevation between Manawainui Valley and Kuiki Peak. Maui Parrotbills also occur in the koa-ohia forests of Waikamoi Preserve (U.S.F.W.S., unpub. data).

The total population is about 500 ± 230 (95% CI) birds (Table 11). Maui Parrotbills occur from 1200 to 2150 m elevation with highest densities at 1700–2100 m (Table 20). The habitat response graphs (Fig. 98) show that highest densities are in wet ohia forests above 1500 m elevation. Maui Parrotbills are rare in all other forests above or below 1500 m. The regression model (Table 21) explains 6% of the variance, and emphasizes wet high elevation forests. Maui Parrotbills usually forage in subcanopy trees and understory shrubs (Carothers et al. 1983). These plants are more sensitive to pig disturbance than canopy trees, indicating that pigs may have a negative effect on this species.

Subfossils associated with dry lowland habitat near Ilio Point, Molokai (Olson and James 1982b), and near Kaupo, East Maui (S. L. Olson, pers. comm.), suggest that Maui Parrotbills originally occupied a wider range of habitats. Populations in dry forests may have perished during early Hawaiian clearing and burning. Maui Par-

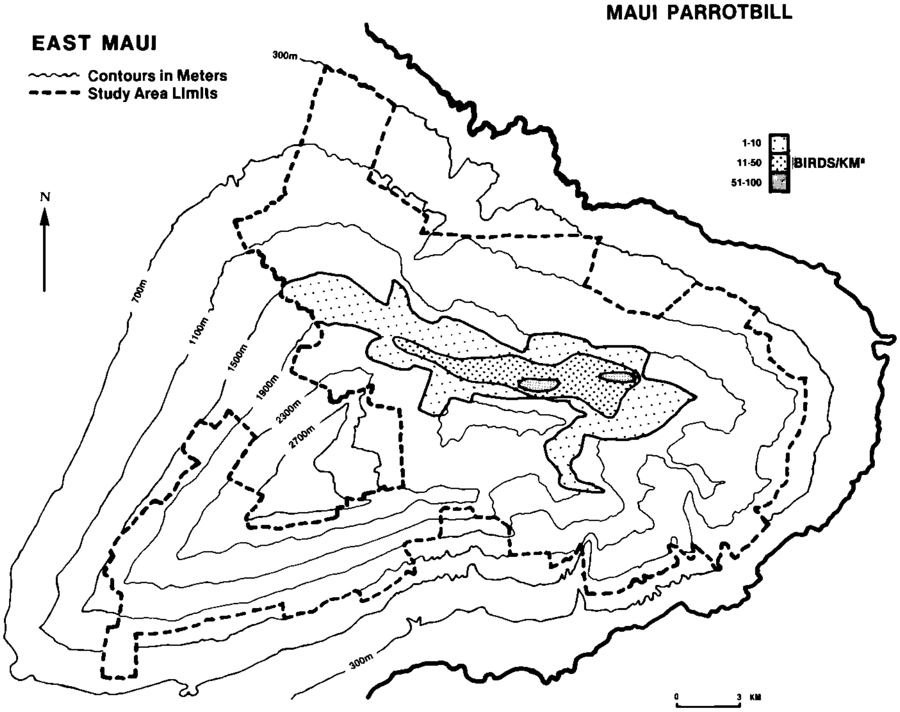
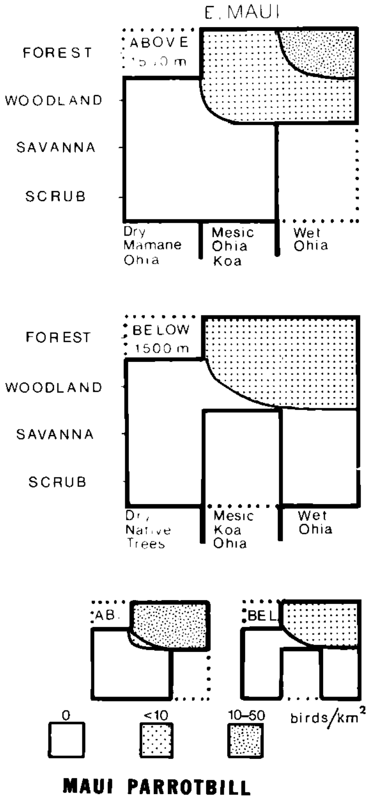


FIGURE 97. Distribution and abundance of the Maui Parrotbill in the East Maui study area.



rotbills were not known historically from Molokai, a relatively well-collected island; moreover, Hawaiians apparently had no name for this distinctive species and did not recognize it (Perkins 1903, Munro 1944). By the time early ornithologists explored Maui and Molokai, the range had probably long since contracted to remote forests because of habitat modification and early release of mosquitoes on Maui (Warner 1968, Pratt 1979).

COMMON AMAKIHI
Hemignathus virens

COMMON AMAKIHI (*Hemignathus virens*)

This species, widely known as the Amakihi, was common and generally distributed on all the main islands except Niihau and Kahoolawe during the 19th century (Perkins 1903). Munro (1944) found the species common everywhere but on Lanai, where the population declined in the 1920s and 1930s. Numbers on Kauai appeared to diminish after 1891 (Palmer in Rothschild 1893–1900; Perkins 1893, 1903). In Hawaii Volcanoes National Park, birds were fairly common from 700 to 2300 m elevation in the 1940s and 1970s, and the frequency of occurrence increased over this period in dry ohia woodland at 700 m (Baldwin 1953, Conant 1975, Banko and Banko 1980). Birds were considered rare on Molokai in 1975 (Scott et al. 1977). Fossils are known from Kauai and Oahu, but are surprisingly absent from Molokai (Olson and James 1982b). Seasonal movements between areas have been noted (Baldwin 1953), and may explain some of the patterns we observed. Common Amakihi feed on nectar, insects, other invertebrates, and fruit (Perkins 1903, Baldwin 1953, Pimm and Pimm 1982). Nectar levels affect local population densities, breeding success, and individual movements on Mauna Kea (van Riper 1984). The breeding biology has been studied extensively in dry (van Riper 1978c) and wet forests (Eddinger 1970).

Common Amakihi are among the most common of native birds. They are abundant on Hawaii, Maui, and Kauai, locally common on Molokai (Tables 10, 11, Figs. 99–108), uncommon on Oahu (M. Morin, pers. comm., *contra* Berger 1981), but have not been found on Lanai since 1976 (Hirai 1978) and may be extinct there.

On Hawaii they occur in all study areas and locally attain densities of 1600 birds/km^2 in the mamane and mamane-naio forests near Puu Laau on Mauna Kea and in the subalpine ohia forests of Kau (Figs. 99 and 102). An estimated 870,000 ± 11,000 (95% CI) birds inhabit the study areas on Hawaii, with the largest proportions of that population in the Kona (40%), Hamakua (20%), and Kau (18%) study areas. The species has a strong association with dry and mesic forests. Unlike other native passerines, Common Amakihi have fairly high densities at low elevations in Puna and along the margins of the Kau Desert. Low-elevation wet forests typically support low Com-

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FIGURE 98. Habitat response graphs of the Maui Parrotbill. (Graphs give mean density above and below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

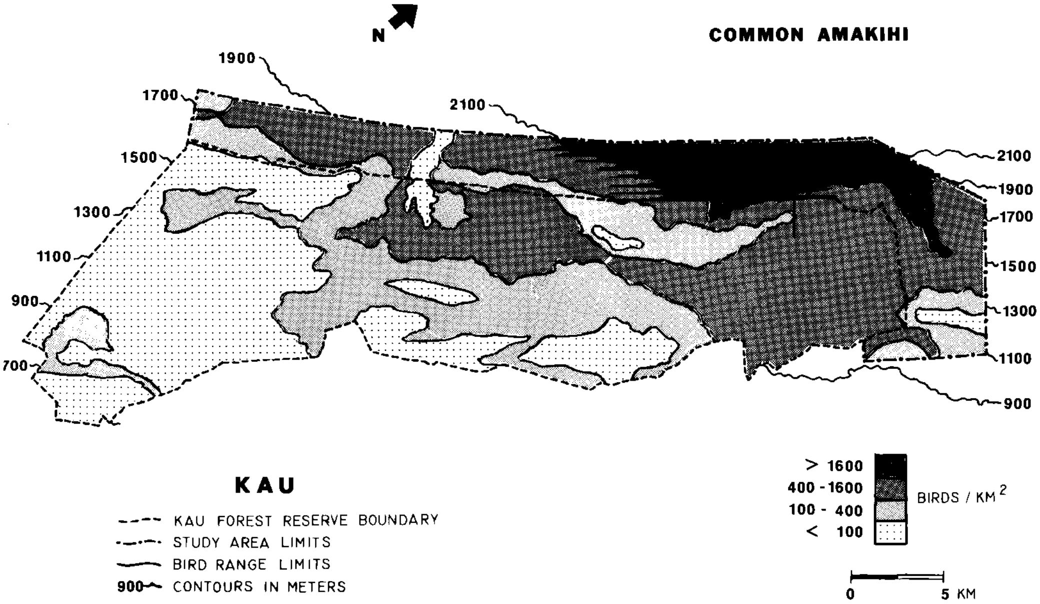

FIGURE 99. Distribution and abundance of the Common Amakihi in the Kau study area.

mon Amakihi densities, notably in Hamakua and Kohala. Deforestation due to lava flows, residential development, and grazing is the probable cause for the low densities between the Kau and Kona populations, and for the loss of birds at lower elevations in Kona east of Kailua and northeast of Kealakekua Bay.

Although densities were lower on Maui than on Hawaii, large populations of 44,000 ± 3500 (95% CI) and 3000 ± 800 birds occur on East and West Maui, respectively (Figs. 104 and 105). The low densities in dry forests on Maui contrast with high ones on Hawaii (Fig. 109), and reflect extensive habitat degradation by feral ungulates. Common Amakihi and Apapane are the only remaining native passerines on the largely deforested dry south slope of East Maui. Common Amakihi are seasonally attracted to mamane flowers in the sparse vegetation of Haleakala Crater. On windward East Maui, they are uncommon at lower elevations. Near absence at low elevations west of Waikamoi Stream marks the mesic/wet habitat transition, but seems anomalous and may reflect seasonal movement out of the area (see Baldwin 1953). On West Maui, abundance varies predictably with habitat, from high densities in dry to mesic montane forests, to virtual absence in very wet forests, bogs, and grasslands.

Common Amakihi have a limited range on Molokai and a total population of only 1800 ± 700 (95% CI) birds. Densities of 100 birds/km² occur locally in the north central part of the study area (Fig. 106), in Waikolu, Pelekunu, and Wailau Valleys, and on the Olokui and Ohialele Plateaux.

The densities on Kauai appear to be one-half to one-third those found in similar habitats on Hawaii and East Maui (Fig. 107). High densities of Anianiau and Kauai Creeper in the Alakai possibly depress Common Amakihi densities via competition for food resources. The 2300 ± 400 (95% CI) birds in the Alakai Swamp study area suggest a substantial increase over the 600 ± 250 birds in the same area for the 1968–1973 period (Sincock et al. 1984), but may reflect seasonal movement into the area during our survey. On Kauai, Common Amakihi are more abundant in the drier koa-ohia forests west of the Alakai, and Sincock et al. (1984) estimated a population of 11,000 ± 2000 birds for all of Kauai. During 1968–1973 birds occurred on the slopes above Waimea Canyon, the Na Pali plateaux, the Alakai Swamp, and the Makaleha Mountains (Fig. 108).

Common Amakihi occur in a wide variety of habitat types (Table 22). They reach highest densities on the island of Hawaii above 1500 m in drier woodlands and forests, as seen in the habitat response graphs (Fig. 109) and regression models (Table 23). In similar habitat types, densities are lower on Maui than on Hawaii. Densities are lower in dry ohia savannas than in dry ohia scrub, although this may reflect a seasonal

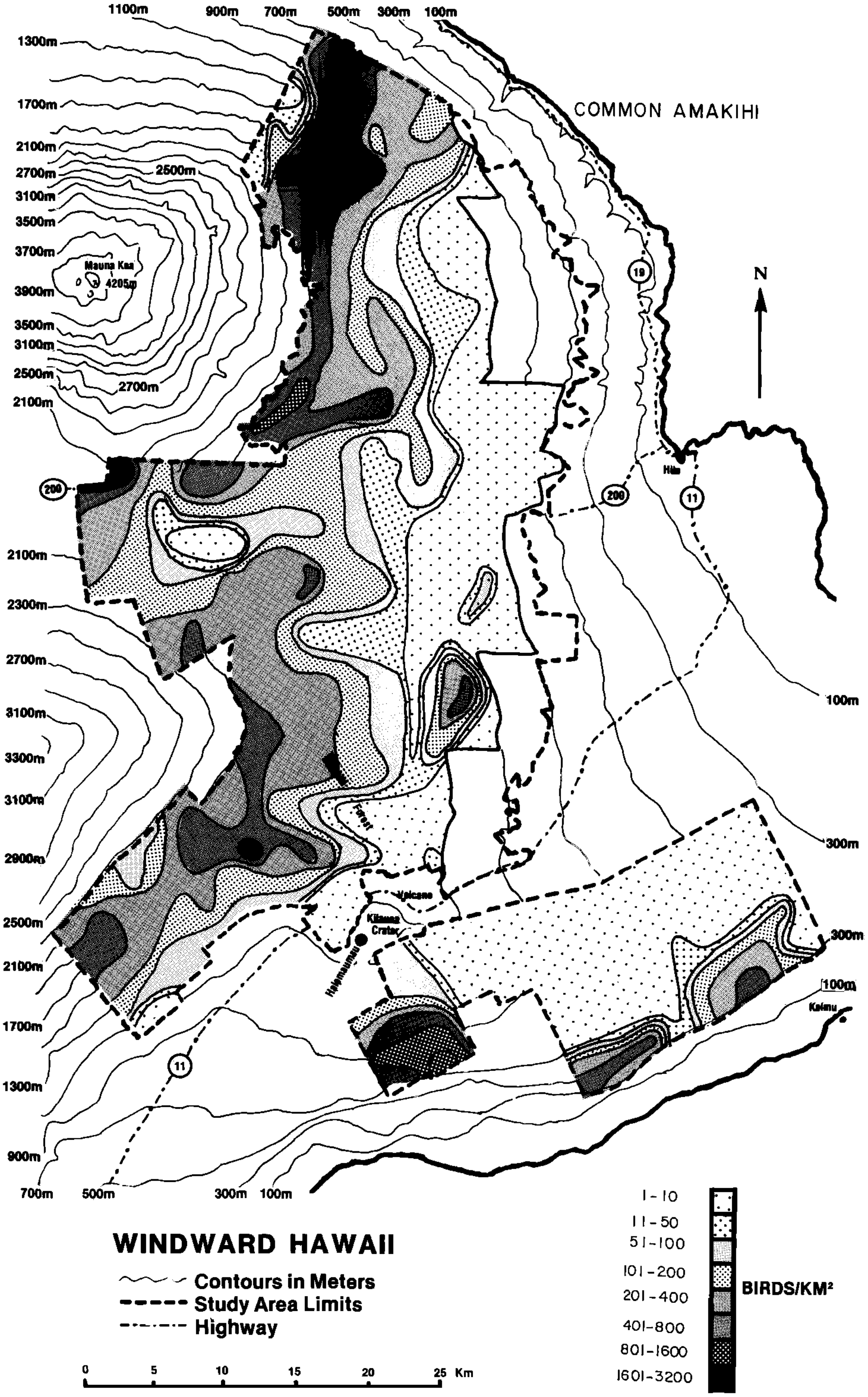

FIGURE 100. Distribution and abundance of the Common Amakihi in the windward Hawaii study areas.

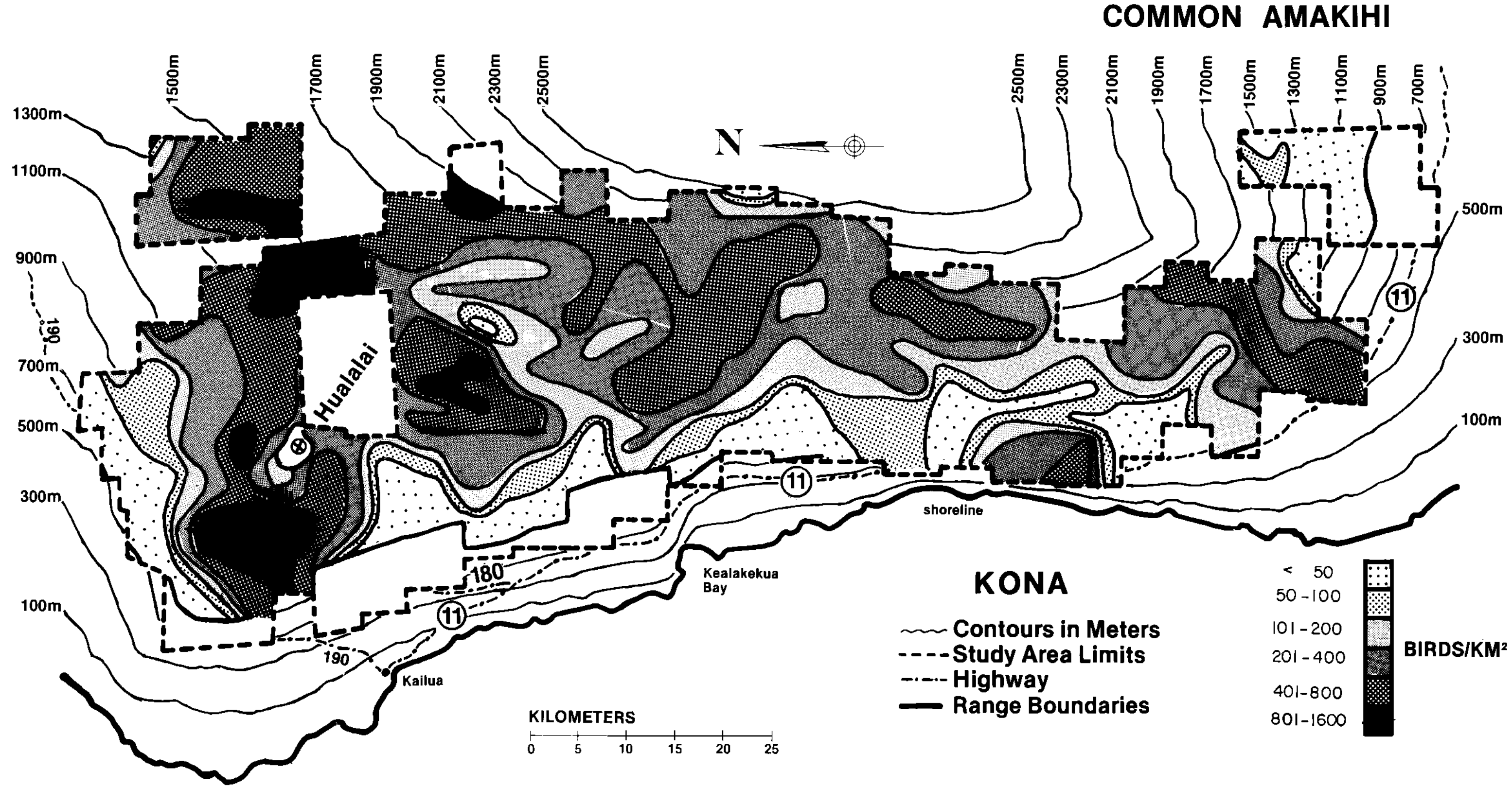

FIGURE 101. Distribution and abundance of the Common Amakihi in the Kona study area.

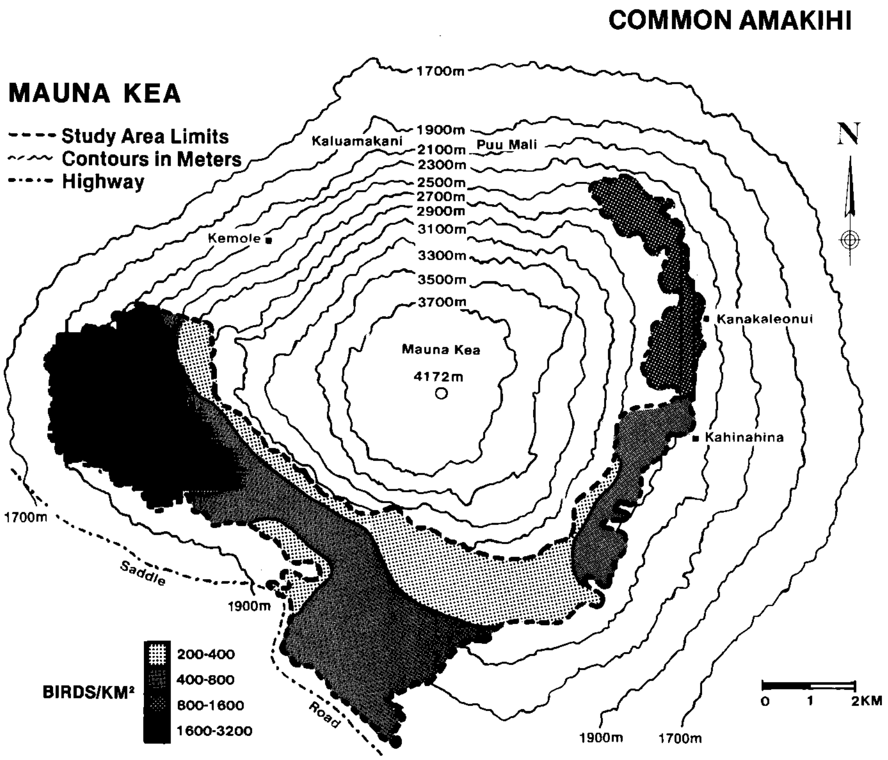

FIGURE 102. Distribution and abundance of the Common Amakihi in the Mauna Kea study area.

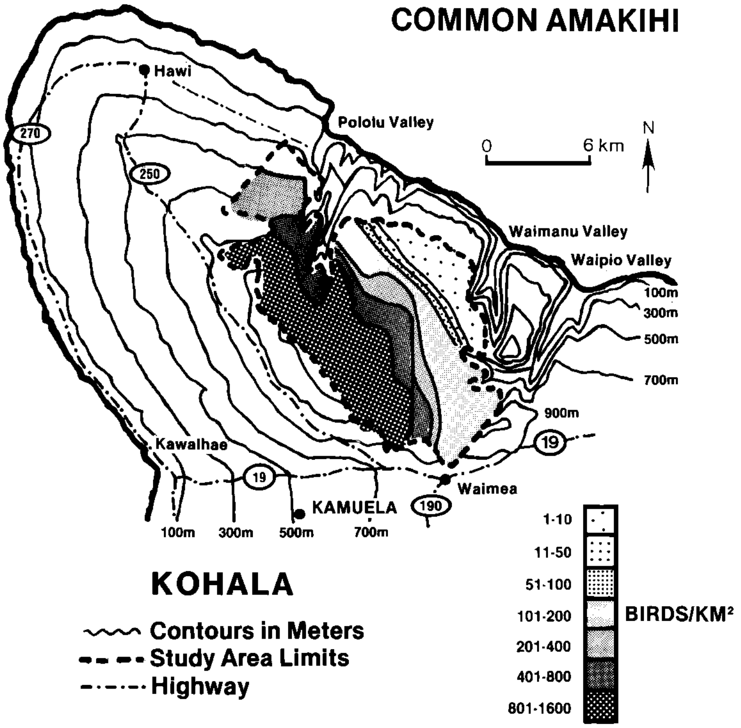

FIGURE 103. Distribution and abundance of the Common Amakihi in the Kohala study area.

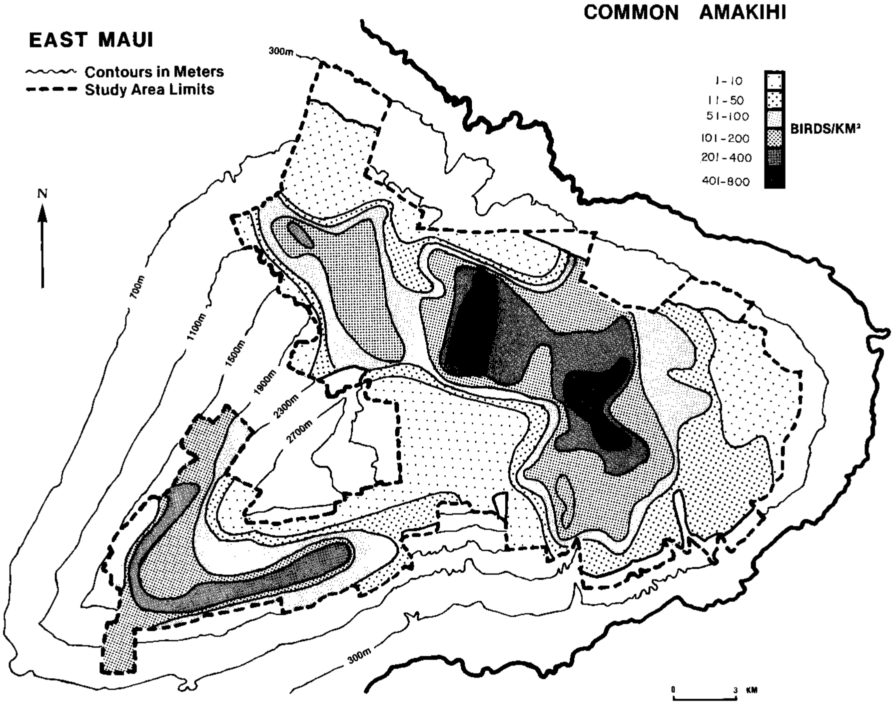

FIGURE 104. Distribution and abundance of the Common Amakihi in the East Maui study area.

pattern or sampling error. Negative moisture terms occur in six of nine regression models. No terms enter the Kauai model, indicating uniform response within the rather homogeneous study area. Common Amakihi have a negative response in three models to matted ferns; the positive term in the Maui model reflects fairly high densities in some ohia dieback areas. Birds are attracted to banana poka infestations for the copious nectar, reflected in the positive terms for passiflora. Native herbs, typical of forest interiors and alpine grasslands, have negative terms in three models. Variables indicating open disturbed forest (introduced herbs, introduced grasses) have positive responses in seven models. Ohia flowers have positive terms in five models, probably reflecting the nectarivorous diet (Baldwin 1953). On Maui, the negative term for mamane flowers reflects low densities in the cinder desert in Haleakala Crater.

Common Amakihi are usually quite uncommon below 500 m elevation, perhaps reflecting a negative response to introduced vegetation, high levels of mosquito infestation, or, less likely, intense competition for food with introduced birds. Exceptions occur where higher densities correspond with dry to mesic native forest at low elevations on Hawaii and Molokai. These patterns are the reverse of the elevational responses shown by other native forest birds. On Hawaii, such areas occur in the Puna study area and below the Kona study area on the Kapua Tract (Table 2). On Molokai, the low-elevation populations occur near the bases of valley headwalls, in a narrow band of mesic to dry forests on precipitous slopes. Common Amakihi thrive in these low-elevation native forests despite the dense populations of mosquitoes and introduced birds. In Pelekunu Valley, Molokai, Common Amakihi move in numbers to low elevations (100 m) during the winter months, but are absent during summer (C. Soares, pers. comm.).

MacMillan (1974) studied the bioenergetics of Common Amakihi from wet montane forest on Kauai and dry subalpine woodland on Hawaii. As with Anianiau, he found that they had thermoregulatory adaptations to the low nocturnal temperatures typical of their environment. Such adaptations to cold montane climates may impede population movement and dispersal between lowland and montane habitats.

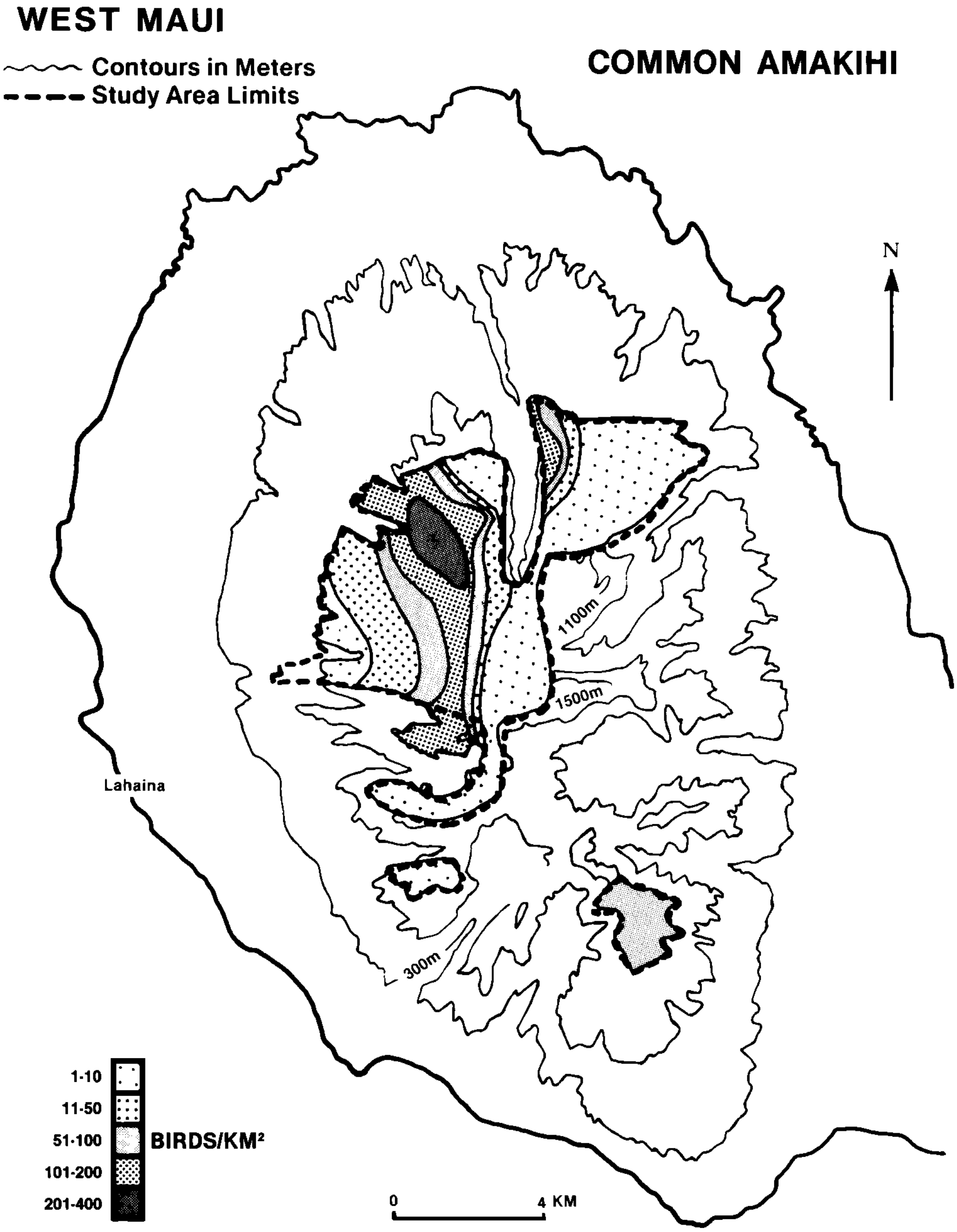

FIGURE 105. Distribution and abundance of the Common Amakihi in the West Maui study area.

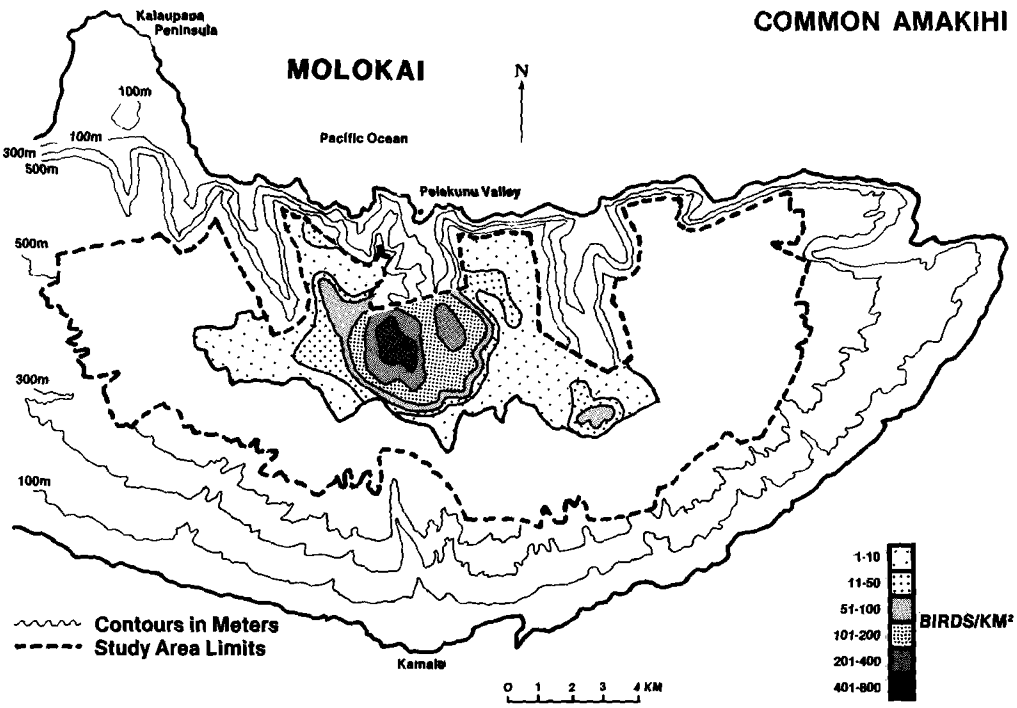

FIGURE 106. Distribution and abundance of the Common Amakihi in the Molokai study area.

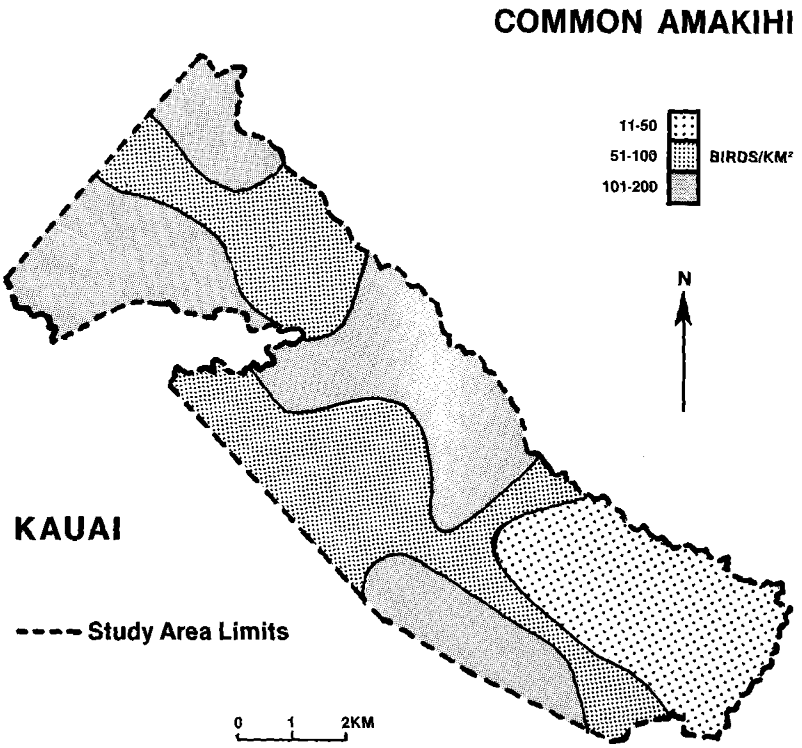

FIGURE 107. Distribution and abundance of the Common Amakihi in the Kauai study area.

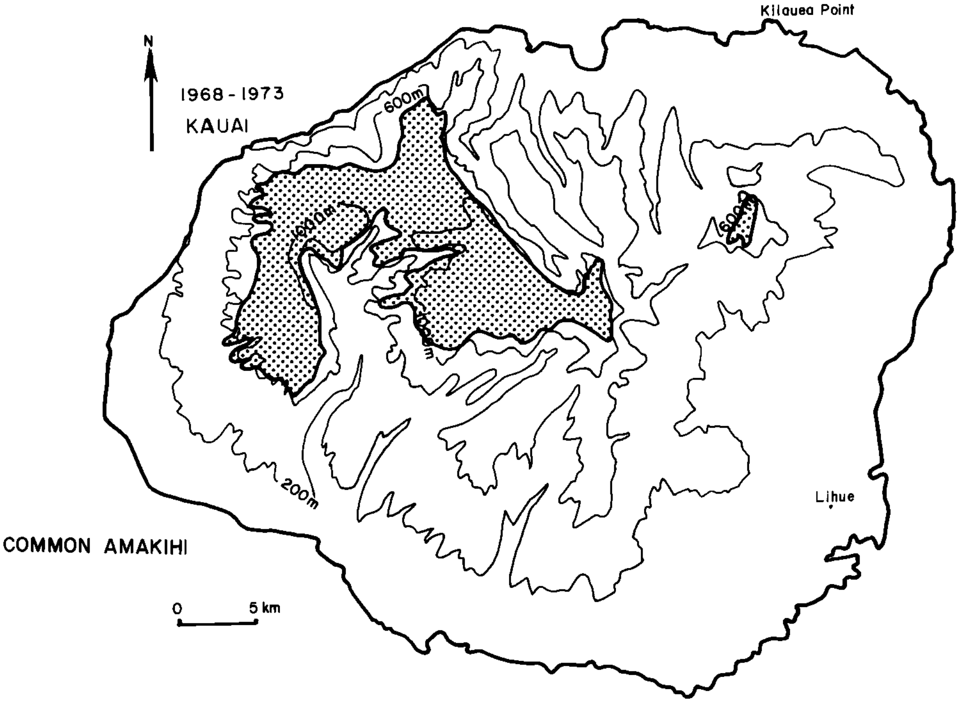

FIGURE 108. Range of the Common Amakihi on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

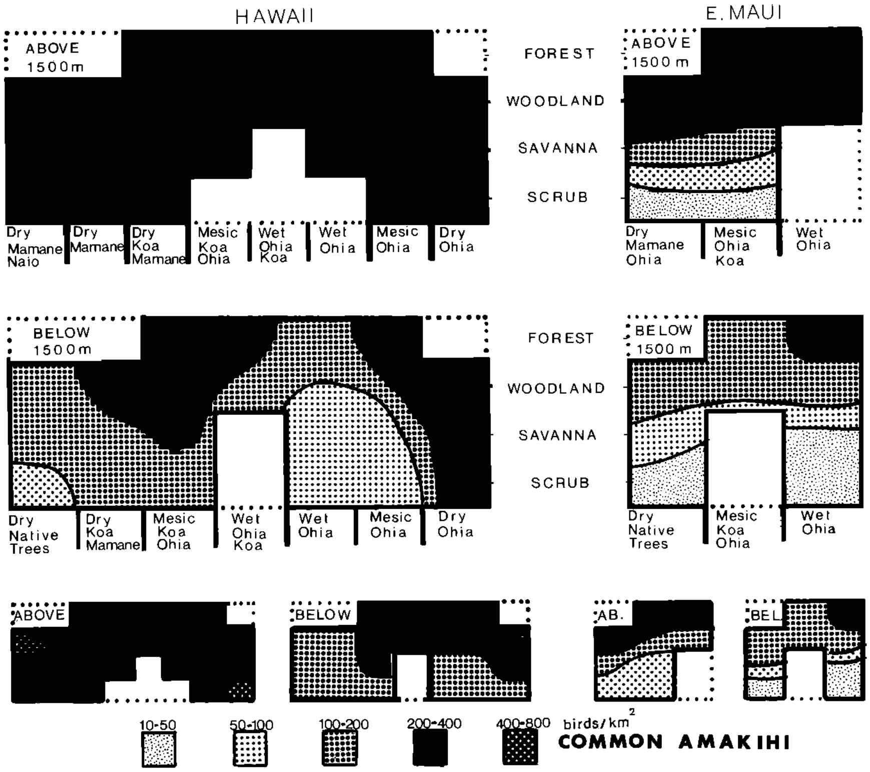

FIGURE 109. Habitat response graphs of the Common Amakihi. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 22

DENSITY [MEAN (SE)] OF THE COMMON AMAKIHI BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Kauai
Elevation											
100–300 m	···	···	···	···	···	···	···	···	···	138 (47)	···
300–500 m	···	0	47 (11)	···	387 (74)	···	0	0	···	222 (60)	···
500–700 m	133 (64)	2 (2)	41 (13)	···	152 (20)	···	59 (43)	91 (23)	62 (62)	83 (35)	···
700–900 m	63 (15)	89 (15)	175 (44)	···	103 (10)	···	215 (61)	53 (10)	69 (18)	*	···
900–1100 m	171 (23)	129 (16)	330 (45)	···	131 (12)	···	198 (34)	138 (15)	140 (42)	10 (5)	···
1100–1300 m	217 (27)	102 (9)	15 (8)	25 (11)	281 (16)	···	296 (36)	189 (19)	85 (15)	16 (4)	97 (11)
1300–1500 m	440 (30)	211 (15)	···	141 (16)	479 (16)	···	472 (41)	203 (20)	48 (9)	31 (26)	74 (10)
1500–1700 m	483 (40)	377 (23)	···	316 (22)	424 (14)	···	684 (56)	221 (19)	4 (4)	···	···
1700–1900 m	597 (41)	469 (34)	···	259 (20)	480 (19)	···	···	220 (23)	+ (+)	···	···
1900–2100 m	1428 (102)	381 (31)	···	234 (13)	448 (21)	826 (77)	···	160 (19)	···	···	···
2100–2300 m	1662 (291)	334 (57)	···	265 (31)	290 (16)	940 (106)	···	56 (11)	···	···	···
2300–2500 m	···	···	···	···	139 (27)	709 (68)	···	27 (12)	···	···	···
2500–2700 m	···	···	···	···	···	618 (47)	···	2 (2)	···	···	···
2700–2900 m	···	···	···	···	···	369 (37)	···	+ (+)	···	···	···
2900–3100 m	···	···	···	···	···	239 (79)	···	···	···	···	···
Habitat											
Ohia	341 (22)	116 (5)	136 (16)	257 (11)	375 (9)	···	323 (22)	201 (10)	79 (12)	51 (13)	87 (8)
Koa-ohia	655 (30)	351 (16)	···	192 (22)	343 (13)	···	···	143 (12)	···	···	···
Koa-mamane	···	271 (40)	···	274 (23)	326 (13)	···	···	···	···	···	···
Mamane-naio	···	···	···	···	346 (38)	747 (39)	···	···	···	···	···
Mamane	···	···	···	···	255 (15)	532 (43)	···	30 (21)	···	···	···
Other natives	···	231 (37)	···	97 (25)	118 (19)	···	···	123 (12)	···	0	···
Intro. trees	···	161 (72)	···	···	183 (37)	···	486 (102)	139 (15)	0	123 (33)	···
Treeless	1512 (174)	4 (3)	31 (13)	67 (24)	112 (18)	···	···	32 (2)	+ (+)	+ (+)	0

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2, 0 indicates stratum was outside range but was sampled, ··· indicates stratum was not sampled in study area; * indicates stratum was not sampled in range but was sampled elsewhere in study area.

TABLE 23
Regression Models for Habitat Response of the Common Amakihi[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai
R^2	0.42*	0.48*	0.65*	0.60*	0.46*	0.26*	0.43*	0.31*	0.24*
Moisture	−4.5*	···	−10.8*	−2.1	−8.3*	X	X	−2.3	−3.0
Elevation	···	8.6*	···	14.3*	11.7*	···	9.2*	6.5*	−5.3*
(Elevation)^2	12.1*	−4.0*	···	−12.9*	−7.2*	···	···	−4.1*	4.8*
Tree biomass	···	−3.2	···	4.5*	···	2.9	3.0	11.5*	···
(Tree biomass)^2	···	···	7.4*	···	9.7*	···	···	···	···
Crown cover	···	4.5*	···	···	−5.2*	···	···	···	···
Canopy height	···	···	···	···	2.4	5.2*	···	···	···
Koa	13.1*	6.8*	X	···	−5.2*	X	X	···	X
Ohia	···	···	···	4.4*	3.8*	X	···	2.0	2.9
Naio	X	X	X	4.6*	2.1	···	X	X	X
Mamane	X	···	···	···	4.0*	···	X	···	X
Intro. trees	X	···	···	X	−2.6	X	···	···	···
Shrub cover	···	6.7*	3.5*	···	···	−3.1	···	···	···
Ground cover	···	−2.1	···	···	−3.6*	···	···	···	···
Native shrubs	···	···	···	···	3.0	X	2.4	···	···
Intro. shrubs	X	4.2*	···	−2.7	−4.7*	X	···	···	···
Ground ferns	X	X	···	···	8.7*	X	···	···	4.0*
Matted ferns	···	−4.8*	−5.9*	···	···	X	−3.3	3.8*	···
Tree ferns	4.3*	X	−5.3*	X	−3.5*	X	−3.4*	···	···
Ieie	X	X	···	X	−5.1*	X	X	4.2*	X
Passiflora	X	4.2*	X	X	3.9*	X	···	4.2*	X
Native herbs	X	X	−2.9	−4.3*	−3.1	X	···	···	···
Intro. herbs	X	X	···	···	5.5*	···	2.5	···	2.7
Native grasses	···	···	−4.2*	3.4*	···	···	···	2.8	···
Intro. grasses	2.6	2.6	···	6.1*	···	···	···	3.8*	···
Ohia flowers	···	8.6*	3.2	···	3.7*	X	···	4.2*	2.8
Olapa fruit	···	−2.3	···	···	−2.7	X	···	···	···
Mamane flowers	X	X	X	···	X	···	X	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

ANIANIAU
Hemignathus parvus

ANIANIAU (*Hemignathus parvus*)

Anianiau, also known as Lesser Amakihi, inhabit the ohia rainforests of Kauai (Berger 1981). They were extremely numerous in all Kauai forests in the 19th century (Perkins 1903, Munro 1944) and were still common over a smaller area 40–50 years later (Munro 1944). Richardson and Bowles (1964) considered them moderately common residents of native forest areas above 450 m elevation. Fossils of this species have been found only on Kauai (Olson and James 1982b). Anianiau feed on insects and nectar (Richardson and Bowles 1964, Berger 1981). Their nesting biology has been studied by Berger et al. (1969) and Eddinger (1970).

We found Anianiau widespread and abundant throughout the Alakai Swamp study area (Tables 11, 20, Fig. 110). Densities are somewhat higher towards the interior of the area. The 6100 ± 600 (95% CI) birds in the area compare closely to the 5500 ± 900 birds estimated for the same area in 1968–1973 (J. L. Sincock, pers. comm.) and suggest a healthy population. Sincock et al. (1984) estimated a total of 24,000 ± 3000 birds for Kauai, and found them in Kokee State Park, the Na Pali plateaux, the Alakai Swamp, Laau Ridge, Namolokama Mountain, Kapalaoa Ridge, and Makaleha Mountains (Fig. 111). Anianiau occur in ohia and koa-ohia forests from near sea level at Nualolo Kai State Park to 1550 m elevation near the summit of Waialeale (Sincock et al. 1984).

The regression model (Table 21) shows that higher Anianiau densities are associated with ground ferns and lower ones with introduced shrubs, but otherwise little habitat response is seen. This generally reflects sampling within fairly homogeneous habitat.

GREATER AMAKIHI
(*Hemignathus sagittirostris*)

Greater Amakihi were poorly known birds from Hawaii. The Hawaiians apparently had no name for them, but early collectors called them Green Solitaires. Greater Amakihi were mostly insectivorous but also fed occasionally on nectar (Perkins 1903). Perkins (1903) indicated that they gleaned insects from ieie and the loose bark of ohia trees in lowland koa-ohia forests. This species was found from 150 to 1200 m elevation along the Wailuku River and in adjacent forests above Hilo, Hawaii. The restriction of this species to the low-elevation forests was unusual among historically known forest birds. No close ecological equivalent was known from higher elevations.

The call of this species was distinctive but rather similar to that of Common Amakihi (Perkins 1903). We therefore assumed that the effective detection distances of the two species were identical. In assessing the historical range, we assumed the Greater Amakihi occurred from transects 12 through 26 as high as 1300 m. The probability that an extant population went un-

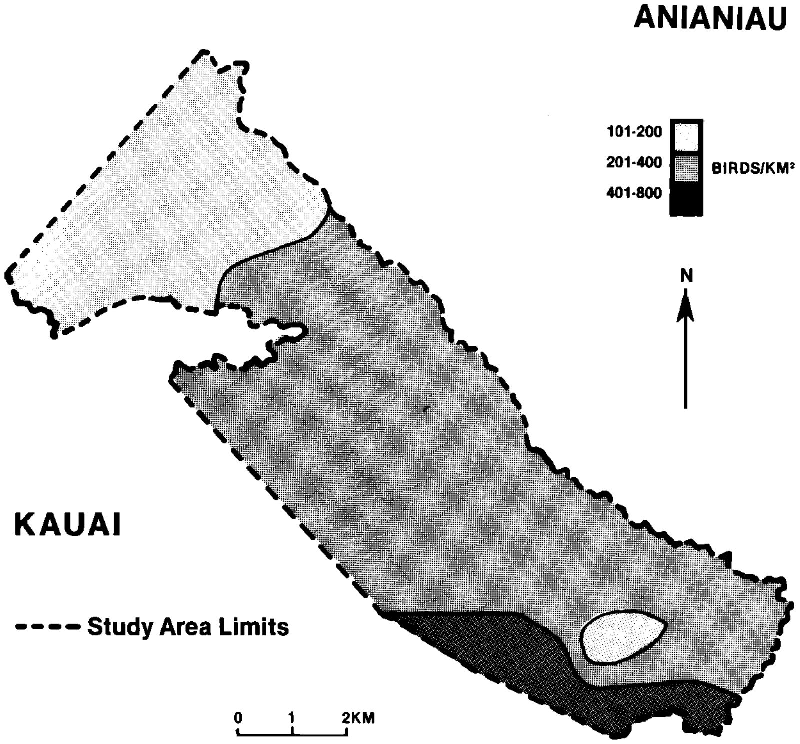

FIGURE 110. Distribution and abundance of the Anianiau in the Kauai study area.

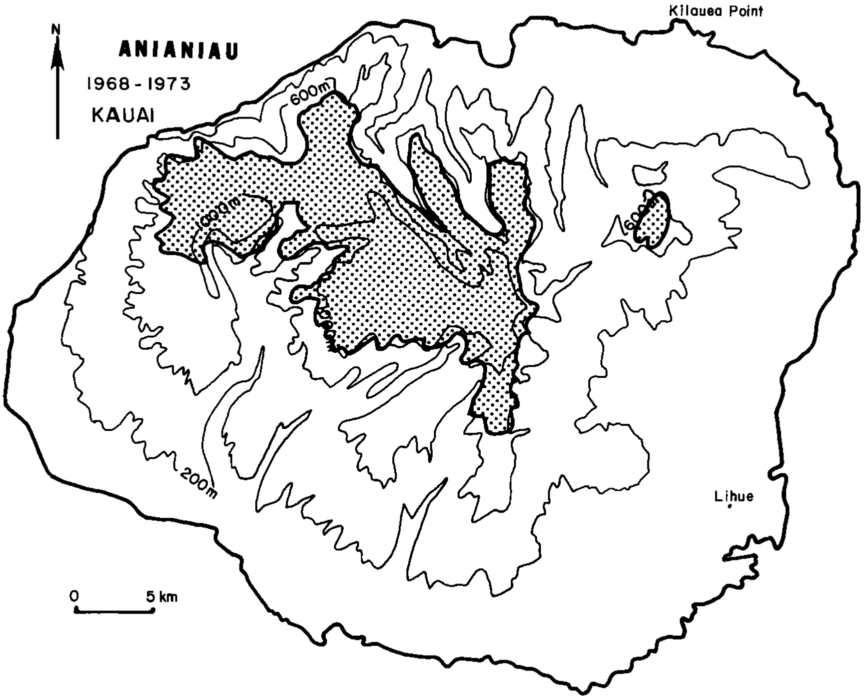

FIGURE 111. Range of the Anianiau on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

detected during the HFBS is moderate (Table 12), but we believe the species is extinct. There have been no records since the last collection in 1901, and virtually all of the habitat in the historical range has been replaced by introduced plant species.

HAWAIIAN AKIALOA (*Hemignathus obscurus*)

Hawaiian Akialoa, also known as Akialoa, were first collected in 1779 during Cook's stay at Kealakekua Bay, Hawaii (Stresemann 1950). They were historically found on Hawaii, Lanai, and Oahu; fossils are also known from Molokai (Olson and James 1982b). Wilson and Evans (1890–1899) reported them as scarce and restricted to forests from 350 to 750 m elevation, and failed to find them in the higher forests of Kona. Perkins (1903) and Munro (1944), however, found them to be "not uncommon" in many localities and to occur throughout Hawaii above 150 m elevation. In the 1890s they were abundant in koa-ohia forests 5 km from Kilauea Crater (Perkins *in* Banko and Banko 1980). Data on specimen labels indicate that Hawaiian Akialoa occurred in several areas on Hawaii as high as 1800 m (Banko 1979). Munro (1944) and Baldwin (1953) failed to find Hawaiian Akialoa in the 1930s and 1940s. The Lanai subspecies was apparently rare even when first collected in 1892 (Rothschild 1893–1900).

Hawaiian Akialoa fed with their enormous sickle-shaped bill on the nectar of ohia and lobeliads (Perkins 1903). They also frequently fed on insects and spiders by gleaning and probing in the bark of trees, under lichens, and in the bases of ieie leaves (Munro 1944).

The call note of this species was easily recognized and birds could be traced by the audible tapping made by the bill against bark (Perkins 1903). This same sound helps present-day observers identify Akiapolaau. The song was described as a short vigorous trill similar to that of Akiapolaau and Common Amakihi; the call note was louder than that of Common Amakihi (Perkins 1903).

Based on these descriptions, we assumed that the effective detection distance for Hawaiian Akialoa (39 m) would be intermediate to those of Common Amakihi and Akiapolaau. We further assumed a distribution similar to that described by Perkins (1903), except that they would now be absent below 1500 m elevation. There have been no documented records for this species since the turn of the century, except for one possible sighting in 1940 high on the windward side of Hawaii (Greenway 1958). It seems unlikely that this species is still extant (Table 12).

KAUAI AKIALOA (*Hemignathus procerus*)

The Kauai Akialoa may best be considered a subspecies of the Hawaiian Akialoa (Pratt 1979). It is abundant in the Kauai fossil record (Olson and James 1982b). This species was numerous on Kauai in the 1890s but apparently declined in numbers shortly after 1900. Munro (1944) knew of only one record since 1920. Richardson and Bowles (1964) rediscovered the species in 1960. They described it as a "rare resident of the undisturbed native forest of the Alakai Swamp." The last well-documented bird was seen in 1965 (Huber 1966). Despite intensive searches and rumors that Kauai Akialoa still exist, no further convincing sightings have been made (Sincock et al. 1984).

Munro (1944) reported that these birds frequently came to the forest edge and to low elevations. He suggested that this habit exposed them to introduced diseases to which they were susceptible, and Perkins (1903) described several birds incapacitated by parasites and apparent pox lesions.

The feeding habits were similar to those described for Hawaiian Akialoa. We assumed the effective detection distance to be the same as well (Table 12). In assessing the probability of missing this species during our survey, we assumed that it would have occurred throughout the survey area. The Kauai Akialoa is on the verge of extinction, if not already gone.

NUKUPUU
Hemignathus lucidus

NUKUPUU (*Hemignathus lucidus*)

Nukupuu are one of the rarest honeycreepers, although they were not uncommon in the 1890s (Perkins 1903, Wilson and Evans 1890–1899). On Maui, all recent sightings have been on the northeast slopes of Haleakala or in Kipahulu Valley from 1450 to 2000 m elevation in wet ohia and koa-ohia forests with well-developed native understories (Banko 1968, Conant 1981). There are no recent records west of Koolau Gap. Perkins (1903) found Nukupuu from 1200 to 1400 m elevation in the koa forests that formerly covered the northwest slopes of Haleakala. On Kauai, Perkins (1903) found birds as low as 600 m and in the Alakai Swamp. Perkins noted that Nukupuu on Kauai were especially associated with koa trees, and inferred from earlier reports and vegetation remnants that they had been associated with koa on Oahu prior to extinction. Like Akiapolaau, Nukupuu probably prefer to foraage on koa instead of ohia because of the greater abundance of borers on koa (Gressitt and Samuelson 1981).

We saw one Nukupuu on Maui during the HFBS (Fig. 112). This bird was sighted on transect 8 at 1600 m elevation in wet ohia forest with about 60% canopy cover and a closed native understory dominated by shrubs. From recent sightings on Maui we infer that Nukupuu inhabit wet ohia forest and woodlands and the upper portions of mesic koa-ohia forests (Table 20). Perkins (1903) remarked that Maui Parrotbills had a wider elevational range than Nukupuu, suggesting that Maui Parrotbills may tolerate a wider range of habitat, as supported by recent data in the wider range of elevation and habitat types that Maui Parrotbills occupy. This inference, if correct, may explain why Maui Parrotbills are more common than Nukupuu.

We estimated a population of 28 ± 56 (95% CI) Nukupuu on Maui. An immature bird, significant as an indication of successful breeding, was observed in July 1983 in the Hanawi watershed (S. Mountainspring, pers. observ.). An undetected Nukupuu population may inhabit the koa-ohia forest from 1500 to 1900 m elevation above Manawainui Valley, east of Kaupo Gap.

Most records of Nukupuu on Kauai since 1960 fall within 1 km of the Wainiha Pali in the Alakai Swamp (Fig. 113), with the most recent record in 1975 (Sincock et al. 1984). We failed to locate the species during our survey of the Alakai and any remaining population must be very small (Table 12). During 17 years of field work, J. L. Sincock (pers. comm.) saw only two Nukupuu.

Van Riper (1982) reported observing a Nukupuu in 1971 on Kohala Mountain; however, he originally reported the bird as an Akiapolaau (van Riper 1973a). On biogeographical grounds, the Akiapolaau or Common Amakihi appear more plausible from this area, but one Nukupuu specimen in the U.S. National Museum was collected by Titian Peale between 1838 and 1842 from the island of Hawaii (S. L. Olson, pers. comm.).

Nukupuu feed on boring larvae, spiders, and weevils, although they excavate less than Akiapolaau (Perkins 1903). Unlike Akiapolaau, Nukupuu occasionally feed on or among ohia flowers (Perkins 1903; J. L. Sincock, pers. comm.), indicating that ohia forests have resources available for this species. Nukupuu also formerly fed from the flowers of banana and orange on Oahu and Kauai (Perkins 1903); the birds are adapted for facultative nectarivory because their tongue can roll into a tube for sucking and both mandibles are slender and decurved (Amadon 1950).

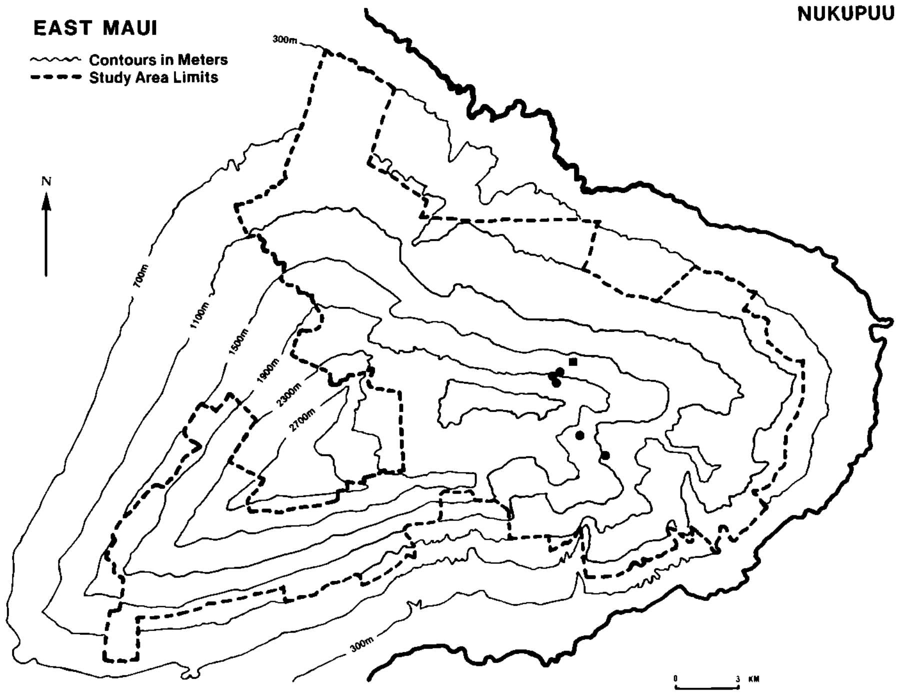

FIGURE 112. Distribution and abundance of the Nukupuu in the East Maui study area. (Square indicates location of birds observed during the HFBS; circles indicate location of other recent records.)

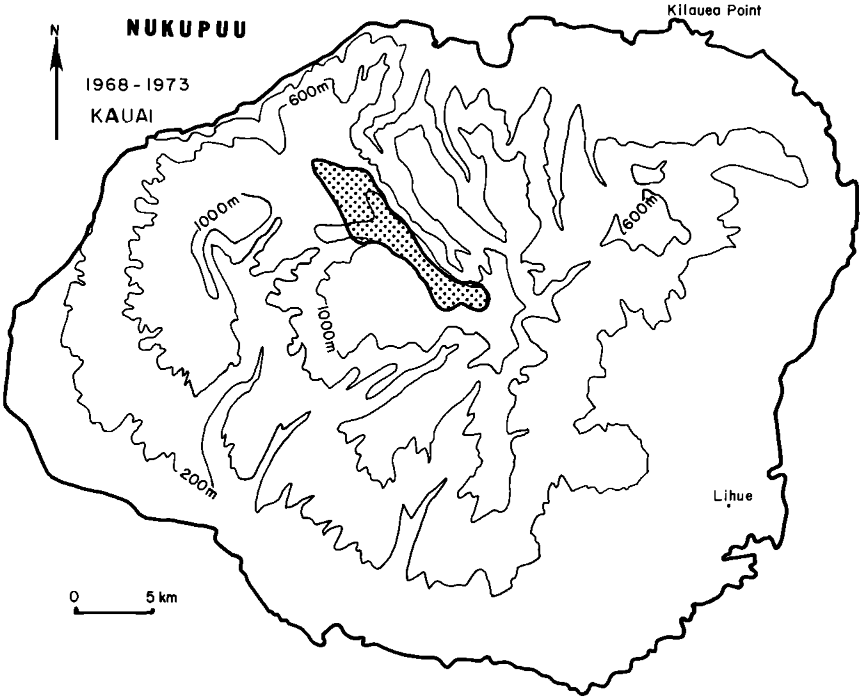

FIGURE 113. Range of the Nukupuu on Kauai, based on 1968–1973 survey and incidental sightings (J. L. Sincock, unpub. data).

AKIAPOLAAU
Hemignathus munroi

AKIAPOLAAU (*Hemignathus munroi*)

Akiapolaau are bizarre honeycreepers with a stout, woodpecker-like lower bill, and a slender, decurved, sickle-like upper bill. Akiapolaau use their lower bill in woodpecker fashion to excavate burrowing insect larvae and their upper bill to probe and pry in surface deformities (Perkins 1903). They also capture invertebrates by gleaning (C. J. Ralph, pers. comm.).

Akiapolaau are rare to uncommon inhabitants of mesic to wet koa-ohia forest and dry mamane-naio woodland on Hawaii. In the 1890s Akiapolaau had a wide distribution and were fairly abundant on Hawaii (Perkins 1903). In central Kona, Perkins found them abundant above 1100 m elevation in mixed koa-mamane-naio forest, but not at lower elevations in wet koa forest lacking naio. In koa forests near Hilo, Perkins found Akiapolaau as low as 500 m; he also noted birds in koa in Kau and in mamane on Mauna Kea. This implies that Akiapolaau had a wider and more continuous distribution then than today. Originally the mesic and dry forests were continuous, particularly from the mamane woodland on east Mauna Kea to the upper montane forests of koa, mamane, and naio in Hamakua. A series of dry forest communities bridged the gap from the mamane-naio forest on the west side of Mauna Kea to the north slopes of Hualalai and the Mauna Loa-Hualalai saddle, connecting with the koa-mamane-naio forests of Kona (Rock 1913). Goat, cattle, and sheep activity in the 19th century (Tomich 1969, Kramer 1971) and sandalwood harvest in the early 19th century (Rock 1913, Judd 1927) fragmented and deforested this extensive upper-elevation dry forest. Akiapolaau were probably once found throughout the mesic and dry forests, but the populations occurring in mamane-naio on Mauna Kea, in koa in Hamakua, Kau, and Kona have been separated by deforestation. Whether individual birds attempt to move from one area to another is unknown.

In the 1890s, Perkins (*in* Banko and Banko 1980) considered Akiapolaau to be common around Kilauea Crater, finding as many as 12 birds in one day. Munro (1944) indicated that they still occurred in fair numbers in the 1930s near Hawaii Volcanoes National Park, and Richards and Baldwin (1953) reported them as "rather common locally above 1200 m on the eastern slope of Mauna Loa and the northeastern slope of Mauna Kea." During the 1940s, Baldwin (1953) found this species on 48 of 110 plot-counts in koa-ohia parkland at 1700 m elevation along the Mauna Loa Strip Road in the national park; extensive searches in the 1970s failed to find the species in the park (Conant 1975, Banko and Banko 1980, HFBS data). The most recent survey of ornithological records prior to the HFBS concluded that Akiapolaau occurred only at Puu Laau on Mauna Kea and in the Keauhou-Kilauea area north of the national park (Berger 1972).

Akiapolaau presently have four disjunct populations totalling 1500 ± 400 (95% CI) birds (Tables 10, 24, Figs. 114–117). The Hamakua population of 900 ± 200 birds is five times more abundant in koa-ohia forest than in ohia forest. These birds are separated from the Mauna Kea population by 3 km of open pasture and from the Kau population by 25 km of scrub and deforested rangeland. The 500 ± 300 birds in Kau are virtually confined to koa-ohia forest, where the species achieves its highest density of 12 birds/km^2. The 50 ± 50 birds on Mauna Kea have two population nuclei—the main one at Puu Laau, and a secondary one in a relict mamane woodland near Kanakaleonui. A small popula-

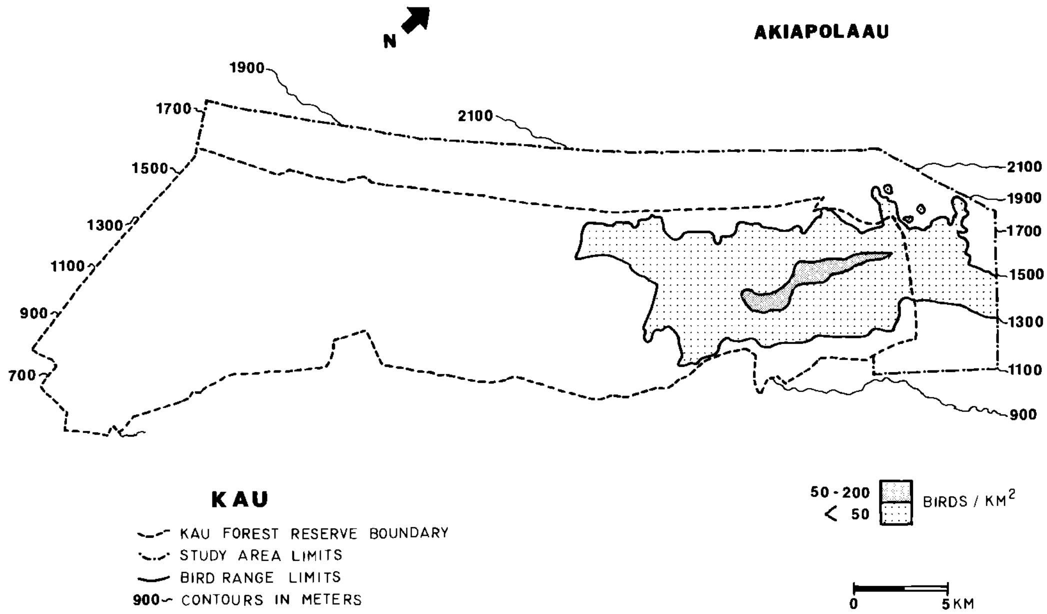

FIGURE 114. Distribution and abundance of the Akiapolaau in the Kau study area.

TABLE 24
DENSITY [MEAN (SE)] OF THE AKIAPOLAAU AND POO-ULI BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Akiapolaau					Poo-uli
	Kau	Hamakua	Kipukas	Kona	Mauna Kea	E. Maui
Elevation						
100–300 m	···	···	···	···	···	···
300–500 m	···	0	···	0	···	0
500–700 m	0	0	···	0	···	0
700–900 m	0	0	···	0	···	0
900–1100 m	+ (+)	0	···	0	···	0
1100–1300 m	2 (2)	1 (1)	0	0	···	0
1300–1500 m	20 (9)	3 (1)	0	1 (1)	···	63 (63)
1500–1700 m	16 (6)	5 (1)	0	+ (+)	···	+ (+)
1700–1900 m	5 (3)	2 (1)	1 (1)	1 (+)	···	+ (+)
1900–2100 m	14 (14)	+ (+)	0	0	+ (+)	+ (+)
2100–2300 m	0	0	0	0	+ (+)	+ (+)
2300–2500 m	···	···	···	0	1 (1)	0
2500–2700 m	···	···	···	···	+ (+)	0
2700–2900 m	···	···	···	···	+ (+)	0
2900–3100 m	···	···	···	···	+ (+)	···
Habitat						
Ohia	+ (+)	1 (+)	+ (+)	+ (+)	···	12 (12)
Koa-ohia	12 (3)	5 (1)	2 (2)	+ (+)	···	0
Koa-mamane	···	0	0	0	···	···
Mamane-naio	···	···	···	0	+ (+)	···
Mamane	···	···	···	0	1 (+)	0
Other natives	···	0	0	0	···	0
Intro. trees	···	0	···	0	···	0
Treeless	0	0	0	0	···	0

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

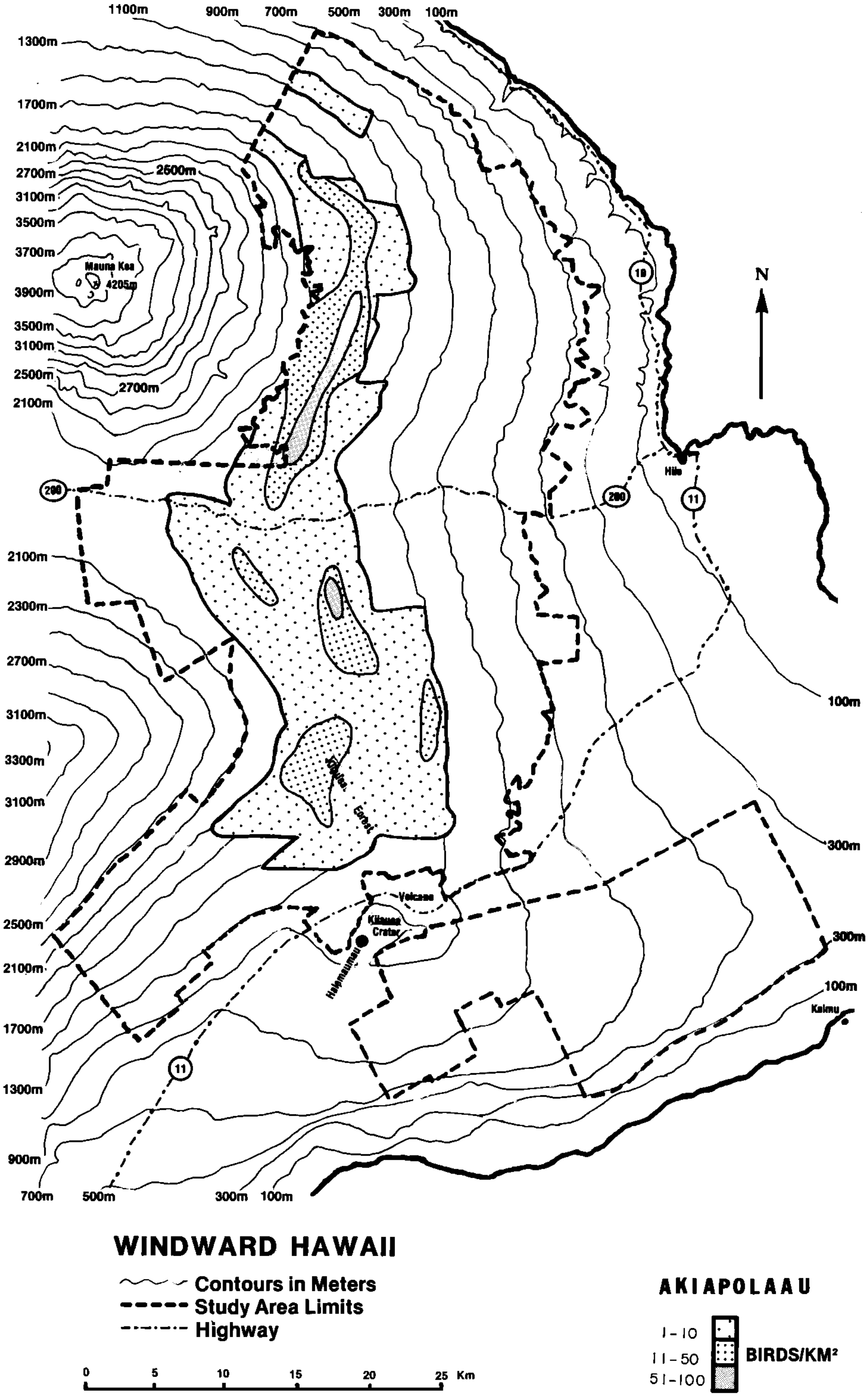

FIGURE 115. Distribution and abundance of the Akiapolaau in the windward Hawaii study areas.

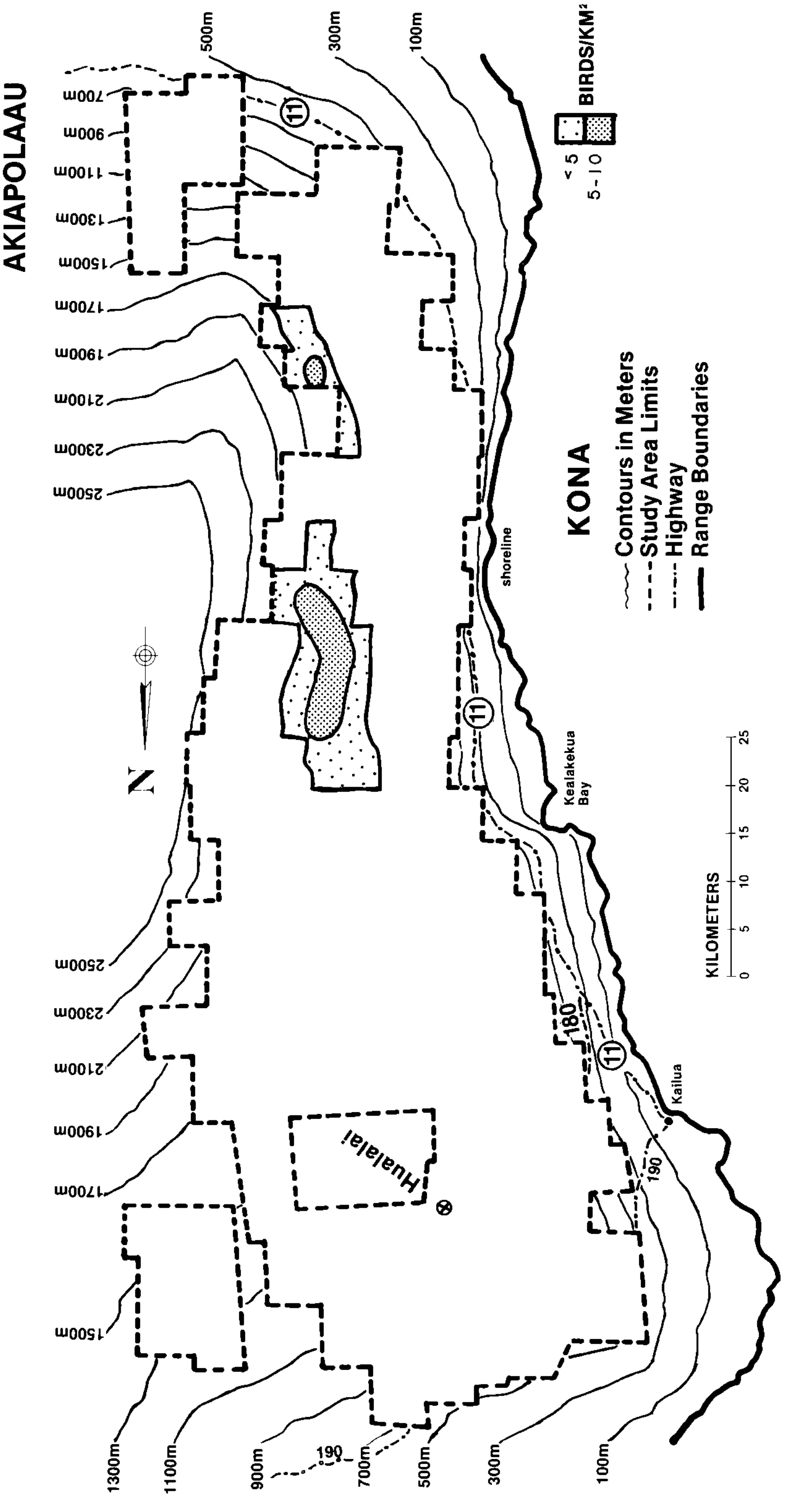

FIGURE 116. Distribution and abundance of the Akiapolaau in the Kona study area.

AKIAPOLAAU

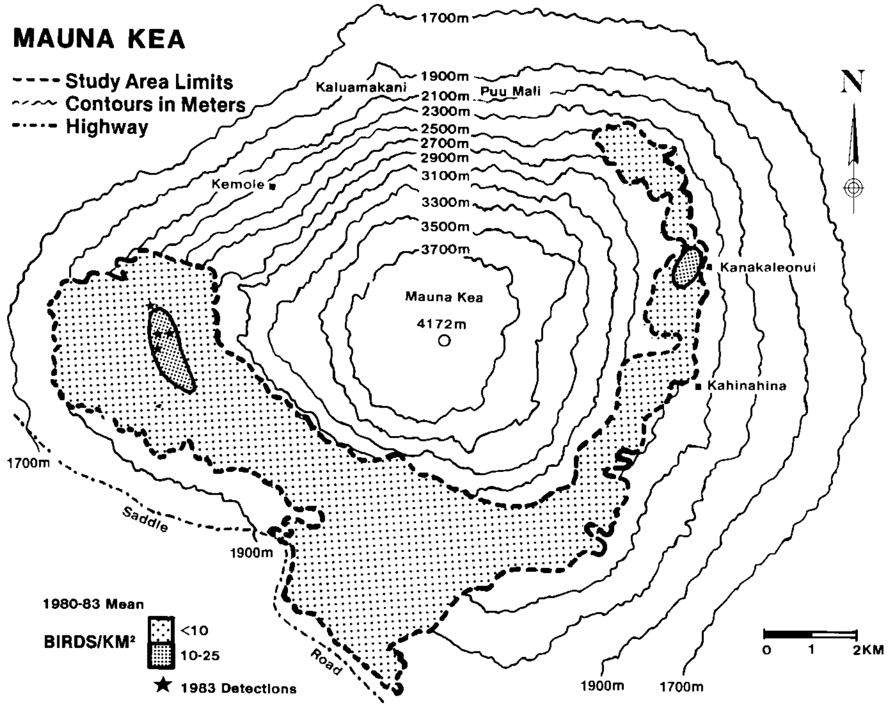

FIGURE 117. Distribution and abundance of the Akiapolaau in the Mauna Kea study area.

tion of about 20 ± 5 birds is on the verge of extinction in central Kona, with one additional record from south Kona (Sakai and Ralph 1980). The absence of birds from the 16 km² koa-ohia forest on north Hualalai where Akepa and Hawaii Creeper occur implies that that "habitat island" is too small to sustain a viable population. Based on Akiapolaau densities in similar habitat (koa-ohia forest with introduced understory) in windward Hawaii, we predict that the Hualalai area could support 5 birds/km², or a total population of about 80 birds. The only recent record on Hualalai was of a single bird in 1971 at 1700 m elevation on the western slopes (van Riper 1973a); this bird was probably a vagrant.

Annual surveys of the Mauna Kea area show significant fluctuations in Akaipolaau population between years. Populations in 1980 and 1981 were 345 ± 196 (95% CI) and 803 ± 462 birds, significantly higher than the 31 ± 42 and 46 ± 52 birds of 1982 and 1983; 1984 was intermediate with 169 ± 75 birds (HFBS data). Ongoing monitoring will determine whether such fluctuations are normal for this population, part of a trend toward extinction, or a result of migration between isolated populations.

The fragmented relictual nature of Akiapolaau populations increases their jeopardy of extinction. Linking the populations would improve the prospect for long-term survival. A vigorous reforestation effort in the upland pastures of Keauhou and Kapapala would reestablish the historical link between the Kau and Hamakua populations, and reforestation of upland koa-mamane and koa-ohia forests would link the Mauna Kea and Hamakua populations. Koa forest along the Mauna Loa Strip Road in Hawaii Volcanoes National Park regenerated naturally after the area was fenced and the goats and cattle removed, and will provide potential transplant locations as the habitat matures.

Akiapolaau range from 1000 to 2100 m elevation in Kau, Hamakua, and Kona, with greatest densities at 1300–2100 m in Kau and at 1300–1900 m in Hamakua. The upper limit is lower in Hamakua because of deforestation at higher elevations. On Mauna Kea, Akiapolaau range from 1900 to 2900 m elevation.

The habitat response graph shows that Akiapolaau reach greatest densities in mesic koa-ohia woodland and forest (Fig. 118). Because of low densities and irregular occurrence, relatively few patterns appear in the regression models (Table 21), but the positive association with koa is quite

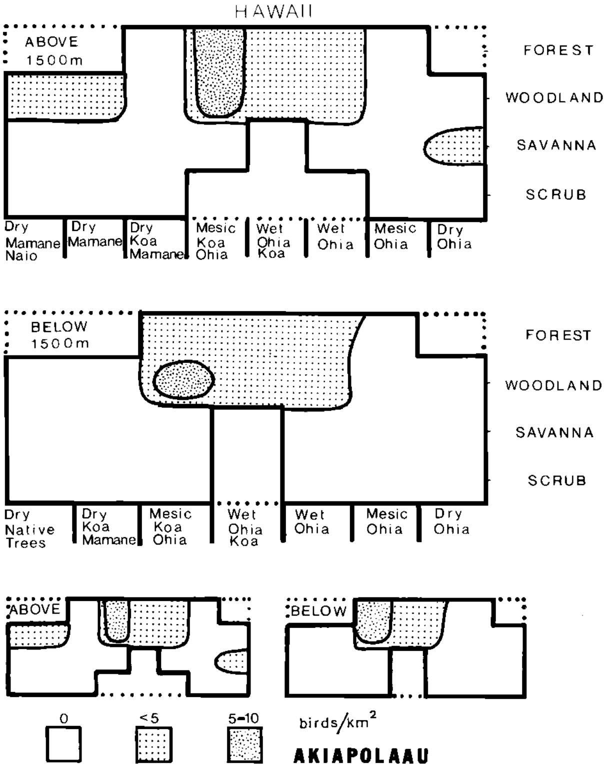

FIGURE 118. Habitat response graphs of the Akiapolaau. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

clear in every model. The invasion of passiflora coincides with depressed Akiapolaau numbers. A number of other variables enter only one model, usually at low levels of significance, or enter no models at all, and thus may be of minor or only local importance in determining habitat response.

The association of Akiapolaau with koa forests probably reflects exploitation of koa for foraging substrates. In a mixed koa-ohia-naio forest, C. J. Ralph (pers. comm.) found that Akiapolaau spend 63–83% of their time in koa trees, a significant difference from the 15–36% of bark surface area constituted by koa. He also found that Akiapolaau seldom use ohia (6–16% of the time vs. 59–71% of bark surface area) and use naio in proportion to its availability. In the Mauna Kea woodland, Ralph found that Akiapolaau feed on both mamane and naio in proportion to their abundance. The underlying cause for these tree preferences is probably related to the abundance of prey, particularly cerambycid borers. In rainforest near Kilauea Crater, Gressitt and Samuelson (1981) found that cerambycid borer larvae are virtually absent in ohia, relatively common in koa, moderately common in naio, and rather sparse overall. This suggests that the distribution of food resources plays a major role in shaping the habitat response of Akiapolaau.

KAUAI CREEPER
Oreomystis bairdi

Kauai Creeper (*Oreomystis bairdi*)

Kauai Creepers, or Akikiki, were common and widely distributed in the 1890s from low to high elevation forests on Kauai (Perkins 1903). They are similar in habits to Hawaii Creepers, and until recently all five Hawaiian creeper species were considered conspecific (Pratt 1979). This species forages for insects and other invertebrates by moving slowly along branches and trunks, probing and prying in cracks and beneath the bark, and gleaning from foliage.

Munro (1944) found Kauai Creepers on the "wet mountain tops above [900 m], being common above [1200 m]." Richardson and Bowles (1964) found them abundant in some regions of native forest in or near the Alakai Swamp area, almost always in loose flocks.

We found Kauai Creepers common through-

TABLE 25

Density [Mean (SE)] of the Kauai Creeper, Hawaii Creeper, and Maui Creeper by Elevation, Habitat, and Study Area[a]

	Kauai Creeper	Hawaii Creeper			Maui Creeper
	Kauai	Kau	Hamakua	Kona	E. Maui
Elevation					
100–300 m	···	···	···	···	···
300–500 m	···	···	0	0	0
500–700 m	···	+ (+)	0	0	0
700–900 m	···	6 (6)	4 (3)	0	0
900–1100 m	···	+ (+)	10 (4)	0	20 (15)
1100–1300 m	57 (11)	4 (3)	3 (1)	11 (11)	104 (24)
1300–1500 m	93 (14)	3 (2)	14 (2)	2 (1)	247 (45)
1500–1700 m	···	20 (6)	48 (7)	4 (1)	511 (88)
1700–1900 m	···	39 (11)	61 (11)	5 (2)	495 (60)
1900–2100 m	···	10 (10)	3 (2)	0	374 (48)
2100–2300 m	···	0	+ (+)	0	35 (23)
2300–2500 m	···	···	···	0	+ (+)
2500–2700 m	···	···	···	···	+ (+)
2700–2900 m	···	···	···	···	0
2900–3100 m	···	···	···	···	···
Habitat					
Ohia	74 (9)	15 (3)	11 (2)	0	380 (34)
Koa-ohia	···	12 (4)	50 (6)	4 (1)	110 (32)
Koa-mamane	···	···	2 (2)	5 (5)	···
Mamane-naio	···	···	···	0	···
Mamane	···	···	···	0	0
Other natives	···	···	0	0	0
Intro. trees	···	···	0	0	141 (34)
Treeless	+ (+)	0	0	0	77 (34)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

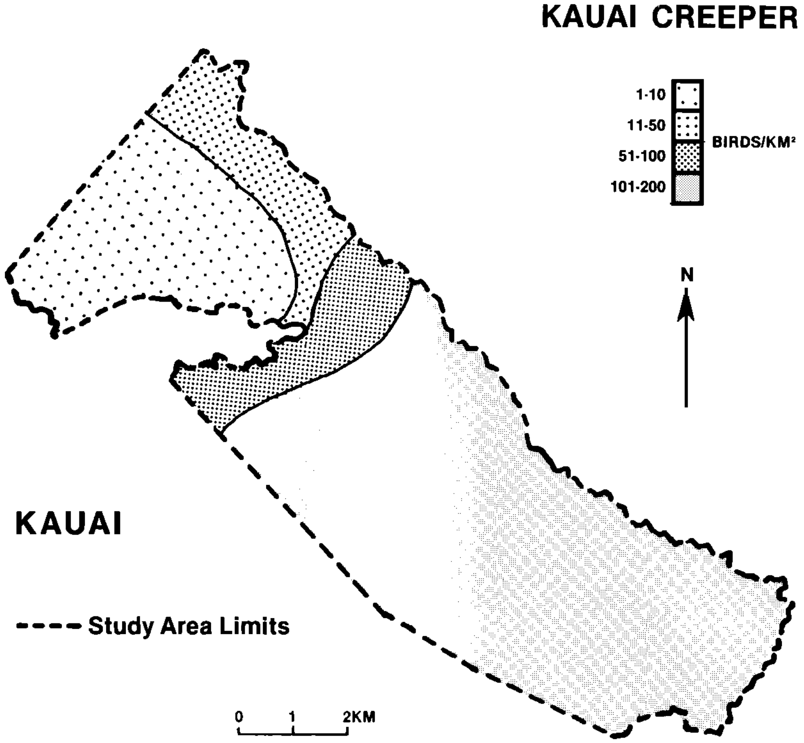

FIGURE 119. Distribution and abundance of the Kauai Creeper in the Kauai study area.

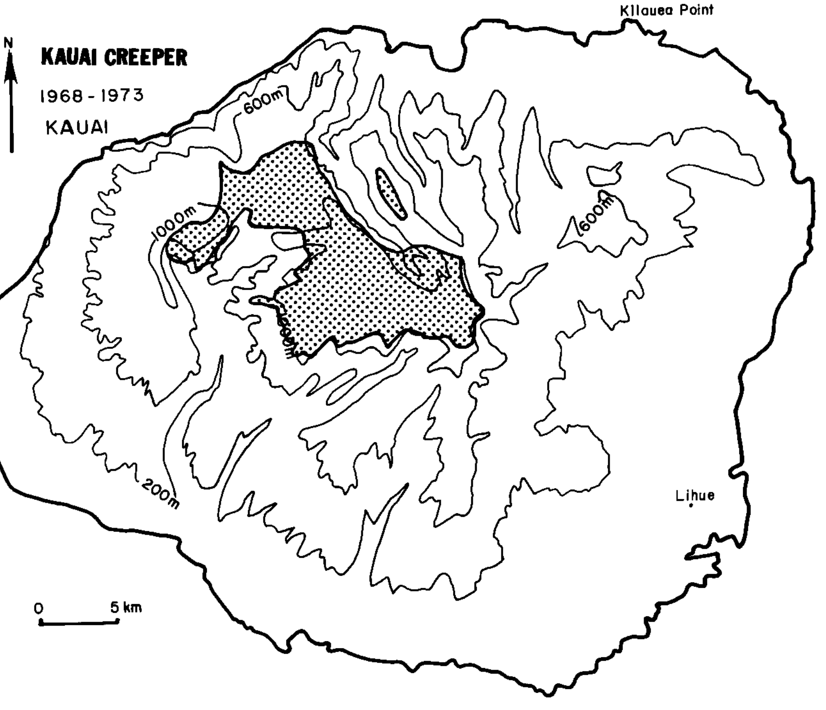

FIGURE 120. Range of the Kauai Creeper on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

TABLE 26

REGRESSION MODELS FOR HABITAT RESPONSE OF THE KAUAI CREEPER, HAWAII CREEPER, AND MAUI CREEPER[a]

	Kauai Creeper	Hawaii Creeper			Mau Creeper
	Kauai	Kau	Hamakua	Kona	Maui
R^2	0.08	0.05*	0.19*	0.07*	0.44*
Moisture	X	···	5.3*	···	6.4*
Elevation	2.4	5.7*	···	···	13.2*
(Elevation)^2	···	···	16.5*	···	···
Tree biomass	···	5.1*	···	···	···
(Tree biomass)^2	···	···	3.2	···	13.3*
Crown cover	···	···	···	···	···
Canopy height	···	−2.7	−2.6	···	···
Koa	X	−2.5	5.1*	5.8*	−6.6*
Ohia	X	···	···	···	···
Naio	X	X	X	8.6*	X
Mamane	X	X	−5.4*	−6.5*	−3.8*
Intro. trees	X	X	···	···	···
Shrub cover	···	···	5.0*	···	−3.4*
Ground cover	···	···	4.3*	···	4.1*
Native shrubs	···	···	···	···	···
Intro. shrubs	···	X	···	···	···
Ground ferns	···	X	X	2.2	···
Matted ferns	···	···	···	···	···
Tree ferns	2.6	···	X	···	−6.1*
Ieie	···	X	X	···	3.1
Passiflora	X	X	−4.5*	6.2*	···
Native herbs	···	X	X	···	···
Intro. herbs	···	X	X	···	−2.1
Native grasses	···	···	−4.7*	3.2	5.5*
Intro. grasses	···	···	−4.3*	···	···
Ohia flowers	···	···	−4.7*	···	3.7*
Olapa fruit	···	···	−2.7	···	···
Mamane flowers	X	X	X	X	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

out the more remote sections of the Alakai Swamp (Tables 11, 25, Fig. 119), but the distribution indicates that the interior of the Alakai may be the last refuge for the species. It has definitely declined in numbers since the Richardson and Bowles (1964) survey. They indicated that Kauai Creepers were three times more common than either Anianiau or Common Amakihi, but we found that creepers are rarer than those species. The 1968–1973 (Sincock et al. 1984) survey also showed that creepers were rarer than those species over all of Kauai, but were more common than Common Amakihi within the Alakai. Sincock et al. (1984) estimated a total population of 6800 ± 1900 (95% CI) birds, with the range limited to the upper elevation forested slopes of Waimea Canyon, Kokee State Park, the Alakai Swamp, and Laau Ridge (Fig. 120). The species has retreated from the Kokee region since 1973 (J. L. Sincock, pers. comm.). The 1650 ± 450 birds we found were similar to the 2300 ± 700 birds found in the same part of the Alakai ten years earlier (J. L. Sincock, pers. comm.). This species fits into the pattern of population decline and retreat to the remote Alakai interior seen among the endangered Kauai passerines.

The regression model for the Kauai Creeper (Table 26) shows that they tend to be more common in the upper reaches of the Alakai and in areas with tree fern understories.

HAWAII CREEPER
Oreomystis mana

HAWAII CREEPER (*Oreomystis mana*)

Hawaii Creepers are uncommon in wet montane forests on Hawaii, where they feed on insects, spiders, and invertebrates gleaned from trunks and larger branches. In the 1890s they occupied a wide range of habitats from dry upper forests in Kona to rainforests in Hamakua, occurring above 1000 m elevation in Kona and at lower elevations near Hilo (Perkins 1903). Perkins noted that they were very abundant and generally distributed but had puzzling gaps in distribution, especially at lower elevations. Henshaw (1902) indicated that they were common in some districts but rare in others and generally found above 600 m elevation. The historical status is clouded by the difficulty of identification and uncertainty of field marks (Scott et al. 1979). Berger (1972) stated that "so little is known about the present distribution of the Hawaii Creeper that we do not know whether it is uncommon or so rare that it is on the verge of extinction."

In the 1890s Hawaii Creepers were common in the vicinity of Kilauea Crater (Perkins *in* Banko and Banko 1980). A dramatic decline in numbers apparently occurred in that area during the late 1930s to early 1940s. In the 1940s Baldwin (1953) found birds to be rare from 1100 to 1700 m elevation in the national park, but reports virtually ceased after the 1950s (Banko and Banko 1980). Because both this species and the Japanese White-eye are arboreal insectivores, the decline may have been due to interspecific competition (Dunmire 1961). In the Christmas bird counts for this area, the number of Hawaii Creep-

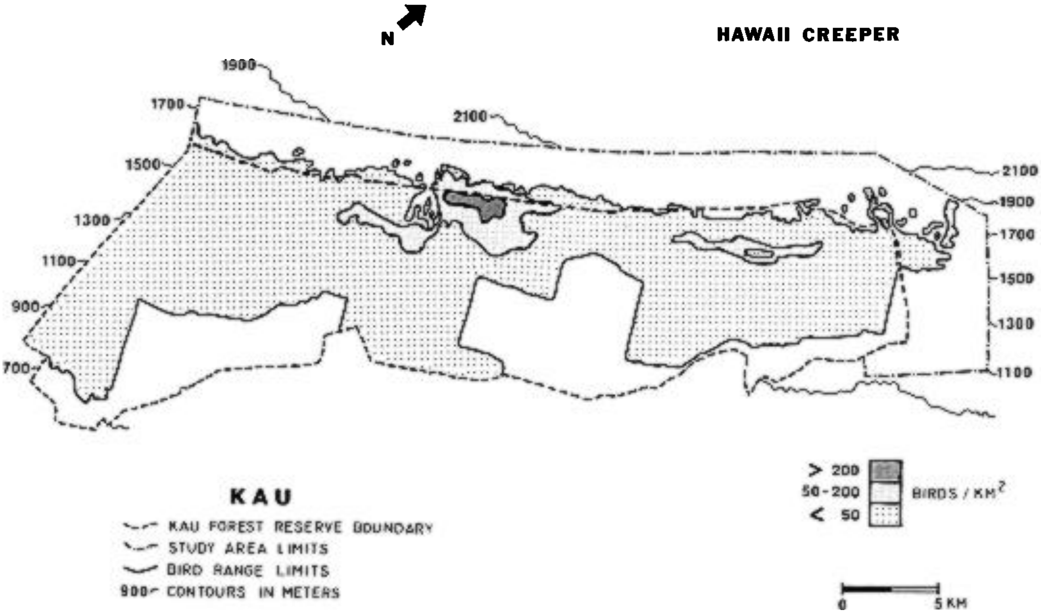

FIGURE 121. Distribution and abundance of the Hawaii Creeper in the Kau study area.

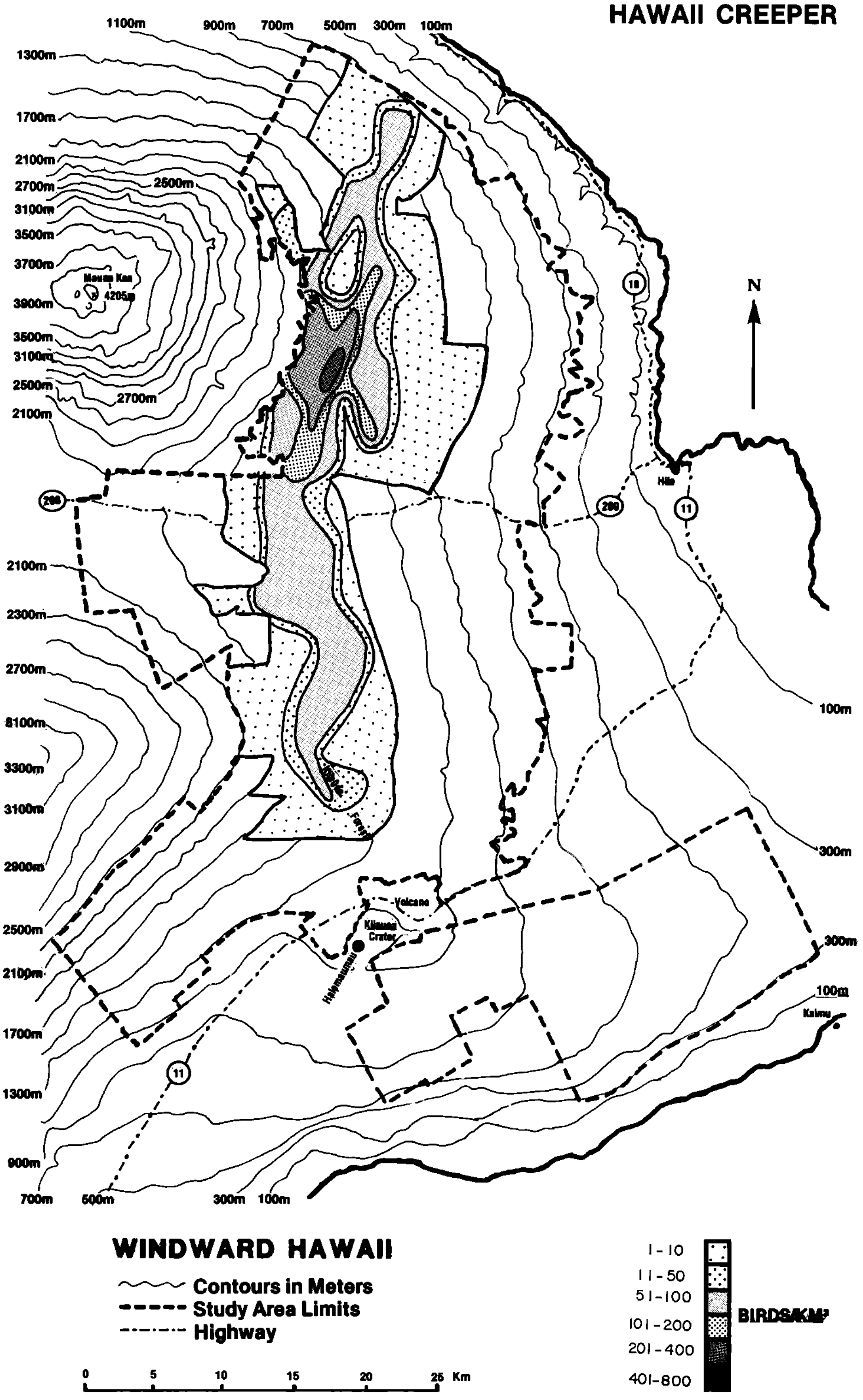

FIGURE 122. Distribution and abundance of the Hawaii Creeper in the windward Hawaii study areas.

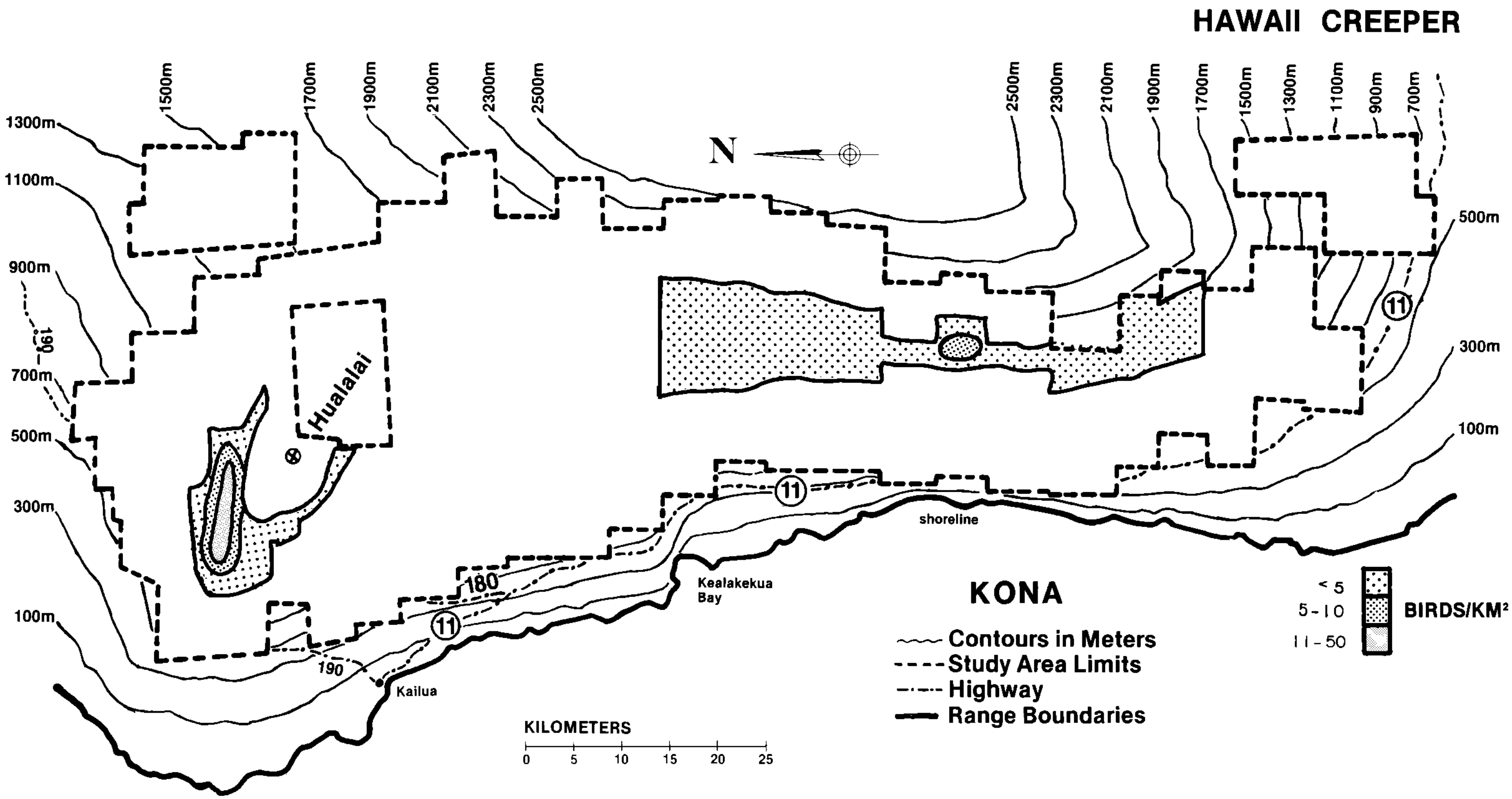

FIGURE 123. Distribution and abundance of the Hawaii Creeper in the Kona study area.
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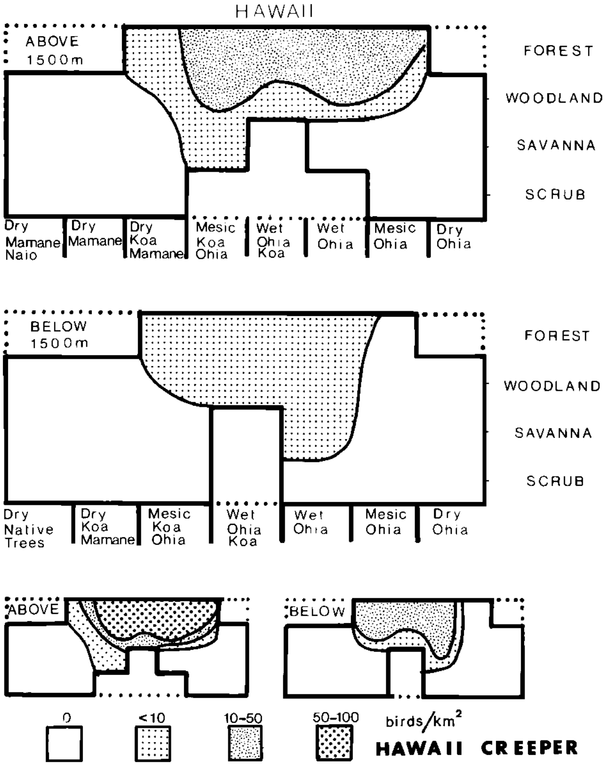

FIGURE 124. Habitat response graphs of the Hawaii Creeper. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

ers dropped from 26 in 1937 to 0 in 1939 and 1940, but no Japanese White-eyes were recorded during these years. If these data were typical for the year round, then other factors probably caused the decline of the species in this area. On the other hand, the results of our competition analysis (Mountainspring and Scott 1985) showed that densities of Hawaii Creepers and Japanese White-eyes were negatively related in the Hamakua study area, possibly reflecting gradual displacement of Hawaii Creepers through interspecific competition for food. An alternate explanation for these patterns is that the spread of avian disease caused the declines, and may be correlated with the spread of Japanese White-eyes.

Hawaii Creepers have four disjunct populations totalling 12,500 ± 2000 (95% CI) birds (Tables 10, 25, Figs. 121–123). About 2100 ± 1100 birds occur over nearly the whole length of Kau in both ohia and koa-ohia forests, and extend below 700 m elevation. A 27-km gap between the Kau population and the 10,000 ± 1600 birds in the Hamakua study area coincides with deforested habitat on the Kapapala Tract. In Hamakua, Hawaii Creepers are, overall, nearly five times more common in koa-ohia than in ohia. As in Kau, creepers extend to low elevations in Hamakua, particularly in stands with large old koa trees.

Two populations totalling 300 ± 150 (95% CI) birds inhabit Kona, primarily in koa-ohia forests. About 220 birds live in the koa-ohia forests on north Hualalai and extend down to 1100 m elevation. The central Kona population of only 75 birds is restricted to areas above 1500 m elevation. The two populations are separated by 35 km of open pasture.

Van Riper (1982) reported 11 Hawaii Creepers during 47 counts on Kohala Mountain in 1972, although these may have represented multiple records of as few as two birds (C. van Riper III, pers. comm.). We failed to find this species during our Kohala survey despite thorough familiarity with it. The probability of our missing a population of 100 birds is small (Table 12). Other recent observers have also failed to find the species in that area.

Hawaii Creepers occur from 700 to 2200 m elevation, but only in the wet forest of Kau and Hamakua are they found below 1100 m. Highest densities occur at 1500–1900 m in Kau and Hamakua. The habitat response graph shows that Hawaii Creepers are most common in the mesic and wet forests above 1500 m elevation (Fig. 124).

The regression models (Table 26) indicate that Hawaii Creepers are most common in wet, dense forests at higher elevations with more koa and less tree fern than average. Hawaii Creepers are positively associated with wetter areas in the Hamakua model. Elevation has positive terms in two models. The low significance of tree biomass, crown cover, and canopy height reflects the range of forest types occupied, although densities are higher in dense forests than in savannas or scrublands. Response to koa is positive in two models and negative in one. Response to understory and phenology variables is generally unimpressive. Passiflora has a negative response in Hamakua, but in Kona passiflora occurs in the north Hualalai refugium and yields a positive response. (A parallel case is seen with Akepa.)

Further insight into Hawaii Creeper habitat requirements is suggested by nest sites. In a five-year study involving nearly 20 person-years of field effort, Sakai and Johanos (1983) reported finding eight nests, or 1.62 nests/person-year, in an unlogged, ungrazed, closed canopy, mature koa-ohia forest, but only one nest, or 0.07 nests/person-year, in an adjacent open canopy koa-ohia forest that was grazed by cattle and logged for koa for many years. Their study suggests that the species prefers relatively undisturbed koa-ohia forests, and our data show that highest densities occur in areas least modified by logging and grazing.

MAUI CREEPER
Paroreomyza montana

MAUI CREEPER (*Paroreomyza montana*)

Maui Creepers, or Alauwahio, are aberrant honeycreepers bearing little similarity to the Hawaii or Kauai species (Pratt 1979, Berger 1981). They were originally present on East Maui, West Maui, and Lanai. Fossil records suggest that they once occurred on Molokai (Olson and James 1982b).

In the 1890s this species was ubiquitous in Lanai forests above 600 m elevation, abundant in the West Maui mountains even into guava scrub, and extremely abundant in the forests of East Maui (Perkins 1903). Munro (1944) saw a pair on Lanai in 1937, but that population is now extinct (Hirai 1978). The West Maui population was last reported at the turn of the century (Perkins 1903) and is now extinct. The probability of even small populations still occurring

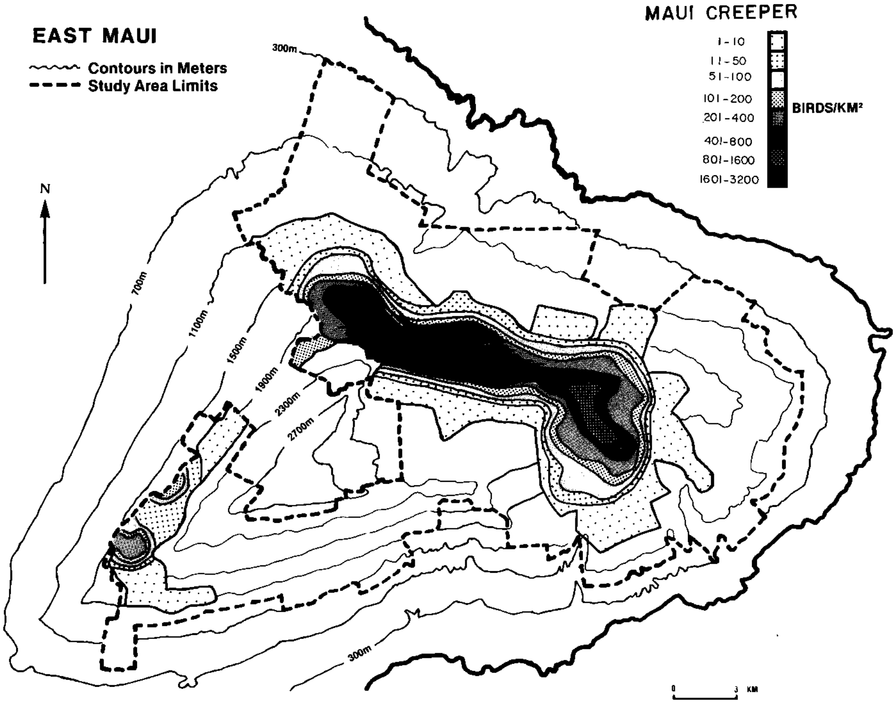

FIGURE 125. Distribution and abundance of the Maui Creeper in the East Maui study area.

on West Maui is small (Table 12). On East Maui, birds were considered "not uncommon" in 1928 (Munro 1944). In the 1960s they were common in upper elevation forests (Berger 1972). Scott and Sincock (1977) found them abundant in the Koolau Forest Reserve in 1975.

Maui Creepers feed on insects and nectar (Berger 1981) and use a wider variety of foraging substrates and maneuvers than Hawaii Creepers (Scott and Sincock 1977). They frequently glean insects from foliage and occasionally take nectar from understory plants (Carothers 1982). Their behavior resembles more nearly that of warblers (Parulinae) than that of creepers (Certhiidae) or nuthatches (Sittidae). Pratt (1979) noted the behavioral similarity to the Black-and-white Warbler (*Mniotilta varia*).

We found Maui Creepers abundant on East Maui, especially at higher elevations in the wet forests, with an estimated population of 35,000 ± 5000 (95% CI) (Tables 11, 25, Fig. 125). Birds are fairly common in high elevation areas of pine, eucalyptus, and other introduced trees at Hosmer Grove and Polipoli State Park. The Polipoli birds are confined entirely to a forest of introduced trees more than 15 km from suitable native habitat. The disjunct distribution reflects the unsuitability of most dry deforested habitats on Maui for this species.

In contrast to Hawaii Creepers, Maui Creepers occur in some savannas and scrublands (Fig. 126). Above 1500 m elevation, they occupy all habitats on the response graph, but are most common in mesic and wet ohia forests. Densities are much higher than those of Hawaii Creepers in similar vegetation types. Maui Creepers occur from 900 to 2500 m elevation and reach highest densities at 1500–2100 m.

The regression model (Table 26) shows that Maui Creepers are most common in dense, wet, high-elevation forests with few tree ferns. Densities are lower in areas with koa or mamane. The positive terms for ground cover and native grasses and the negative term for introduced herbs indicate association with forest interiors that are less damaged by feral pigs.

Maui Creepers are most often found in small flocks. Such flocks are of particular interest in management, because individual birds of three endangered species, Maui Parrotbills, Nukupuu, and Poo-uli, often join these flocks and feed together. On the western dry side of East Maui, far from the main range, we found widely scattered individual birds or family groups, indicating considerable ability of this rainforest species to disperse across extensive areas of dry scrub, grassland, and barren desert. It seems highly probable that if the habitat quality on leeward East Maui

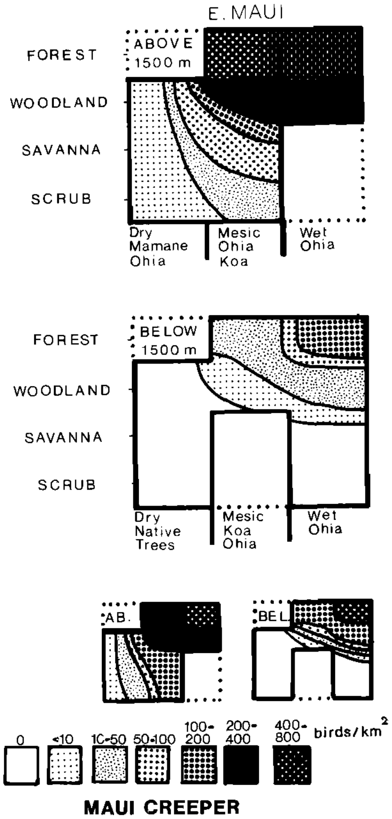

FIGURE 126. Habitat response graphs of the Maui Creeper. (Graphs give mean density above and below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

were improved, Maui Creepers would repopulate these areas.

The numbers and distribution of Maui Creepers suggest that they may be among the first birds to disappear if whatever factor limiting the distribution to upland forests becomes operational at higher elevations. The sharp drop-off of densities at lower elevations is quite striking and suggests that the species is very sensitive to a limiting factor with a mirror image distribution, possibly avian disease. Below 1400 m elevation densities decline drastically west of Waikamoi Stream. Densities on windward East Maui sharply delimit the refugium where the endangered passerines occur. The sharp drop-off of densities at 1600 m elevation in the Hana Forest Reserve parallels the range limits of the Maui Parrotbill and Crested Honeycreeper, suggesting a common limiting factor.

MOLOKAI CREEPER (*Paroreomyza flammea*)

This is the only species of creeper that shows marked sexual dimorphism in plumage. Males of this species are various shades of scarlet, and females are brown with some scarlet markings. Like other creeper species, they glean insects and other invertebrates from trunks and limbs of trees (Bryan 1908). Molokai Creepers are considerably larger than the other creepers.

Perkins (1903) characterized Molokai Creepers as widely distributed and common in the 1890s. Birds were common in 1907 but by the 1930s they were in danger of extinction (Munro 1944). Many have unsuccessfully searched for them since Munro's survey (Richardson 1949, Pratt 1974, Scott et al. 1977). Pekelo (1963a) reported several sightings from the rainforest on the west rim of Pelekunu Valley on the Ohialele Plateau (transect 4 area).

The Hawaiian name for this species, Kakawahie, meant "woodchopping" and was said to describe their chipping call. They were also said to be attracted to observers (Munro 1944). We assumed that the area surveyed at a station for this species was identical to that of the Maui Creeper and that if Molokai Creepers still existed, they would have occurred in any of the native forests we sampled. We failed to find this species, and it may now be extinct (Table 12).

AKEPA
Loxops coccineus

Akepa (*Loxops coccineus*)

Akepa were known from Hawaii, Maui, Oahu, and Kauai. The Kauai subspecies, also known as Ou-holowai, is particularly distinct and possibly a separate species (Pratt 1979, A.O.U. 1983). No fossils have been found yet (Olson and James 1982b). One desiccated specimen found in 1943 at the edge of Lake Waiau, elevation 3968 m, near the summit of Mauna Kea, probably represents a bird carried in a wind storm (Munro 1944). Akepa use their unusual asymmetric bill and jaw musculature (Richards and Bock 1973) to capture insects on koa and ohia by twisting apart ohia leaf buds, prying into woven-together koa phyllodes, and foraging among terminal leaf clusters (Perkins 1903).

On Hawaii in the 1890s, Akepa were "rare in most districts" but "comparatively common in the mixed ohia and koa forests on the north side of the Wailuku river at an altitude of [550 m] upwards; and in the koa forest of Kau" (Henshaw 1902). An elevation of 600 m was specified for 12 of 23 elevations recorded on specimen tags (Banko 1979). Perkins (1903) considered Akepa

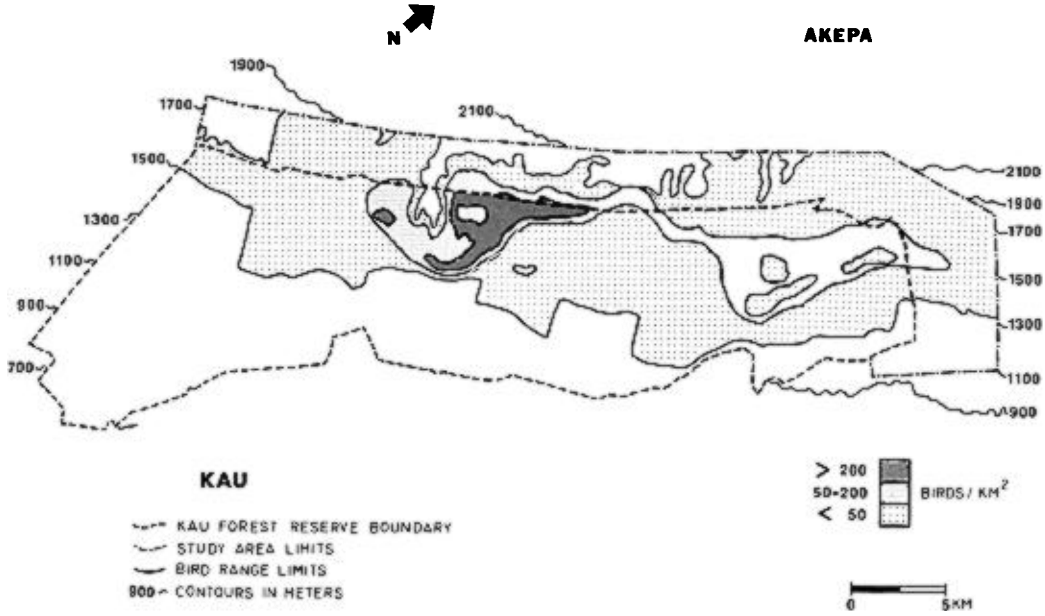

FIGURE 127. Distribution and abundance of the Akepa in the Kau study area.

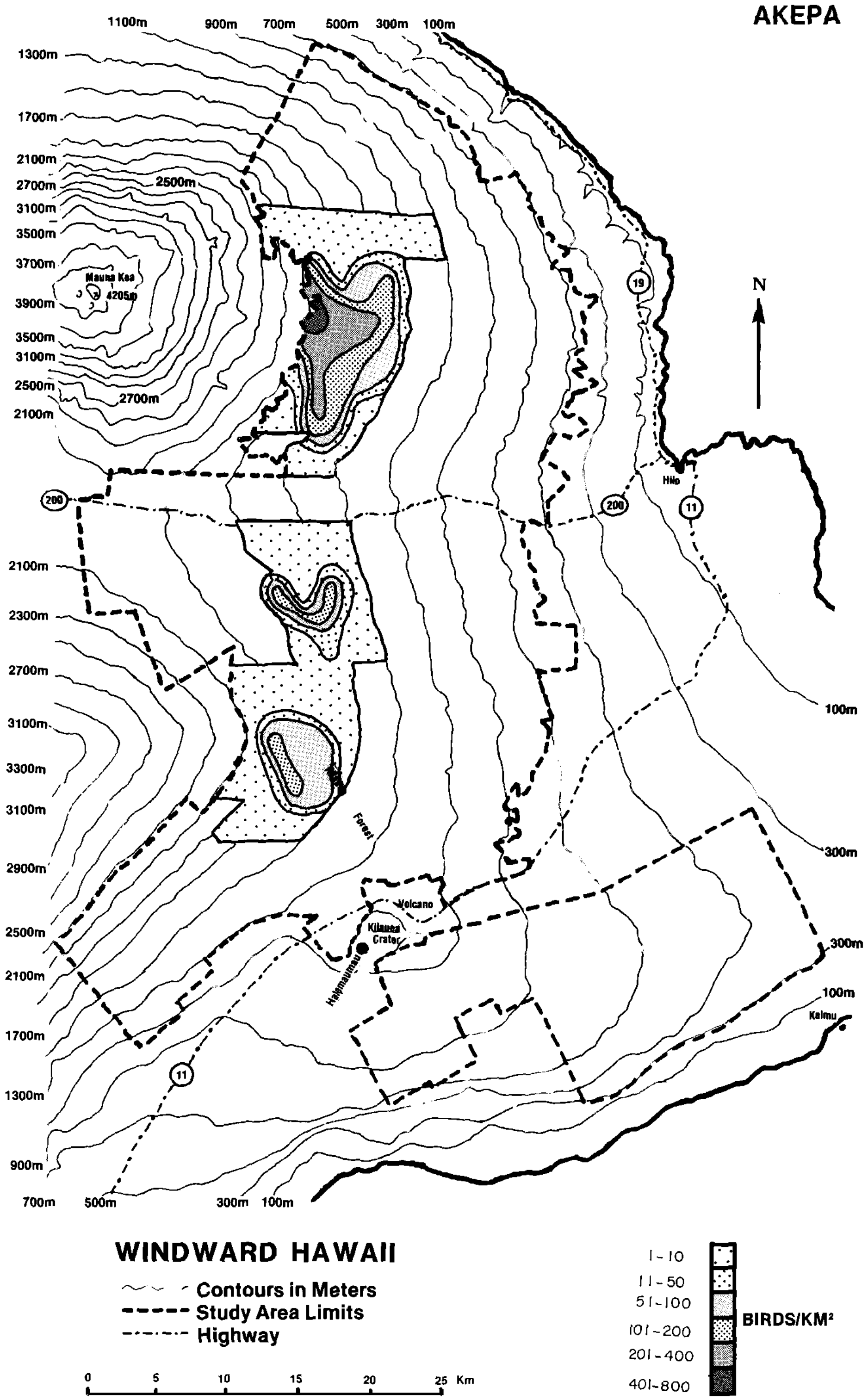

FIGURE 128. Distribution and abundance of the Akepa in the windward Hawaii study areas.

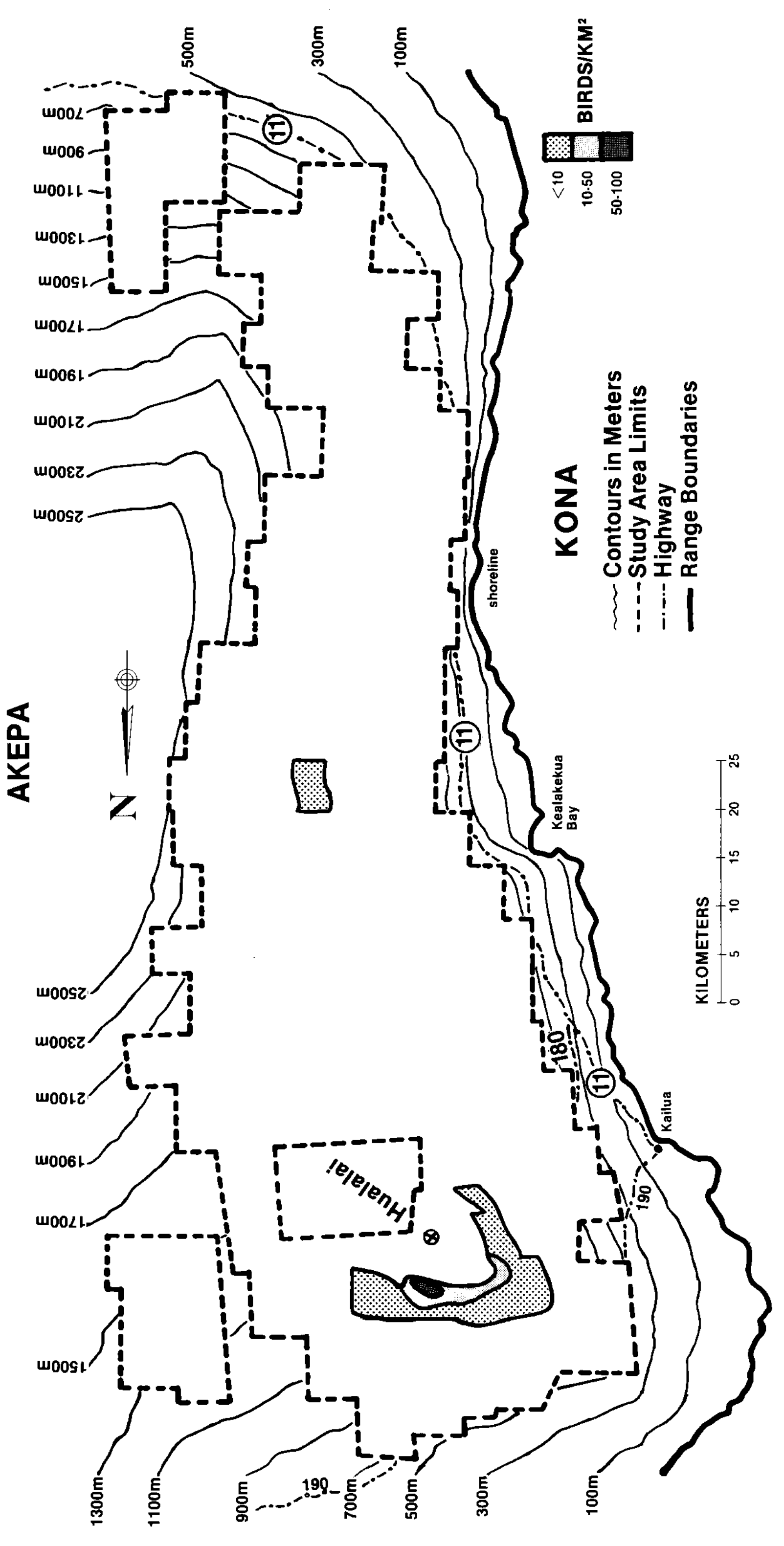

FIGURE 129. Distribution and abundance of the Akepa in the Kona study area.

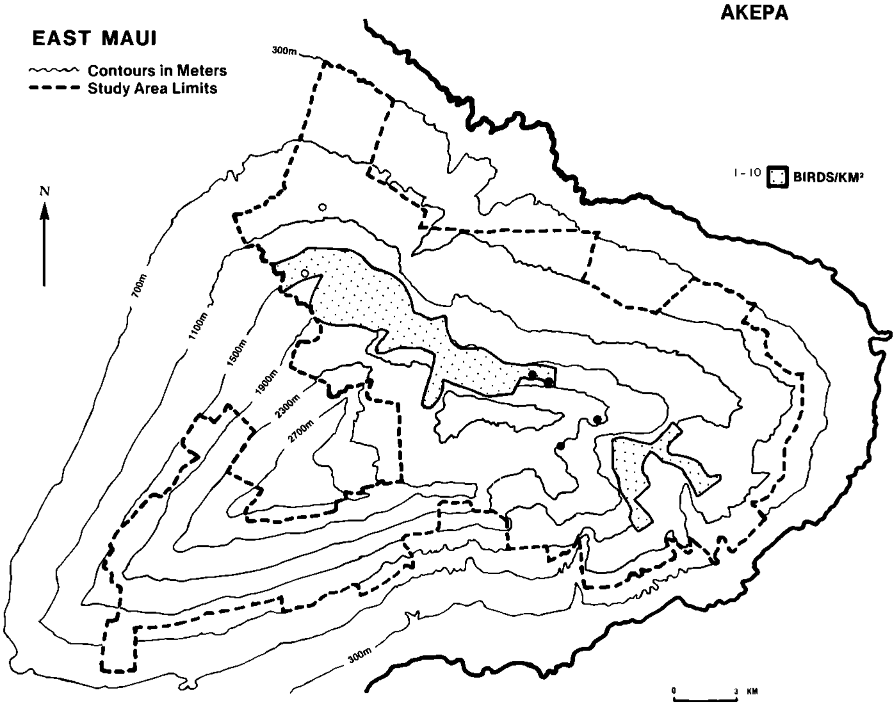

FIGURE 130. Distribution of Akepa in East Maui study area. (Birds recorded as incidentals during the HFBS are indicated by open circles; recent records by other observers are indicated by closed circles.)

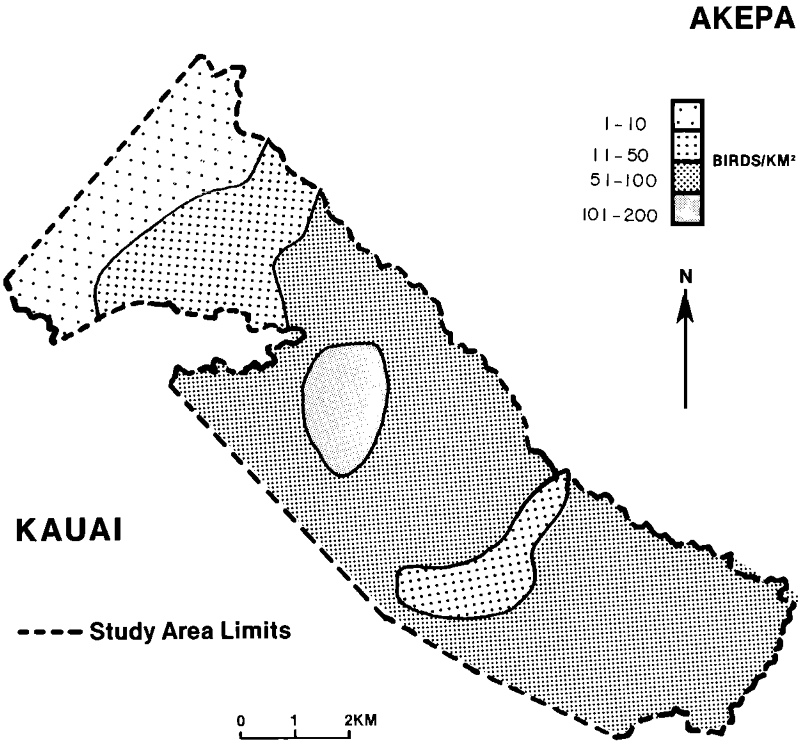

FIGURE 131. Distribution and abundance of the Akepa in the Kauai study area.

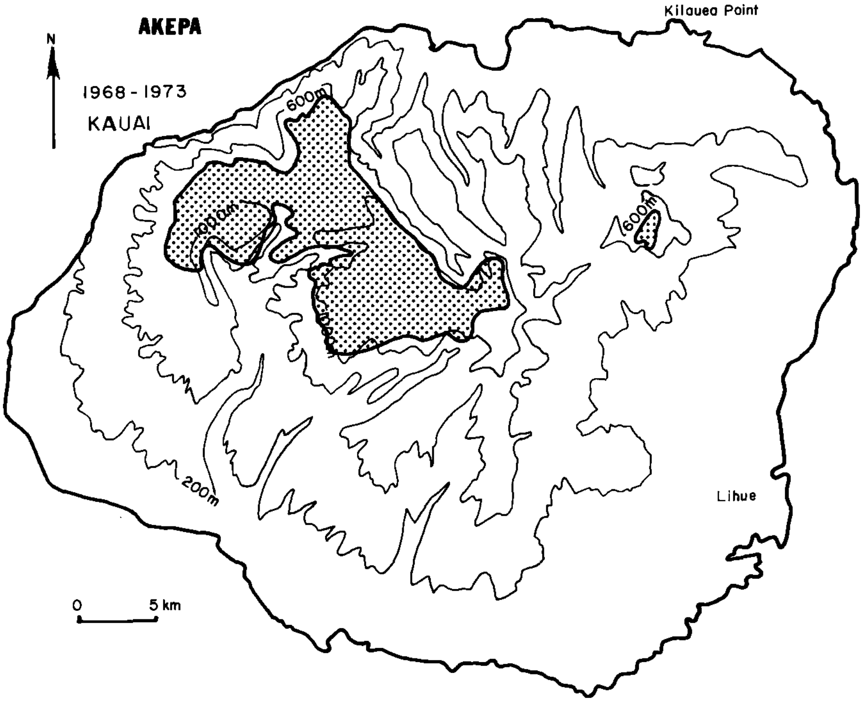

FIGURE 132. Range of the Akepa on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

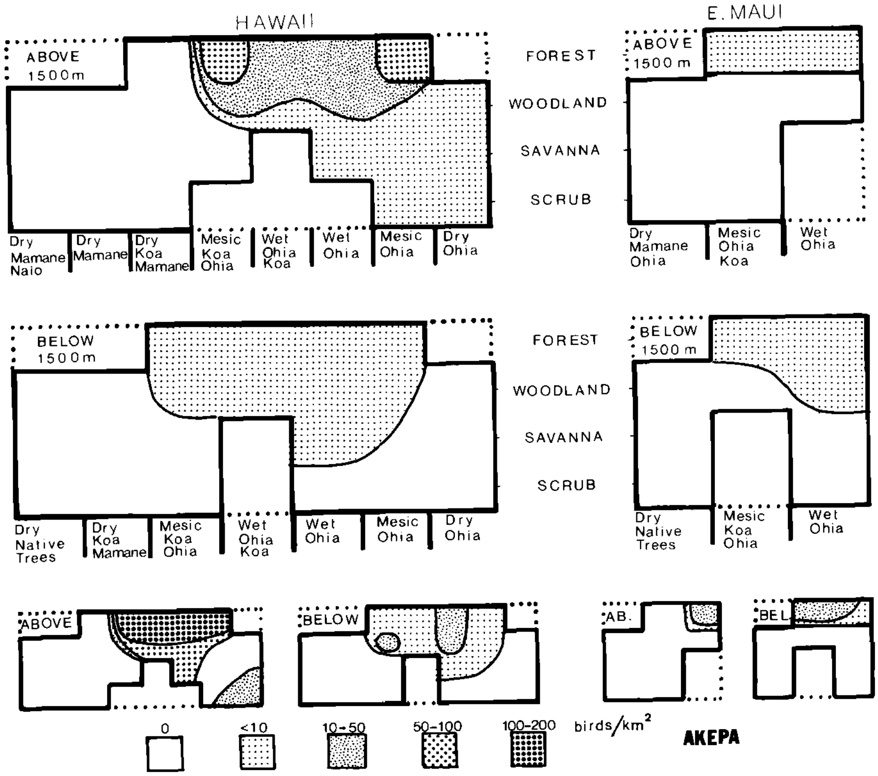

FIGURE 133. Habitat response graphs of the Akepa. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 27
DENSITY [MEAN (SE)] OF THE AKEPA AND CRESTED HONEYCREEPER (AKOHEKOHE) BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Akepa					Crested Honeycreeper
	Kau	Hamakua	Kona	E. Maui	Kauai	E. Maui
Elevation						
100–300 m	···	···	···	···	···	···
300–500 m	···	0	0	0	···	0
500–700 m	0	0	0	0	···	0
700–900 m	0	0	0	0	···	0
900–1100 m	0	0	0	0	···	0
1100–1300 m	11 (8)	0	0	14 (14)	68 (9)	0
1300–1500 m	14 (6)	17 (5)	19 (8)	8 (8)	66 (9)	31 (31)
1500–1700 m	30 (7)	32 (6)	44 (11)	15 (14)	···	64 (12)
1700–1900 m	77 (17)	83 (19)	41 (16)	+ (+)	···	116 (17)
1900–2100 m	24 (11)	77 (33)	0	+ (+)	···	80 (16)
2100–2300 m	+ (+)	0	0	0	···	6 (5)
2300–2500 m	···	···	0	0	···	+ (+)
2500–2700 m	···	···	···	0	···	0
2700–2900 m	···	···	···	0	···	0
2900–3100 m	···	···	···	···	···	···
Habitat						
Ohia	50 (9)	15 (4)	0	10 (7)	68 (6)	92 (9)
Koa-ohia	17 (4)	67 (10)	40 (8)	14 (14)	···	25 (15)
Koa-mamane	···	0	0	···	···	···
Mamane-naio	···	···	0	···	···	···
Mamane	···	···	0	0	···	0
Other natives	···	0	0	0	···	0
Intro. trees	···	+ (+)	0	0	···	0
Treeless	0	0	0	0	0	10 (5)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

very widely distributed and abundant in the Kau, Hilo, Kohala, and parts of the Kona districts. Richards and Baldwin (1953) reported them locally common at higher elevations on eastern slopes of Mauna Loa and scattered as low as 600 m. Berger (1972) stated that Hawaii Akepa were rare. In Hawaii Volcanoes National Park, Perkins (*in* Banko and Banko 1980) found as many as 12 birds in one koa tree in the vicinity of Kilauea Crater in the 1890s. By the 1940s, Akepa were rare in the national park and occurred only in the Ainahou area in dry ohia woodland at 800 m elevation (Baldwin 1953), and by the 1970s they were gone from the national park (Conant 1975, Banko and Banko 1980).

We found Akepa on Hawaii, Maui, and Kauai (Figs. 127–131). The three Hawaii populations are widely separated and total 14,000 ± 2500 (95% CI) birds (Tables 10, 27). Highest densities of 300 birds/km^2 occur in subalpine ohia woodland in Kau. The 5300 ± 1500 birds of that population are well distributed over the study area, except for the south portion. The 7900 ± 1800 birds in Hamakua show an incipient patchy distribution, with a hiatus in the Saddle Road area. Akepa are also absent from the northern fifth of the Hamakua study area. In Kona, 99% of the 660 ± 250 birds inhabit the koa-ohia forests on north Hualalai; there was one incidental observation of a bird in central Kona. Akepa occur from 1100 to 2100 m elevation on Hawaii, with highest densities at 1500–1900 m in Kau and Kona, and at 1500–2100 m in Hamakua. We failed to find Akepa in the Kohala study area (Table 12), as did van Riper (1982).

Akepa were locally abundant on East Maui in the 1890s (Perkins 1903). Munro failed to find them in 1928 and again in 1936. Maui Akepa have been rarely reported since the turn of the century (Richards and Baldwin 1953, Casey 1973, Scott and Sincock 1977). All observers prior to our survey considered it to be very rare (Berger 1972). Perkins (1903) did not find Akepa in the West Maui Mountains. We estimated the Maui population at 230 ± 290 (95% CI) birds with a patchy, relict distribution. Maui Akepa occur from 1100 to 2100 m elevation in ohia and koa-ohia forests, with several records in and west of Waikamoi watershed. An undetected Akepa population may occur above 1500 m elevation

TABLE 28

REGRESSION MODELS FOR HABITAT RESPONSE OF THE AKEPA AND CRESTED HONEYCREEPER (AKOHEKOHE)[a]

	Akepa				Crested Honeycreeper
	Kau	Hamakua	Kona	Kauai	Maui
R^2	0.11*	0.16*	0.11*	0.08	0.34*
Moisture	···	5.7*	···	X	8.9*
Elevation	···	−3.7*	2.5	···	···
(Elevation)^2	10.0*	6.0*	···	···	11.7*
Tree biomass	···	−3.0	···	···	8.1*
(Tree biomass)^2	···	3.3	···	···	···
Crown cover	···	···	···	···	···
Canopy height	6.7*	···	···	···	···
Koa	−2.7	3.4*	2.4	X	−4.5*
Ohia	···	···	2.6	X	···
Naio	X	X	5.4*	X	X
Mamane	X	−5.8*	−2.8	X	−4.6*
Intro. trees	X	···	···	X	−4.2*
Shrub cover	···	···	−2.6	−2.4	···
Ground cover	···	2.7	···	···	···
Native shrubs	···	7.2*	···	···	−2.2
Intro. shrubs	X	2.5	···	···	···
Ground ferns	X	X	7.2*	···	···
Matted ferns	···	···	···	−2.4	−6.7*
Tree ferns	···	X	−4.5*	···	−4.3*
Ieie	X	X	···	···	···
Passiflora	X	−6.0*	10.5*	X	···
Native herbs	X	X	···	···	−4.8*
Intro. herbs	X	X	−3.3	···	···
Native grasses	···	−3.0*	···	···	3.4*
Intro. grasses	···	−2.7*	···	···	···
Ohia flowers	···	···	···	···	4.8*
Olapa fruit	···	···	···	···	2.7
Mamane flowers	X	X	X	X	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

in the koa-ohia forest above Manawainui Valley. Our survey failed to find Akepa in the area of the putative 1950 record on the dry south side of East Maui, 3 km east of Lualailua Hills (Richards and Baldwin 1953).

Kauai Akepa were common in the 1890s "over a large part of the high plateau" (Perkins 1903). Richardson and Bowles (1964) noted that they were fairly common in higher elevation forests. We estimated 1700 ± 300 (95% CI) Akepa in the Alakai Swamp study area, with far higher densities in the remote interior than towards Kokee State Park. Sincock et al. (1984) estimated a population of 5100 ± 1700 for Kauai, with 600 ± 200 birds in our study area. Population levels should be monitored to determine whether a long-term decline is occurring as for Kauai Creeper, although the data suggest otherwise. During the 1968–1973 survey Akepa occurred on the northwest slopes of Waimea Canyon, Kokee State Park, the Na Pali plateaux, the Alakai Swamp, and the Makaleha Mountains (Fig. 132).

Oahu Akepa were apparently rare and locally distributed in the 1890s (Perkins 1903). They were considered extinct by Berger (1981), but in 1976 Shallenberger and Vaughn (1978) reported a probable sighting of a female Akepa in the central Koolau range near the headwaters of Kaukonahua Stream.

Akepa are most common on Hawaii above 1500 m elevation in tall, mesic to wet forests, and are absent from mamane woodland (Tables 27, 28, Fig. 133). The Kauai regression model indicates little response within the fairly uniform Alakai study area. There are too few Maui Akepa sightings to construct a regression model.

Akepa response to understory elements varies between study areas (Table 28). The Kona population is associated with ground ferns and passiflora, but the passiflora infestation in Hamakua is associated with lower Akepa numbers. This difference appears to be due to the fortuitous occurrence of passiflora in the north Hualalai refugium. Native shrubs have a strong positive response in the Hamakua regression model, but the Kau model has no response to any understory element. The absence of ohia flowers and olapa fruit in the models probably reflects the mainly insectivorous diet.

Perkins (1903) found Akepa widespread in koa and ohia forests on Hawaii and Maui, and Sincock et al. (1984) found them in these forest types on Kauai. This is reflected by the positive terms for koa in the Hamakua and Kona models, and by the location of a majority of Maui records in koa habitat. In Kau, however, Akepa have higher densities in ohia than in koa. The Hawaii subspecies nests in cavities; mature trees and snags may be an essential habitat component (Sincock and Scott 1980, Collins 1984).

ULA-AI-HAWANE (*Ciridops anna*)

Ula-ai-hawane are among the least known historically of the Hawaiian forest birds, and only five specimens were collected. This species is known to have occurred only on the island of Hawaii in the Kona, Hilo, and Kohala districts (Perkins 1903). Fossil records show that congeners formerly occurred on Kauai, Molokai, and Oahu (Olson and James 1982b). This species fed on the blossoms and unripe fruit of loulu palms (*Pritchardia* spp.), according to secondhand reports (Perkins 1903); however, the stomach of the sole alcoholic specimen was filled with foliage insects (S. L. Olson, pers. comm.). Nothing more is known of the behavior. The hind limb has a peculiar stout morphology (Olson and James 1982b), and conceivably these birds were adapted to foraging for insects among the foliage of *Pritchardia* palms, much like the palm creeper *Berlepschia rikeri* in the Amazon Basin forages on *Mauritia* palms (Vaurie 1980).

Ula-ai-hawane were quite rare even when first collected in 1859; they have not been seen since 1892 and are probably extinct. Munro (1944) had a possible sighting on Kohala Mountain in 1937. Extensive searches of the Kohala area by us and others (van Riper 1973a, 1982) have failed to yield any evidence that they still exist. We assumed that the effective detection distances for this species (30 m) and the Apapane were similar (Table 12).

IIWI
Vestiaria coccinea

Iiwi (*Vestiaria coccinea*)

The vermilion plumage and sharply decurved, orange bill of Iiwi are spectacular. In the 1890s Iiwi were one of the most abundant and widespread of the native birds (Wilson and Evans 1890–1899, Henshaw 1902, Perkins 1903). Fossils are known only from Oahu (Olson and James 1982b).

Munro (1944) stated that Iiwi, formerly very numerous, were greatly reduced by the 1940s and were absent on Molokai and Lanai. They became extinct on Lanai by 1929 (Munro 1944) and are currently very rare on Oahu (Shallenberger and Vaughn 1978) and Molokai (Pratt 1974, Scott et al. 1977). In Hawaii Volcanoes National Park, Iiwi were fairly common in ohia rainforest and koa-ohia parkland in the 1940s (Baldwin 1953); by the 1970s, occurrences were less frequent below 1300 m elevation but more frequent in koa-ohia parkland at 1700 m (possibly reflecting habitat regeneration since the halt of grazing in the 1940s) (Conant 1975, Banko and Banko 1980).

We found Iiwi in all study areas except Lanai (Tables 10, 11, 29, Figs. 134–142). On Hawaii, Iiwi comprise one or perhaps two populations, depending on the degree to which birds travel across the Waimea Plains. The main population of 340,000 ± 12,000 (95% CI) birds forms a virtually continuous band from the Mauna Kea, Hamakua, and Kipukas study areas to the Kau and Kona study areas; 88% of these birds occur in Hamakua. In the Kapapala Tract, the Kahuku Tract, and around Puu Lehua, deforested areas have low densities and incipient hiatuses.

Iiwi occur at greatly reduced densities below 1000 m elevation, except in Kona where moderate densities occur as low as 300 m. Iiwi occur as low as 700 m in Hamakua at the north end of the study area in old growth koa-ohia forest and areas with exceptional ohia bloom. About 200 Iiwi occur in the Puna study area. Although Iiwi breed on Kohala Mountain (van Riper 1982) and the satellite population of 800 ± 600 (95% CI) birds there may be a deme separate from the main population, it is also possible that all low elevation Iiwi populations on Hawaii and Maui

TABLE 29
DENSITY [MEAN (SE)] OF THE IIWI BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Kauai
Elevation											
100–300 m	···	···	···	···	···	···	···	···	···	0	···
300–500 m	···	0	0	···	82 (24)	···	0	0	···	0	···
500–700 m	0	0	0	···	46 (10)	···	0	56 (19)	0	0	···
700–900 m	26 (14)	35 (9)	1 (1)	···	49 (8)	···	0	50 (11)	+ (+)	0	···
900–1100 m	46 (14)	99 (17)	2 (2)	···	56 (6)	···	0	54 (9)	5 (5)	7 (4)	···
1100–1300 m	68 (11)	119 (7)	4 (4)	0	68 (7)	···	9 (4)	111 (15)	28 (14)	2 (1)	202 (13)
1300–1500 m	199 (14)	365 (17)	···	13 (7)	84 (8)	···	21 (11)	155 (18)	6 (6)	10 (10)	264 (15)
1500–1700 m	414 (25)	638 (34)	···	49 (11)	153 (11)	···	24 (24)	151 (18)	+ (+)	···	···
1700–1900 m	495 (36)	612 (44)	···	32 (8)	81 (10)	···	···	176 (22)	+ (+)	···	···
1900–2100 m	155 (28)	332 (39)	···	7 (4)	34 (7)	0	···	143 (28)	···	···	···
2100–2300 m	25 (25)	57 (30)	···	+ (+)	7 (2)	0	···	11 (7)	···	···	···
2300–2500 m	···	···	···	···	+ (+)	+ (+)	···	+ (+)	···	···	···
2500–2700 m	···	···	···	···	···	25 (11)	···	+ (+)	···	···	···
2700–2900 m	···	···	···	···	···	+ (+)	···	0	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···
Habitat											
Ohia	190 (13)	197 (7)	2 (1)	10 (4)	54 (3)	···	15 (6)	128 (8)	13 (6)	4 (2)	232 (10)
Koa-ohia	328 (20)	518 (24)	···	120 (28)	125 (7)	···	···	82 (12)	···	···	···
Koa-mamane	···	283 (61)	···	41 (8)	40 (8)	···	···	···	···	···	···
Mamane-naio	···	···	···	···	178 (178)	0	···	···	···	···	···
Mamane	···	···	···	···	20 (4)	11 (5)	···	0	···	···	···
Other natives	···	42 (11)	···	78 (78)	0	···	···	26 (26)	···	0	···
Intro. trees	···	338 (127)	···	···	226 (42)	···	31 (31)	24 (11)	0	0	···
Treeless	0	0	0	10 (1)	5 (2)	···	···	7 (3)	+ (+)	0	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

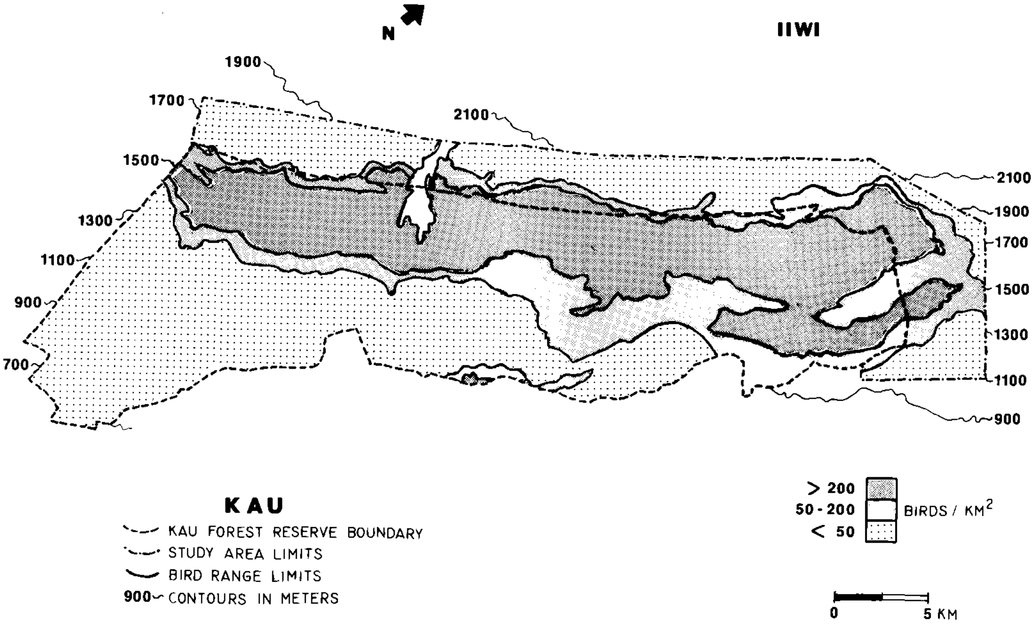

FIGURE 134. Distribution and abundance of the Iiwi in the Kau study area.

are sustained primarily by recruitment of migrants from higher elevations. On Hawaii, Iiwi range from 300 to 2900 m elevation and attain greatest densities at 1300–1900 m.

Mass movements between areas are undertaken by Iiwi in search of flowering plants such as ohia, mamane, and mountain apple (Henshaw 1902, Perkins 1903, Baldwin 1953). Birds on Mauna Kea probably make daily excursions from lower elevations to feed on nectar. In January 1979 hundreds of migrants ("bombers") were seen moving up at dawn from mid-elevation koa-ohia forests in the Hamakua study area to mamane woodland in bloom on Mauna Kea (C. B. Kepler and J. M. Scott, pers. observ.). Although Iiwi were rare on the southwest slopes of Mauna Kea during our 1983 survey, in good flowering years they invade these areas too (J. M. Scott, pers. observ.). Iiwi in the Kipukas study area also seem to move opportunistically into areas with mamane or ohia bloom (see Baldwin 1953, Pimm and Pimm 1982).

The 19,000 ± 2000 (95% CI) birds on East Maui show a sharp drop-off below 1100 m elevation. Mass movements are less pronounced on Maui than on Hawaii, but local concentrations of Iiwi and Apapane are associated with eucalyptus bloom in Hosmer Grove and Polipoli State Park, and with mamane bloom in Hosmer Grove and Haleakala Crater near Paliku. On West Maui 180 ± 150 Iiwi represent a localized, relict population in the vicinity of the Kaulalewelewe Ridge. Incidental observations by many observers over the past 20 years suggest that this population is relatively stable.

On Molokai a population of 80 ± 65 (95% CI) Iiwi has a relict distribution in two areas, Olokui Plateau and Kamakou Preserve. Iiwi are absent from the valleys and confined to ridges and cliffs.

On Kauai our estimate of 5400 ± 500 (95% CI) Iiwi in the Alakai study area suggests a fair-sized population that has perhaps declined from the 7800 ± 2300 birds estimated for that area in 1968–1973 (J. L. Sincock, pers. comm.). Sincock et al. (1984) estimated a total population of 26,000 ± 6000 birds on Kauai. The 1968–1973 range included the area west of Waimea Canyon, Kokee State Park, the Na Pali plateaux, the Alakai Swamp, Kapalaoa Ridge, and Namolokama Mountain (Fig. 143).

Iiwi feed primarily on flower nectar and foliage insects (Henshaw 1902, Perkins 1903, Baldwin 1953, Ralph et al. 1980, Carothers 1982, Pimm and Pimm 1982). The markedly decurved bill perfectly fits the decurved flowers of several lobeliads. Perkins (1903), later corroborated by Spieth (1966), reported that Iiwi feed frequently on lobeliads such as *Clermontia arborescens.* Although lobeliads are not obligately fertilized by honeycreepers (Rock 1919, Spieth 1966), the morphological adaptation of Iiwi points to a long-term association that may have been important when lobeliads were dominant understory elements, before the impact of feral ungulates. This rela-

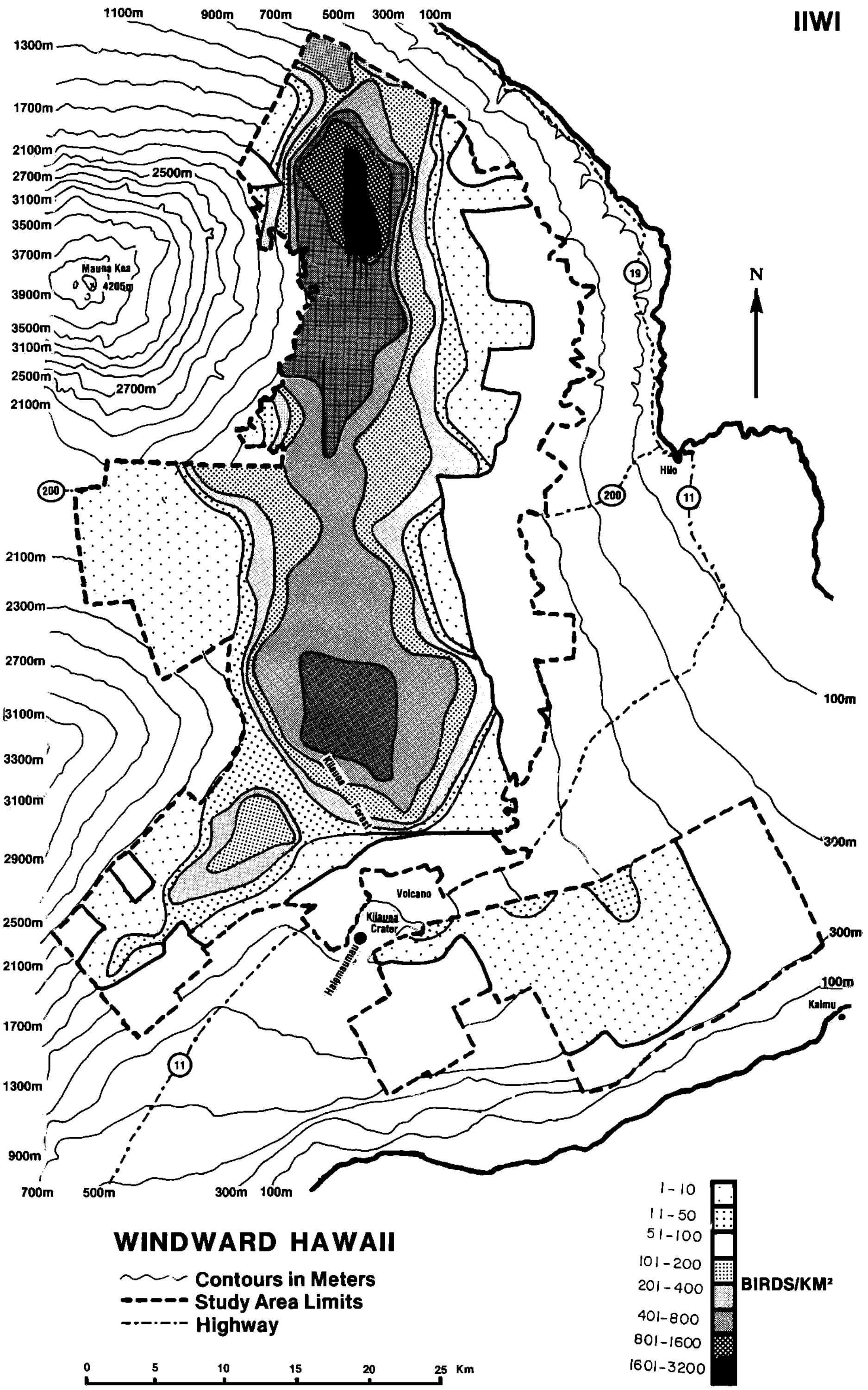

FIGURE 135. Distribution and abundance of the Iiwi in the windward Hawaii study areas.

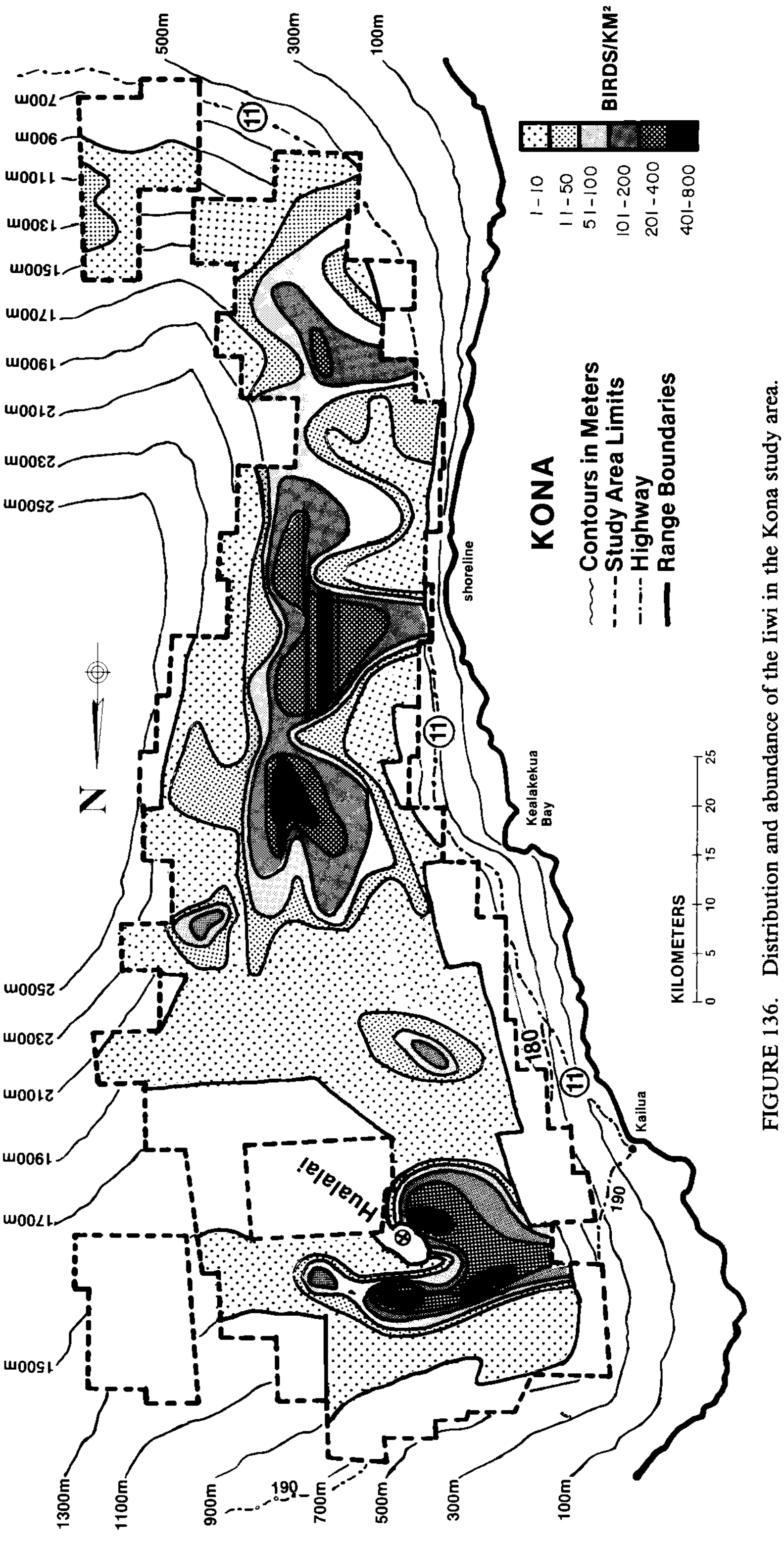

FIGURE 136. Distribution and abundance of the Iiwi in the Kona study area.

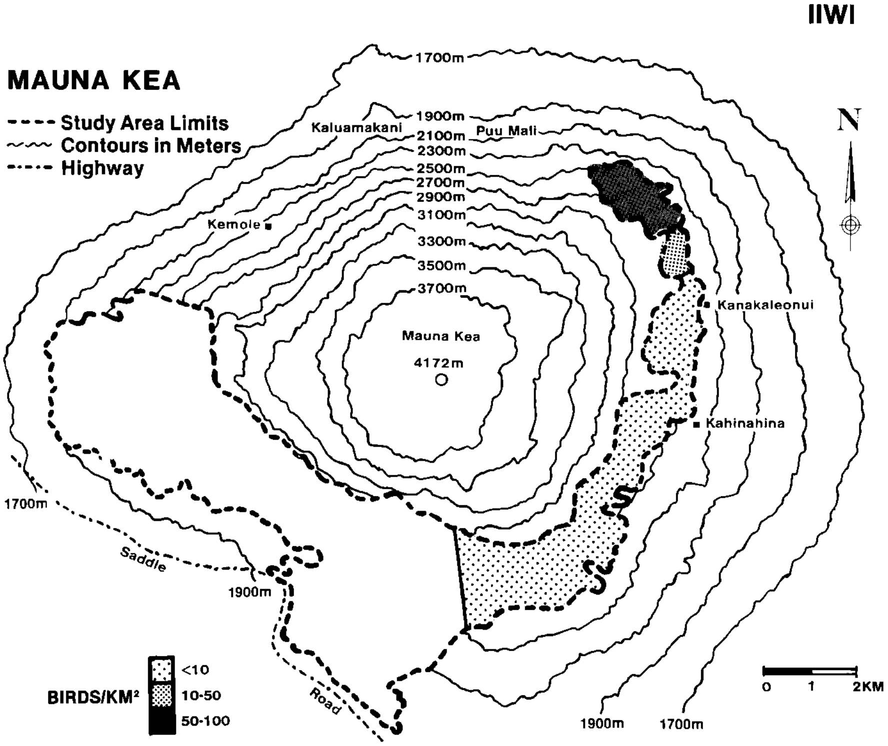

FIGURE 137. Distribution and abundance of the Iiwi in the Mauna Kea study area.

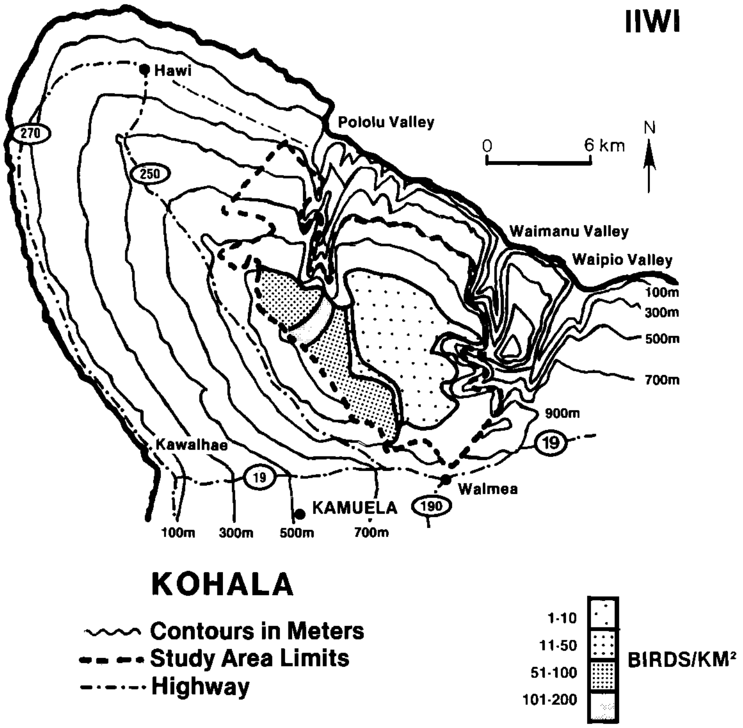

FIGURE 138. Distribution and abundance of the Iiwi in the Kohala study area.

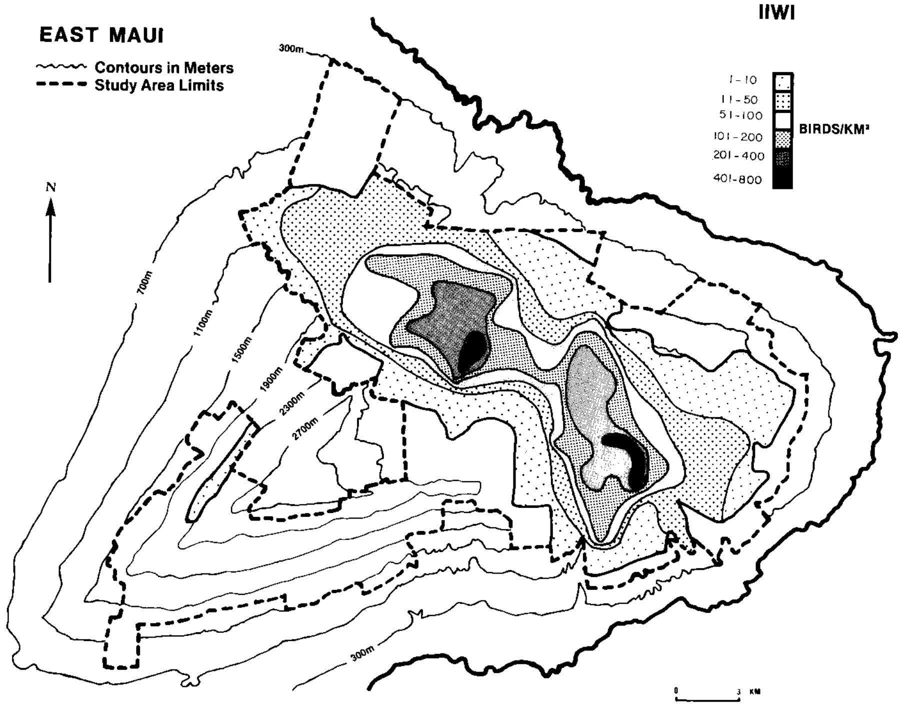

FIGURE 139. Distribution and abundance of the Iiwi in the East Maui study area.

tionship may predate the rise of ohia as a dominant tree, given the putatively greater antiquity of Hawaiian lobeliads (Perkins 1903:403).

The habitat response graphs show that Iiwi are widely distributed on Hawaii and absent only in areas with low rainfall (left end of response graphs, Fig. 144). Iiwi utilize dry mamane and mamane-naio woodlands when they are in bloom. Similar use may be made of other xerophytic native trees (e.g., wiliwili), but only extensive sampling on a seasonal basis would reveal this. Densities are lower below 1500 m elevation on both Maui and Hawaii. Densities on Maui are generally lower than in similar vegetation types on Hawaii. Iiwi are most abundant in mesic to wet forests at higher elevations.

Higher densities are associated with wetter habitat in four regression models (Table 30). In most models a strong response to elevation is evident. The poor fit of the Kauai regression model appears to indicate sampling within a homogeneous cluster. Iiwi generally respond positively to forest development. Iiwi are strikingly associated with passiflora, particularly banana poka. They also respond positively to such other diet items as ohia flowers, olapa fruit, and mamane flowers.

The regression models show that Iiwi have a much weaker response to ohia flowers than do Apapane. This may reflect that Iiwi are less adapted morphologically than Apapane to feed on ohia, although territorial spacing may partly obscure the response. Carpenter and MacMillen (1976) noted that Iiwi are more dependent on nectar than Apapane, and establish feeding territories in the forest interior at moderate densities of ohia flowers. Flocks of Iiwi and Apapane occasionally make towering flights to 100 m or higher, which may help to identify areas with high bloom intensity, as the flowering crowns of ohia and mamane are conspicuous from several kilometers (Perkins 1903).

HAWAII MAMO (*Drepanis pacifica*)

Hawaii Mamo were magnificent, mostly black birds whose yellow feathers were avidly sought by Hawaiians for the construction of feathered war cloaks (ahuula) for ruling chiefs (Brigham 1899). Kamehameha I had a cloak of pure mamo feathers, but cloaks made after Western contact for lesser royalty used oo feathers (Brigham 1899).

Restricted to the island of Hawaii, Hawaii Mamo were first collected in 1778 or 1779 (Stresemann 1950) and last reported in 1899 (Henshaw 1902). Following the great lava flow of 1880 above Hilo, a considerable number were shot for their feathers, but by the 1890s they were extremely rare (Perkins 1903). Hawaii Mamo had a wide range including most leeward and wind-

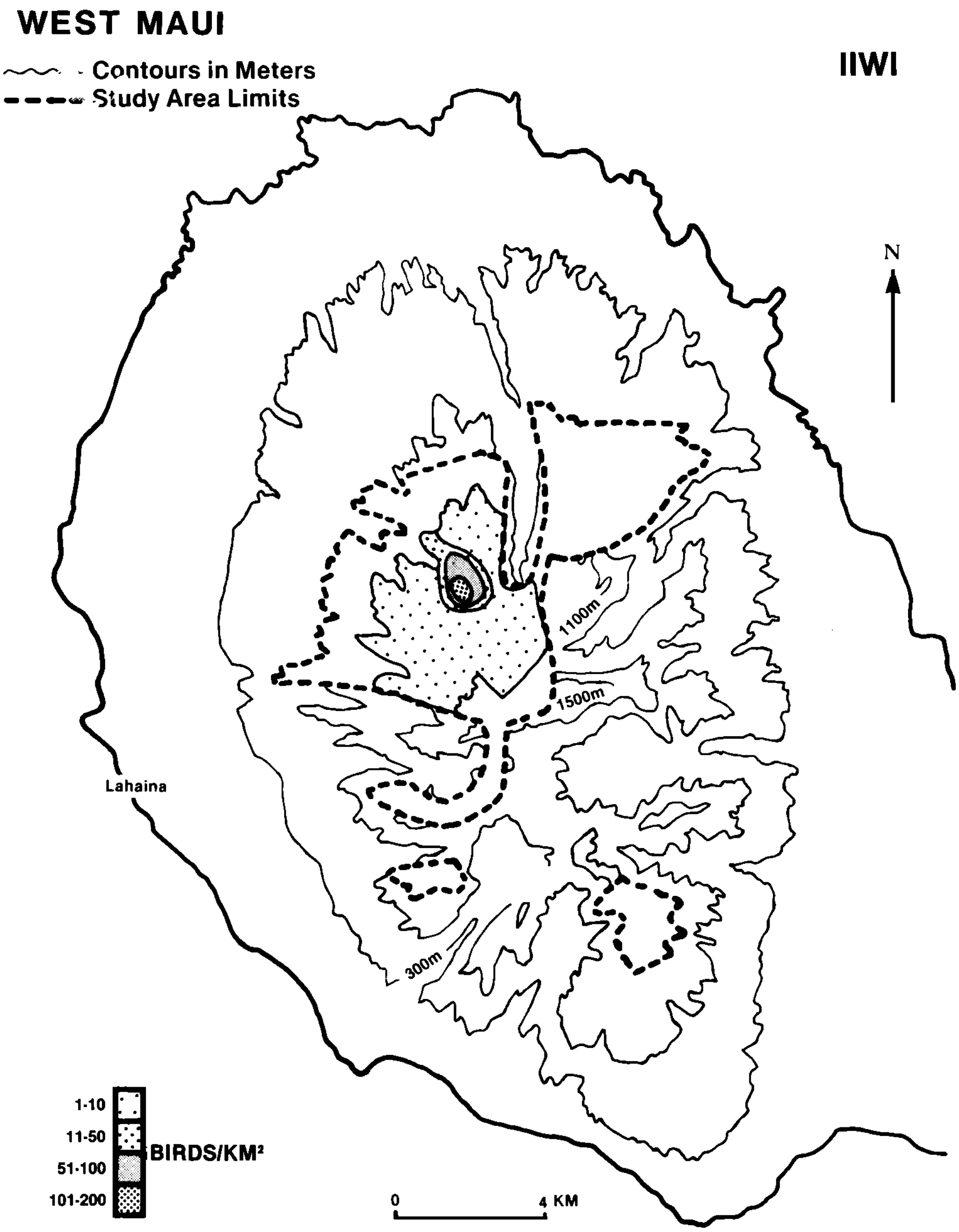

FIGURE 140. Distribution and abundance of the Iiwi in the West Maui study area.

ward forests and Kohala Mountain (Perkins 1903).

Hawaii Mamo used their long decurved bill to feed extensively on the nectar of lobeliads, mamane, ohia, and loulu palms (Perkins 1903), and on insects (Henshaw 1902). They were aggressive, frequently displacing other nectarivores.

The call was described as a single rather long and plaintive note. Henshaw (1902) said he watched birds for more than two hours without hearing them call or sing. We assumed that Hawaii Mamo were less conspicuous than Hawaii Oo (effective detection distance of 40 m), thus the lower probability of detecting this species during our survey (Table 12). Nevertheless, it is extremely doubtful that this species still survives.

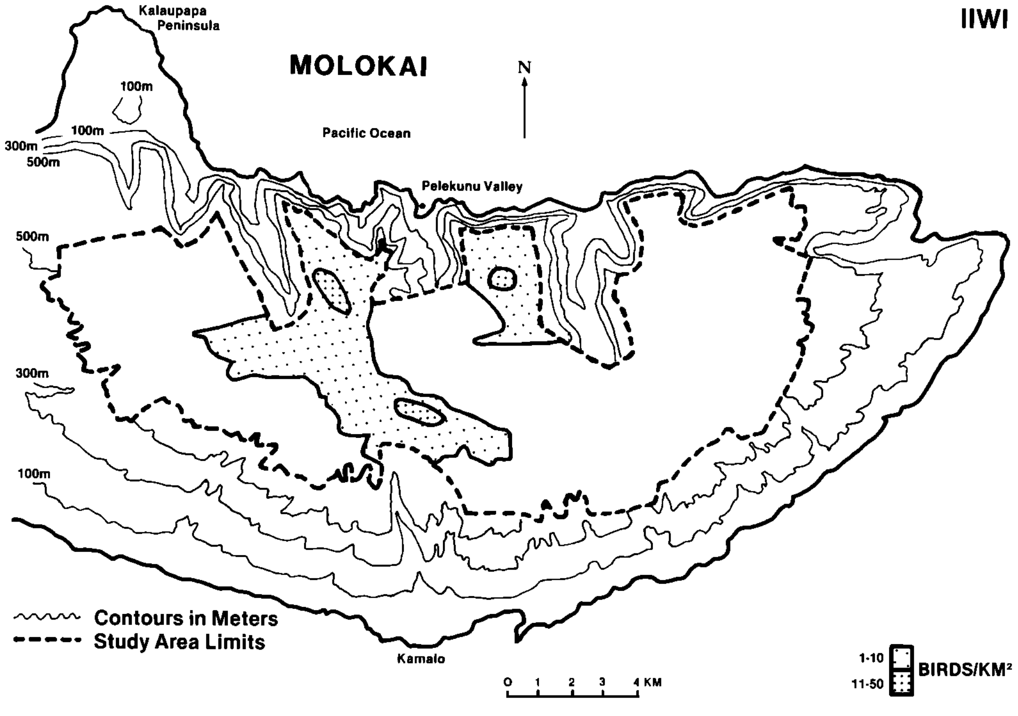

FIGURE 141. Distribution and abundance of the Iiwi in the Molokai study area.

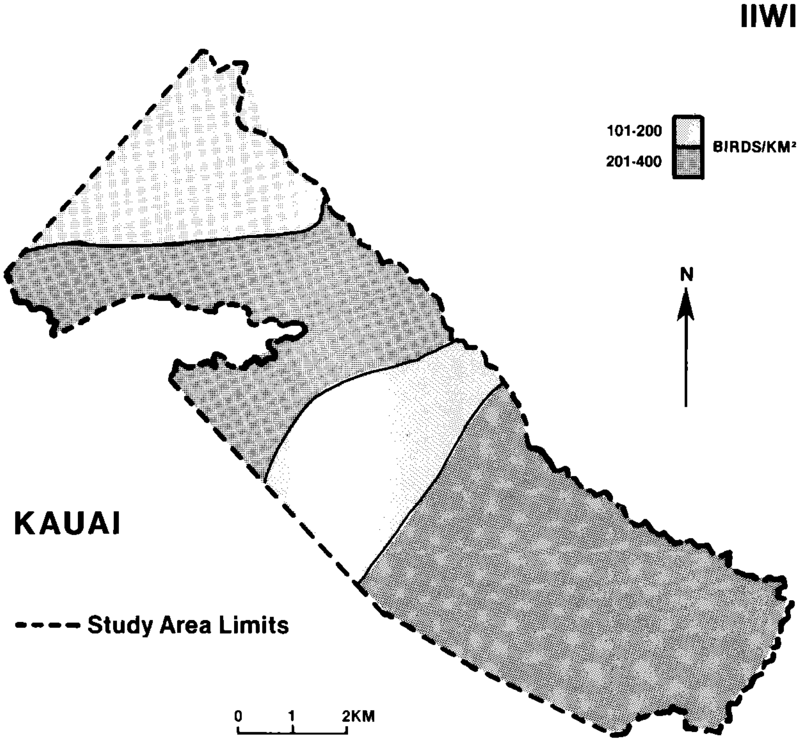

FIGURE 142. Distribution and abundance of the Iiwi in the Kauai study area.

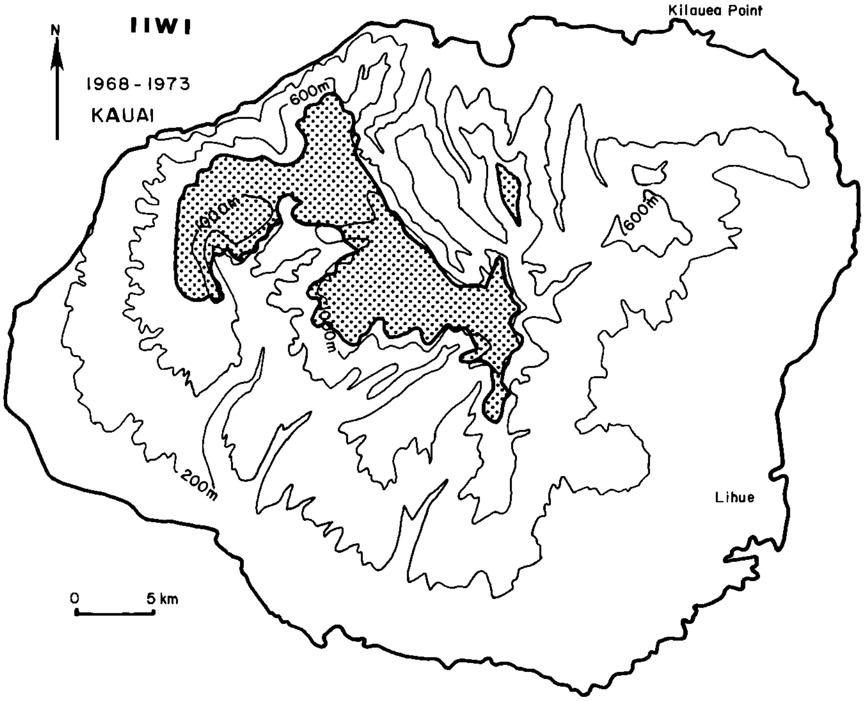

FIGURE 143. Range of the Iiwi on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

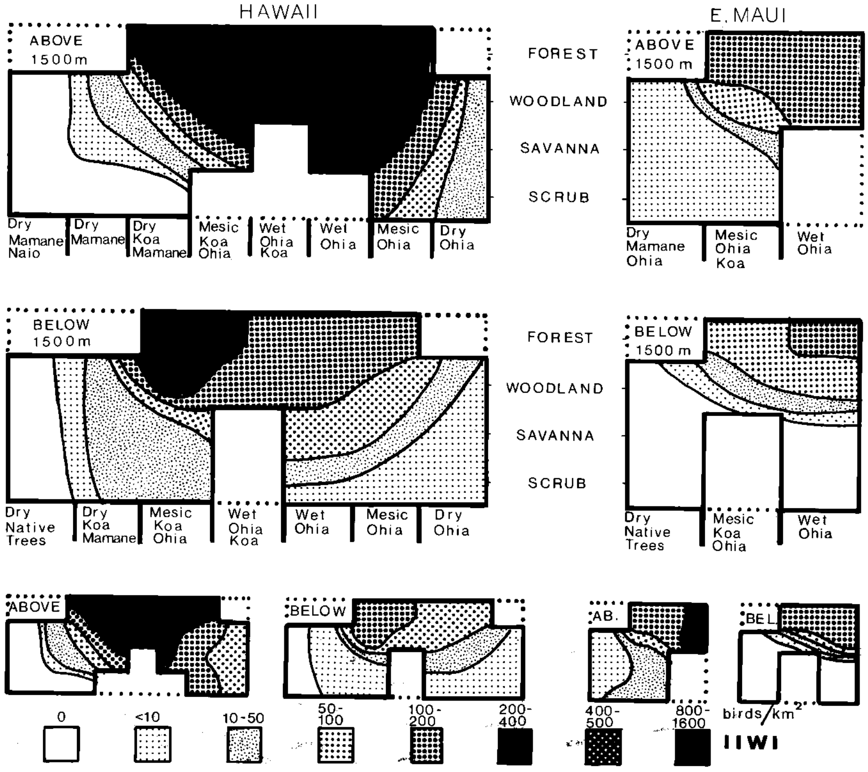

FIGURE 144. Habitat response graphs of the Iiwi. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 30
REGRESSION MODELS FOR HABITAT RESPONSE OF THE IIWI[a]

	Kau	Hamakua	Kipukas	Kona	Kohala	Maui	Kauai
R^2	0.55*	0.65*	0.22*	0.42*	0.15*	0.40*	0.05
Moisture	5.3*	11.5*	···	8.6*	X	6.1*	X
Elevation	6.4*	12.2*	···	···	2.3	6.5*	2.6
$(\text{Elevation})^2$	−2.6	−3.6*	···	10.0*	···	···	···
Tree biomass	···	−2.9	···	−8.0*	···	−5.0*	···
$(\text{Tree biomass})^2$	16.1*	3.8*	6.0*	11.1*	···	8.2*	···
Crown cover	···	···	···	···	···	···	···
Canopy height	···	···	···	···	2.2	···	···
Koa	···	5.6*	···	4.8*	X	−2.4	X
Ohia	···	4.0*	−3.9*	···	···	2.4	X
Naio	X	X	···	···	X	X	X
Mamane	X	···	5.8*	−2.8	X	···	X
Intro. trees	X	3.4*	X	···	···	−2.7	X
Shrub cover	···	···	···	8.6*	···	···	···
Ground cover	2.3	···	···	7.8*	···	···	···
Native shrubs	···	9.4*	···	−6.0*	···	···	···
Intro. shrubs	X	6.7*	−2.8	−9.6*	···	···	···
Ground ferns	X	X	···	7.1*	···	···	···
Matted ferns	···	−7.2*	···	···	···	···	···
Tree ferns	···	X	X	···	···	−5.2*	···
Ieie	X	X	X	−9.1*	X	···	···
Passiflora	X	5.2*	X	5.7*	2.8	···	X
Native herbs	X	X	···	−3.7*	···	···	···
Intro. herbs	X	X	···	−5.5*	···	···	···
Native grasses	···	···	···	···	···	4.0*	···
Intro. grasses	···	···	···	···	···	···	···
Ohia flowers	···	6.8*	···	···	···	···	···
Olapa fruit	···	···	···	···	2.5	3.8*	···
Mamane flowers	X	X	4.1*	X	X	···	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

BLACK MAMO (*Drepanis funerea*)

Known only from Molokai, Black Mamo were known as Oō-nuku-umu or Hoa, and were discovered in 1893 by Perkins (Berger 1981). The last Black Mamo recorded was a specimen taken in 1907 (Bryan 1908). Numerous surveys from 1936 to the present have failed to find the species (Munro 1944, Richardson 1949, Pratt 1974, Scott et al. 1977, HFBS). Black Mamo were originally known from wet forests in Kamakou Preserve (Perkins 1903), the transect 15 area (Bryan 1908), and Wailau Valley (Munro 1944). Neither mamo species is known from the fossil record (Olson and James 1982b), but since both species were nectarivores of higher elevation wet ohia forests, mamo species could have occurred on Maui, Oahu, and Kauai and been unrepresented in the dry area fossil sites at lower elevations. The ecologically similar and still widespread Iiwi is also poorly represented by fossils.

Black Mamo have a long decurved bill and take nectar from the large tubular flowers of lobeliads and sometimes from ohia. Perkins (1903) characterized them as very tame birds of the underbrush. Like their congener on Hawaii, Black Mamo were very aggressive and displaced all other nectarivores except oo from flowers (Perkins 1903).

The call of this species was characterized by Bryan (1908) as a rising, whistled "hoa." Perkins (1903) stated that they uttered a loud call of extraordinary clarity repeatedly at short intervals. We estimated the effective detection distance to be 40 m. The probability of detecting a population of 50 birds on Molokai was 85% (Table 12).

CRESTED HONEYCREEPER *Palmeria dolei*

CRESTED HONEYCREEPER [AKOHEKOHE]
(*Palmeria dolei*)

Crested Honeycreepers, also known as Akohekohe, originally occurred on Molokai and East Maui, and were locally abundant in the 1890s (Perkins 1903). On Molokai they were last seen in 1907 (Bryan 1908) and were considered extinct by 1944 (Richardson 1949), but reports of unidentified black birds in montane rainforests persisted through the 1960s (Pekelo 1967). Recent efforts to find the species on Molokai have been unsuccessful (Pratt 1974, Scott et al. 1977, HFBS). It seems highly unlikely that a population of 50 survives on Molokai or West Maui (Table 12).

Munro (1944) failed to find Crested Honeycreepers on Maui during the 1920s and 1930s. Richards and Baldwin (1953) reported them rare on the north slopes of Haleakala above 1750 m elevation. Greenway (1958) concluded that they were reduced to a small population or perhaps extinct on Maui. Scott and Sincock (1977) reported them very common in the upper Hanawi watershed. Conant (1981) considered them locally common and widespread above Manawainui Valley, in Kipahulu Valley, and from Wai Anapanapa to the upper Hanawi. W. E. Banko (pers. comm.) found this species common at higher elevations in Kipahulu Valley during 1967. This differs from the formal account of the Kipahulu Valley Expedition (Warner 1967), which reported only one or two sightings per person day in the upper valley. Our survey found that they are moderately common in the upper valley, with as many as eight sightings per person day.

We found Crested Honeycreepers only at upper elevations on East Maui (Tables 11, 27, Fig. 145). The population numbers 3800 ± 700 (95% CI) birds. In three areas above 1500 m elevation densities exceed 200 birds/km^2 and the species appears well established: west of Koolau Gap to Waikamoi Stream, east of Koolau Gap to Wai Anapanapa and Kipahulu Valley, and Kuiki Peak to Manawainui Valley. We found birds from 1300 to 2300 m elevation, with highest densities at 1500–2100 m. The densities, distributional patterns, and historical records indicate that the population is more secure than previously thought.

Like Apapane and Iiwi, Crested Honeycreepers feed primarily on the nectar of ohia flowers. Crested Honeycreepers are aggressively dominant over Apapane and Iiwi in the crowns of flowering ohia trees (Perkins 1903). Crested Honeycreepers also feed on foliage insects and fruit, particularly when nectar is scarce (J. H. Carothers, S. Mountainspring, pers. observ.).

The habitat response graphs for Crested Honeycreepers indicate that they are restricted almost entirely to habitats above 1500 m elevation

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FIGURE 146. Habitat response graphs of the Crested Honeycreeper (Akohekohe). (Graphs give mean density above and below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

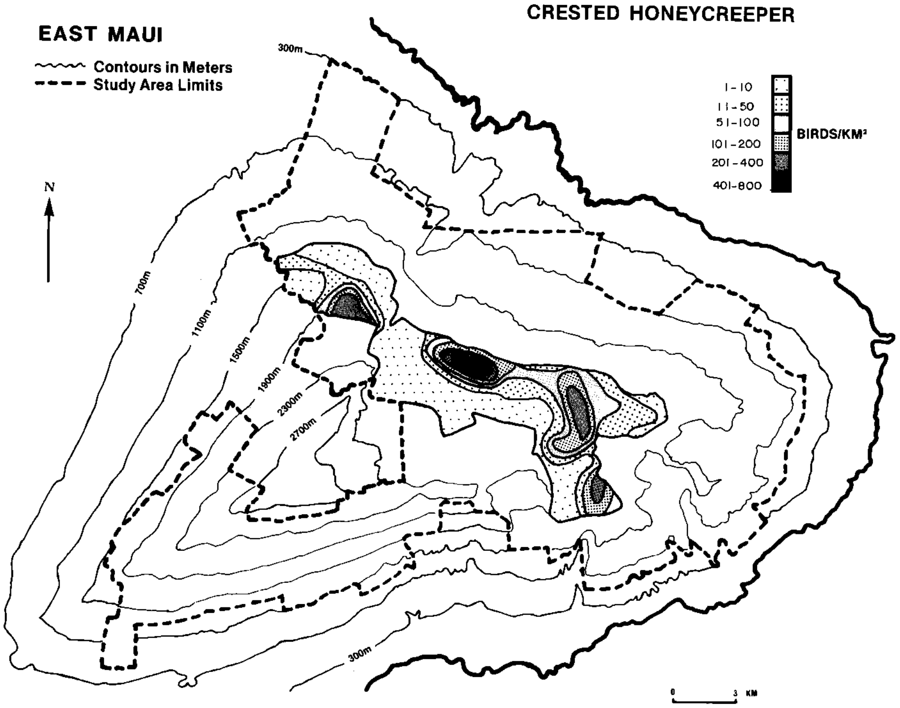
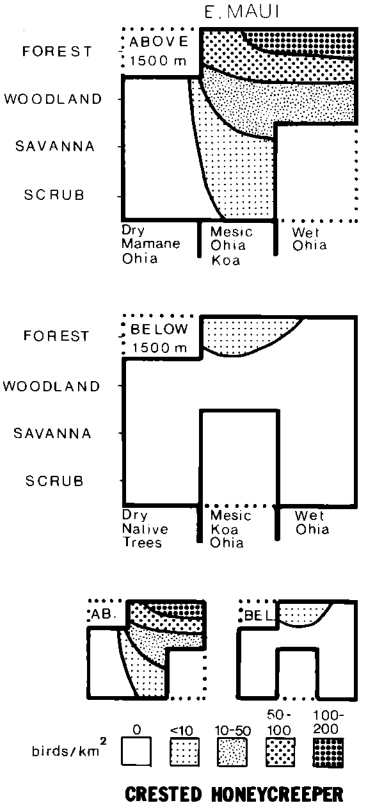


FIGURE 145. Distribution and abundance of the Crested Honeycreeper (Akohekohe) in the East Maui study area.



and are most abundant in mesic ohia-koa and wet ohia forests (Fig. 146). They are completely absent from dry ohia and mamane forests, plantations of introduced trees, and ohia dieback areas (Table 27). Densities are positively associated with forest biomass. Negative responses in the regression models (Table 28) to mamane and introduced trees mainly reflect absence in dry montane forests. Because this species feeds on understory flowers and fruit when ohia is not flowering, the tendency of matted ferns to choke out flowering plants probably lowers habitat quality. The regression model also shows a weak association with ohia flowers and olapa fruit.

Conant (1981) noted seasonal movement in the Kipahulu Valley area. In March, Crested Honeycreepers are found only at higher elevations (1700–2100 m), whereas in June and August, they occur as low as 1100 m elevation. This may represent range contraction during the breeding season followed by postbreeding dispersal. Apapane and Iiwi breed in January–May on Hawaii, with birds more widespread during the non-breeding season (Baldwin 1953); Palila have a similar seasonal cycle (van Riper et al. 1978, van Riper 1980). During July 1980 all Crested Honeycreepers we found at the range periphery were immature birds.

APAPANE
Himatione sanguinea

APAPANE (*Himatione sanguinea*)

Apapane are the most abundant honeycreepers. Early writers noted their abundance on the six principal islands (Perkins 1903). Munro (1944) characterized them as "occurring in fair numbers on Hawaii, Maui, Oahu and Kauai, a few on Lanai and but one seen on Molokai." Baldwin (1953) found Apapane were the most common native birds in Hawaii Volcanoes National Park and documented seasonal movements in response to changes in available food. Apapane appear to have increased slightly in abundance in the national park over the 1940–1975 period (Conant 1975, Banko and Banko 1980).

Apapane feed primarily on the nectar of ohia flowers and on foliage insects (Baldwin 1953). They occasionally visit other flowers (Perkins 1903, Berger 1981) and immature birds sometimes feed on berries when nectar is scarce, but Apapane appear to be less opportunistic than Iiwi in feeding on other flowers. Baldwin (1953) thought their bill was best adapted for probing the cuplike receptacles of ohia flowers. Pollination of ohia by honeycreepers, especially Apapane, is essential for high levels of fruit-set and outbreeding, a possible result of co-evolved mutualism (Carpenter 1976).

Apapane are usually gregarious, with recognition of individuals probably facilitated by their complex vocal repertoire (Ward 1964). An in-

TABLE 31
DENSITY [MEAN (SE)] OF THE APAPANE BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	E. Maui	W. Maui	Molokai	Lanai	Kauai
Elevation												
100–300 m	···	···	···	···	···	···	···	···	···	488 (178)	···	···
300–500 m	···	0	104 (14)	···	604 (96)	···	+ (+)	34 (18)	···	687 (129)	···	···
500–700 m	208 (85)	66 (11)	362 (24)	···	516 (48)	···	51 (28)	116 (23)	125 (81)	229 (37)	+ (+)	···
700–900 m	662 (93)	129 (13)	863 (32)	···	187 (16)	···	143 (42)	183 (22)	306 (40)	153 (25)	51 (18)	···
900–1100 m	568 (64)	310 (23)	1000 (67)	···	238 (14)	···	357 (80)	354 (34)	668 (112)	337 (32)	46 (18)	···
1100–1300 m	477 (37)	500 (24)	473 (47)	252 (47)	225 (14)	···	144 (26)	339 (28)	595 (89)	445 (34)	···	1256 (45)
1300–1500 m	711 (39)	623 (29)	···	204 (23)	179 (10)	···	203 (26)	397 (32)	521 (69)	362 (104)	···	1139 (36)
1500–1700 m	1292 (51)	588 (30)	···	310 (29)	196 (11)	···	443 (55)	586 (56)	213 (40)	···	···	···
1700–1900 m	1524 (77)	577 (42)	···	214 (20)	188 (14)	···	···	455 (59)	302 (55)	···	···	···
1900–2100 m	1286 (101)	576 (68)	···	153 (16)	122 (12)	0	···	291 (37)	···	···	···	···
2100–2300 m	1891 (350)	87 (30)	···	192 (47)	88 (11)	0	···	81 (18)	···	···	···	···
2300–2500 m	···	···	···	···	14 (6)	+ (+)	···	7 (3)	···	···	···	···
2500–2700 m	···	···	···	···	···	4 (4)	···	1 (1)	···	···	···	···
2700–2900 m	···	···	···	···	···	12 (8)	···	+ (+)	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	751 (30)	391 (12)	573 (23)	187 (13)	209 (7)	···	216 (22)	452 (22)	479 (39)	324 (21)	···	1209 (28)
Koa-ohia	1294 (48)	525 (21)	···	263 (26)	288 (10)	···	···	328 (23)	···	···	···	···
Koa-mamane	···	81 (21)	···	309 (30)	68 (6)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	21 (7)	0	···	···	···	···	···	···
Mamane	···	···	···	···	50 (7)	5 (3)	···	21 (12)	···	···	···	···
Other natives	···	128 (31)	···	100 (26)	6 (4)	···	···	116 (20)	···	54 (13)	17 (13)	···
Intro. trees	···	81 (18)	···	···	371 (90)	···	128 (42)	111 (20)	*	447 (58)	56 (15)	···
Treeless	814 (156)	19 (6)	326 (115)	39 (20)	86 (16)	···	···	96 (16)	199 (50)	18 (8)	+ (+)	227 (227)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area; * indicates stratum was not sampled in range but was sampled elsewhere in study area.

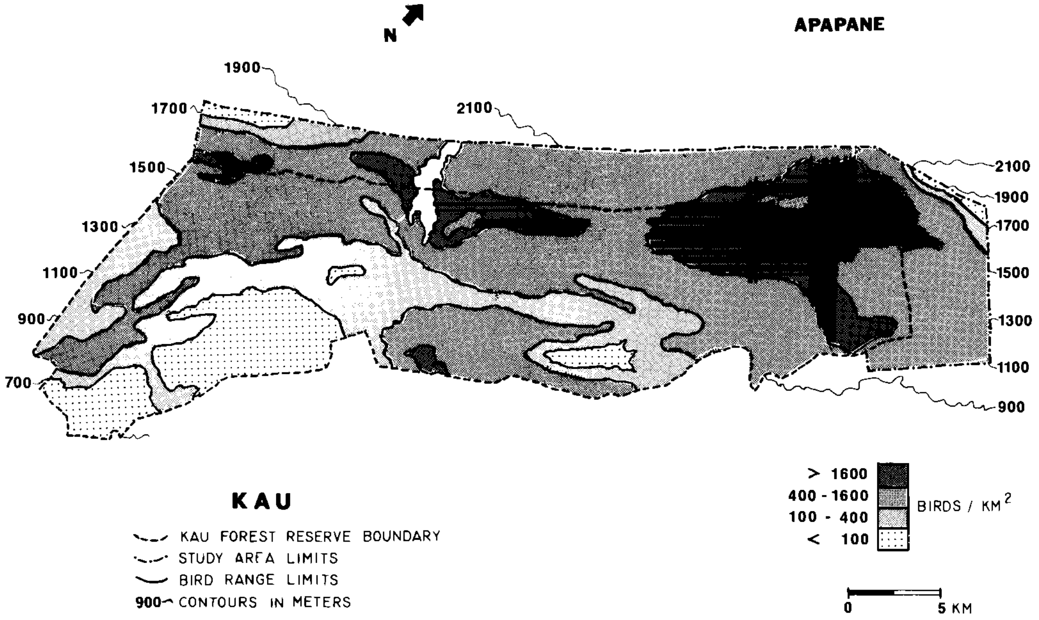


FIGURE 147. Distribution and abundance of the Apapane in the Kau study area.

terspecific social dominance hierarchy of nectarivores is maintained at flowering trees by aggressive interactions. At the base of this hierarchy are Apapane, followed above by Iiwi, then by Crested Honeycreepers on Maui and formerly Molokai (Perkins 1903, Pimm and Pimm 1982). Flocking by Apapane may thwart defense of flowering trees by Iiwi and Crested Honeycreepers. Flocking is also related to large scale mass movements between widely separated (>7 km) roosting and feeding sites (MacMillen and Carpenter 1980). On 26 July 1974 these observers estimated 42,000 Apapane and Iiwi in an evening flight of 1.5 hr duration, presumably gaining an overnight energy savings as a result of thermal protection in mature forest and escape from a nocturnal fog belt. Perhaps because of sharper topographic contrast, smaller land area, and smaller populations, mass flights are less apparent on Maui and the smaller islands than on Hawaii (C. B. Kepler and J. M. Scott, pers. observ.).

We found Apapane in all study areas. They are the most abundant native bird in all areas but Mauna Kea (Tables 10, 11, 31, Figs. 147–156). More than 1,000,000 birds inhabit our study areas on Hawaii, forming two populations that probably exchange individuals.

On Hawaii the main population of 1,080,000 ± 25,000 (95% CI) birds forms a continuous band from Hamakua through Puna and Kau to Kona. Low densities below 2000 m elevation correspond to deforested habitat, particularly in Kona. As with Iiwi, the 200 Apapane in the mamane woodland on Mauna Kea are migrants to areas of high bloom (C. B. Kepler and J. M. Scott, unpub. data). In some years Apapane also occur on the west slopes of Mauna Kea. Apapane are well established throughout Hamakua and Puna, these two areas possessing 50% of the main population. The absence of birds at low elevations north of Hilo and in the northeast corner of the Puna study area corresponded closely to areas lacking ohia bloom. Kau has 25% of the main population. Low densities in the extreme south of the study area again corresponded to areas with low ohia bloom. Bird densities in Kona are also strongly affected by the distribution of ohia bloom, and deforestation accounts for low densities around Puu Waawaa north of Hualalai and around Puu Lehua south of Hualalai (Fig. 149). Apapane occur from sea level below the Puna and Kona study areas to 2900 m elevation on Mauna Kea. Densities exceeding 500 birds/km^2 occur at 300–700 m elevation in Kona, at 700–1100 m in Puna, at 1100–2100 m in Hamakua, and at 700–2300 m in Kau. Similar patterns were found in Hawaii Volcanoes National Park by Conant (1975, 1980). Maximum densities of 2000 birds/km^2 occur in the Kau area and are among the highest bird densities recorded for a noncolonial species (Udvardy 1957). A population of 20,000 ± 3000 (95% CI) birds on Kohala Mountain are separated by 30 km of pastures from the

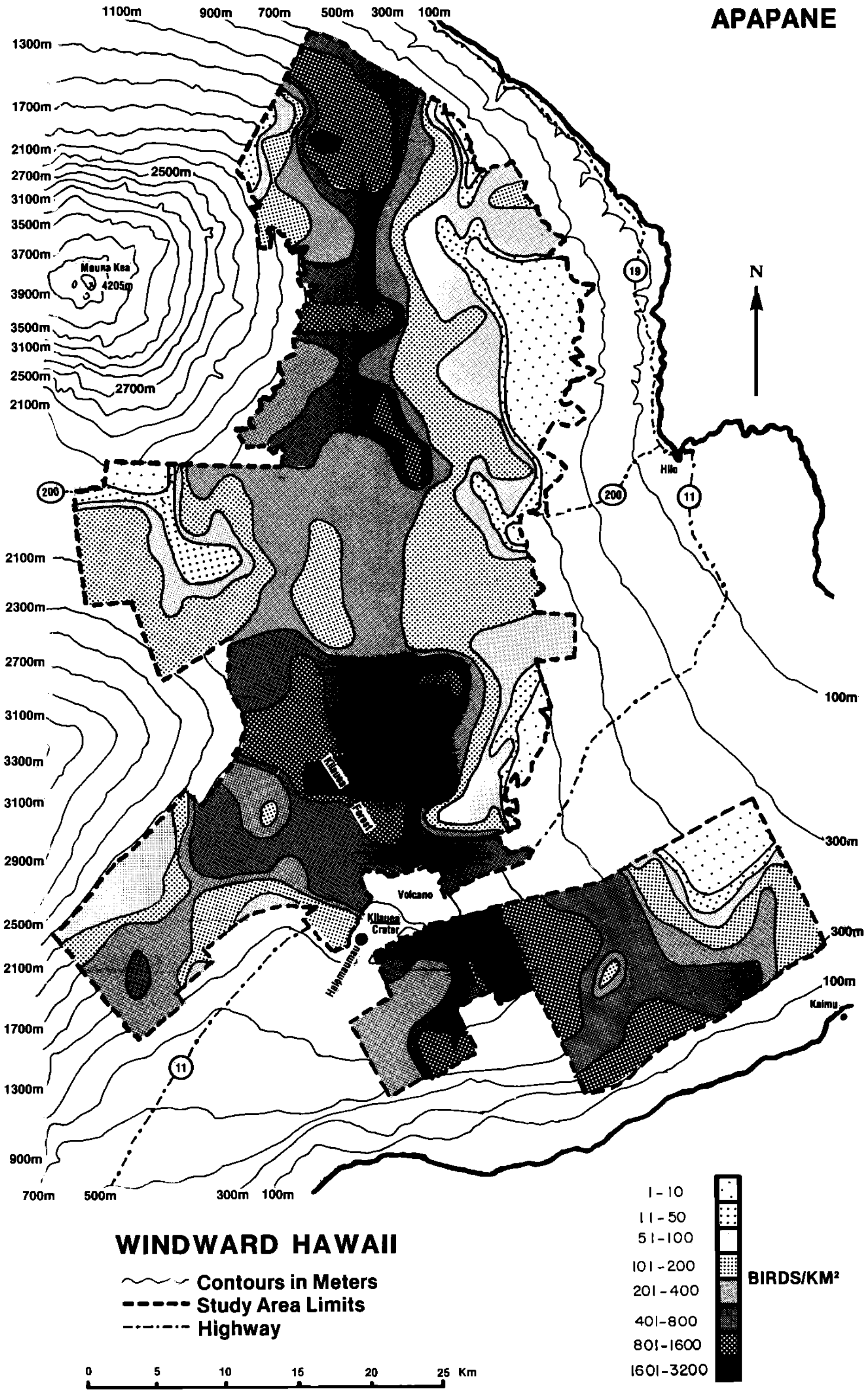


FIGURE 148. Distribution and abundance of the Apapane in the windward Hawaii study areas.

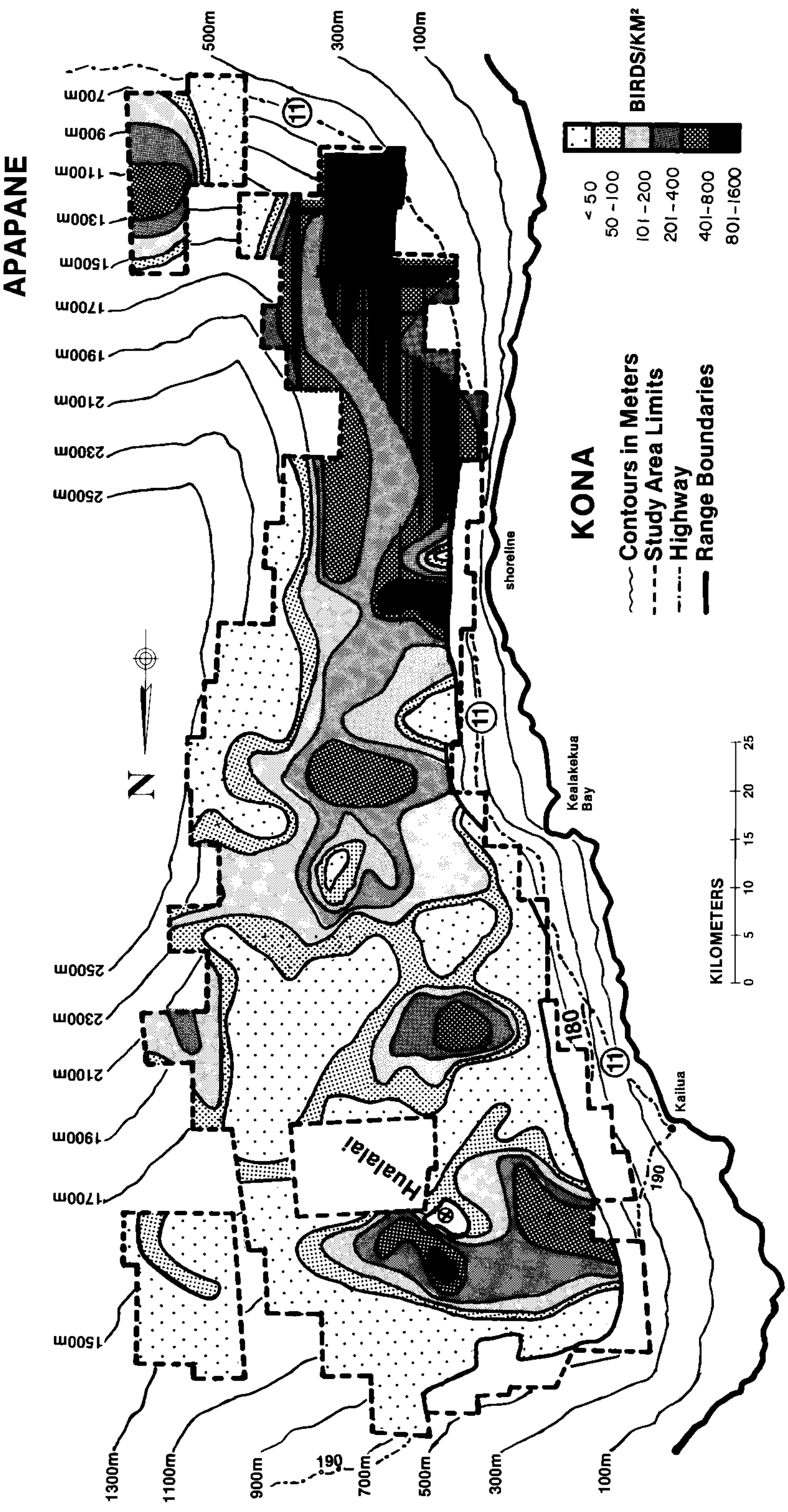


FIGURE 149. Distribution and abundance of the Apapane in the Kona study area.

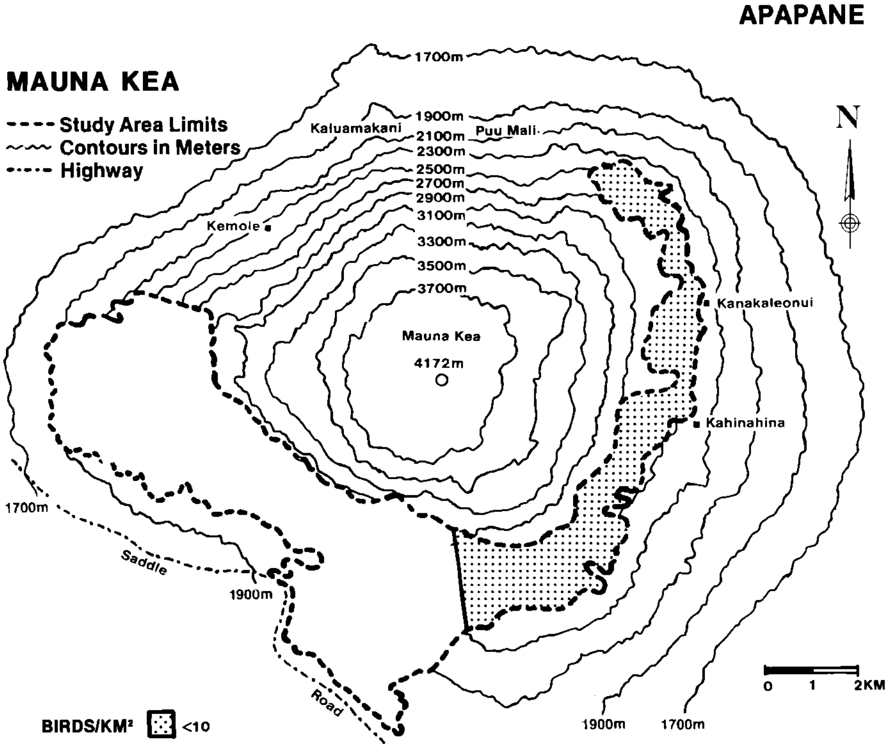


FIGURE 150. Distribution and abundance of the Apapane in the Mauna Kea study area.

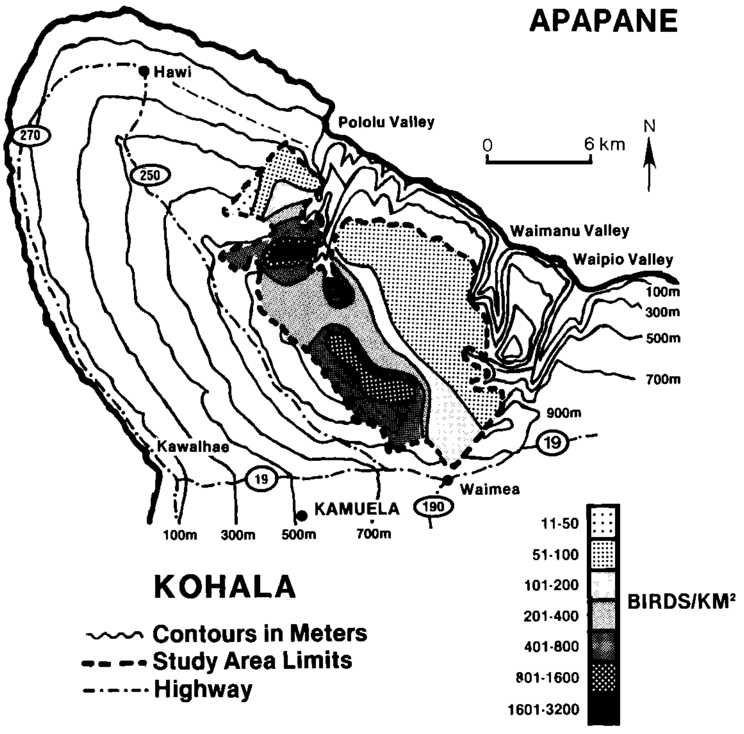


FIGURE 151. Distribution and abundance of the Apapane in the Kohala study area.

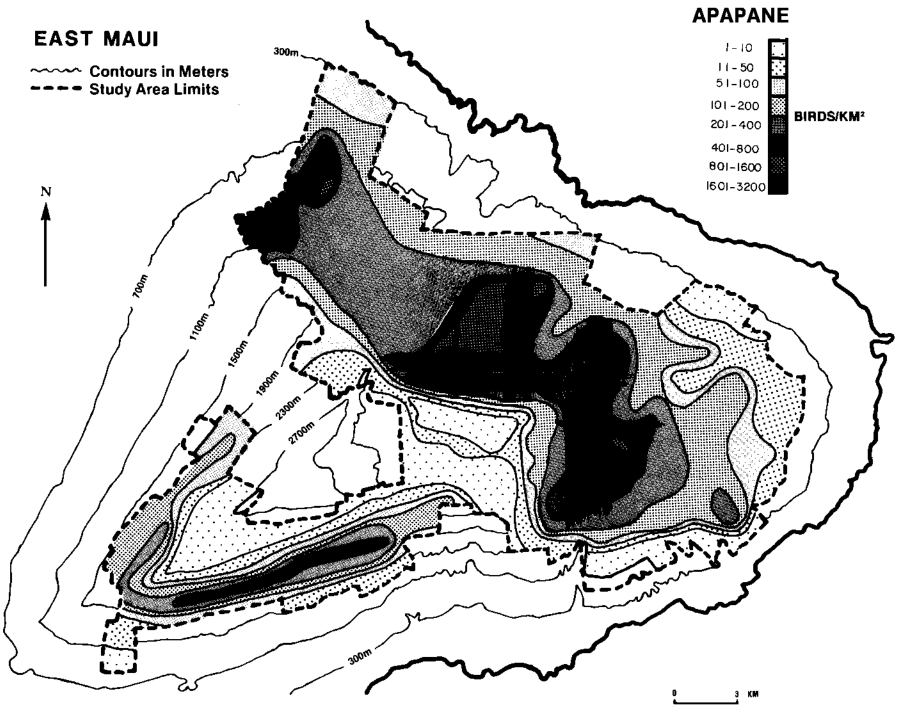


FIGURE 152. Distribution and abundance of the Apapane in the East Maui study area.

main population and are more common at higher elevations.

On East Maui 94,000 ± 7000 (95% CI) Apapane are distributed over the entire study area, with far higher densities in wet ohia forests than in degraded dry woodlands. In Kahikinui, birds are associated with remnant habitat patches. On windward East Maui, densities are lower at lower elevations. Apapane range from 300 to 2700 m elevation on East Maui, reaching highest densities at 1500–1900 m.

West Maui supports a robust population of 16,000 ± 2000 (95% CI) Apapane centered around Puu Kukui and its subsidiary ridges. The near absence of birds on Keahikauo Ridge reflects the presence of bogs and lack of forest in the area.

On Molokai 39,000 ± 5000 (95% CI) Apapane have low densities or are absent due to deforestation on the eastern part of the study area by axis deer, pigs, and cattle, and on the southwest study area margin by deer and goats. Highest densities occur in Pelekunu Valley down to 100 m elevation and in Kamakou Preserve at 900–1500 m.

Only 540 ± 420 (95% CI) Apapane survive on Lanai and have low densities in the remaining native forests. The Lanai population appears to be threatened with extinction, but may be sustained by occasional immigrants from Molokai or Maui.

Apapane are widespread and abundant throughout the Alakai Swamp study area on Kauai. We estimated a population of 30,000 ± 1500 (95% CI) birds that did not differ beyond normal annual variation from the 43,000 ± 9000 birds that J. L. Sincock (unpub. data) estimated for that area for 1968–1973. Sincock et al. (1984) estimated a total of 163,000 ± 23,000 birds for Kauai. The 1968–1973 range showed a virtually continuous population through most areas of native forest on Kauai, with occasional occurrences on the isolated Hoary Head Range (Fig. 157).

Apapane are more abundant above 1500 m elevation on Hawaii than on Maui (Fig. 158). Densities are comparable below 1500 m on the two islands. On all four habitat response graphs, birds occupy every available habitat, but are most common in mesic to wet ohia and koa-ohia forests.

The regression models show that Apapane are especially common in wet, fairly dense, ohia forest at mid to high elevations with good ohia bloom (Table 32). Densities generally increase with tree biomass. In Puna, crown cover and canopy height index the positive response to forest development. Among tree species, ohia have positive terms in four models. Ohia flowers generate pos-

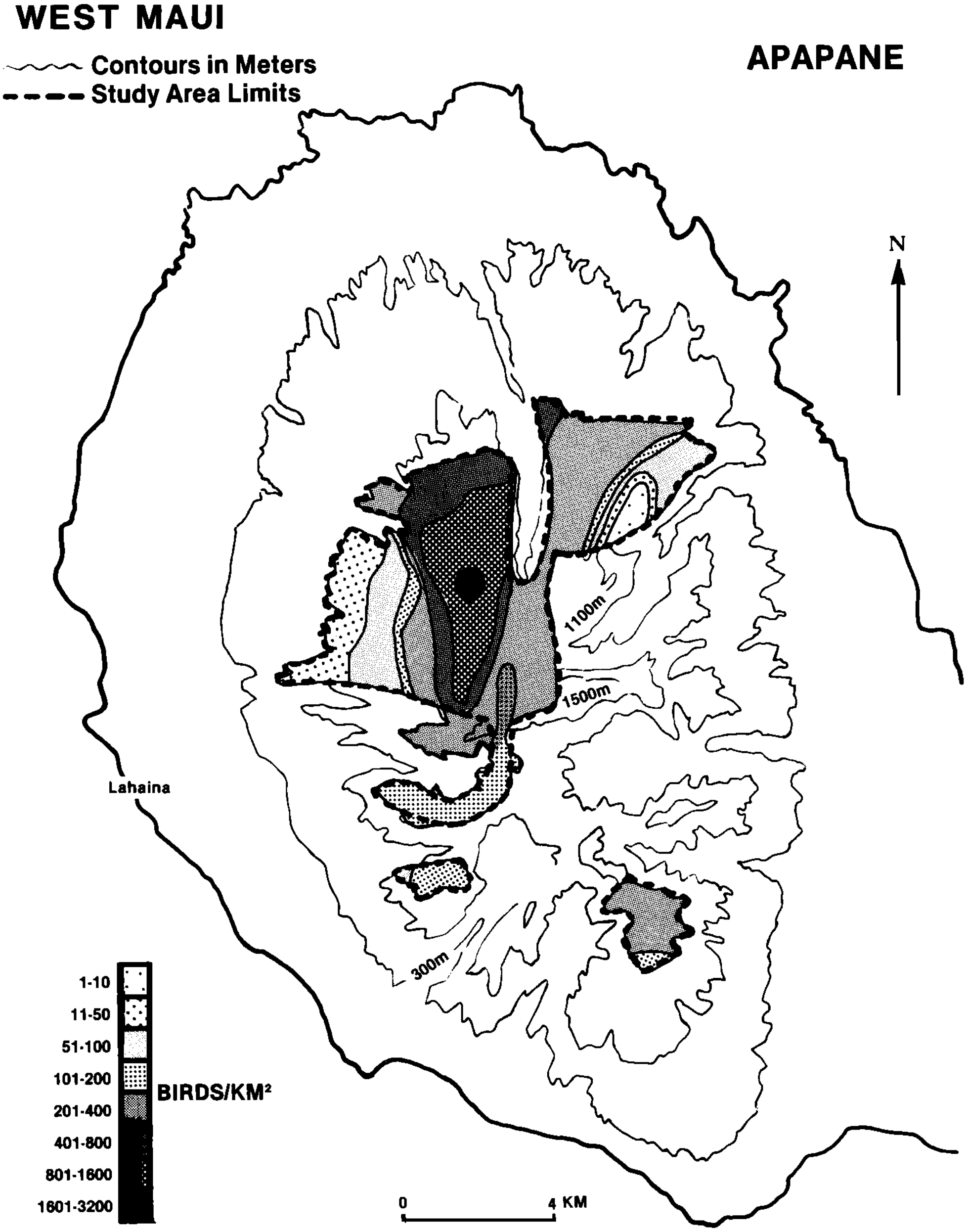


FIGURE 153. Distribution and abundance of the Apapane in the West Maui study area.

itive response in six models and would enter the Puna model at the 0.06 significance level. Responses to other tree species suggest that many combinations provide acceptable habitat. Weak negative responses to introduced trees occur in two models, but densities above 200 birds/km^2 occasionally occur in eucalyptus forests. With few exceptions, Apapane do not respond strongly to understory components, and some of the weaker responses are contradictory between forests. Birds are often associated with native graminoids, an indicator of undisturbed communities and forest interiors.

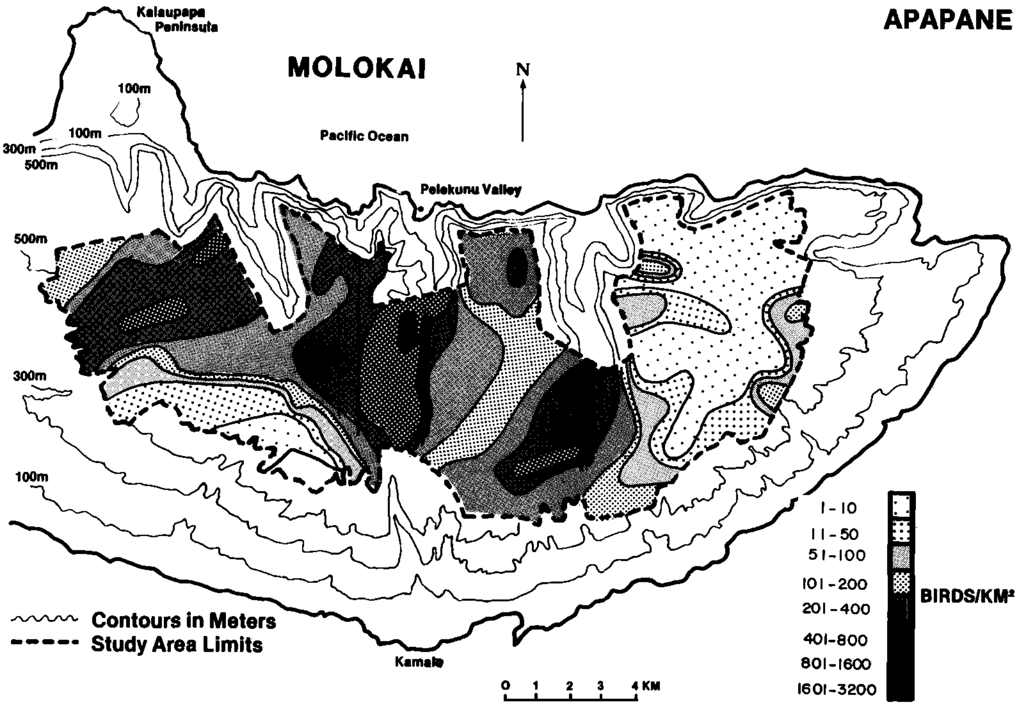


FIGURE 154. Distribution and abundance of the Apapane in the Molokai study area.

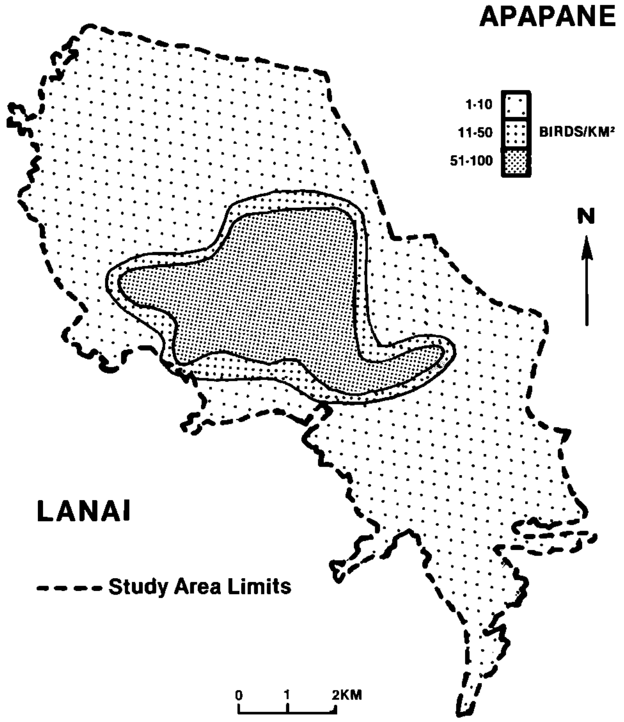


FIGURE 155. Distribution and abundance of the Apapane in the Lanai study area.

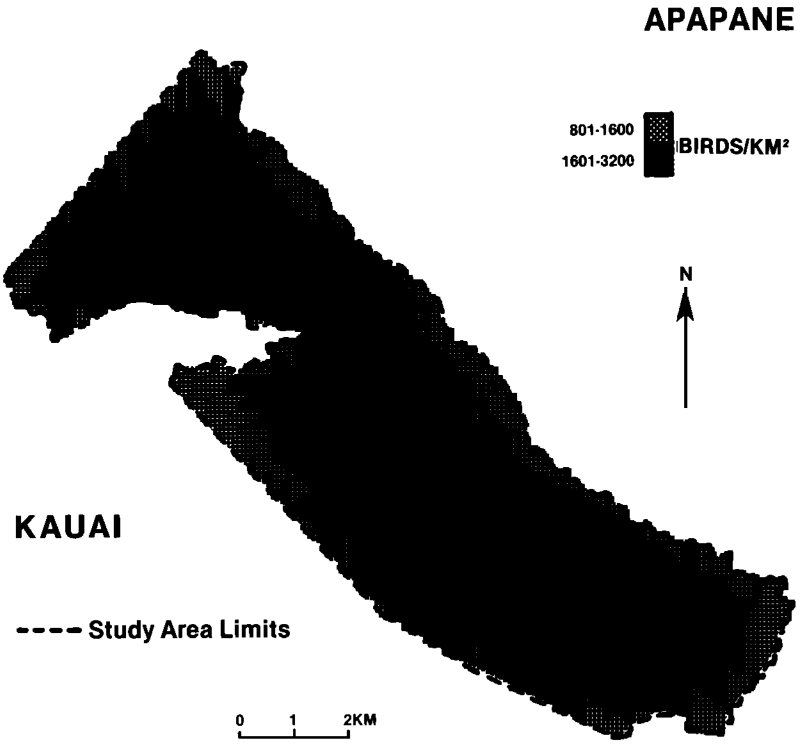


FIGURE 156. Distribution and abundance of the Apapane in the Kauai study area.

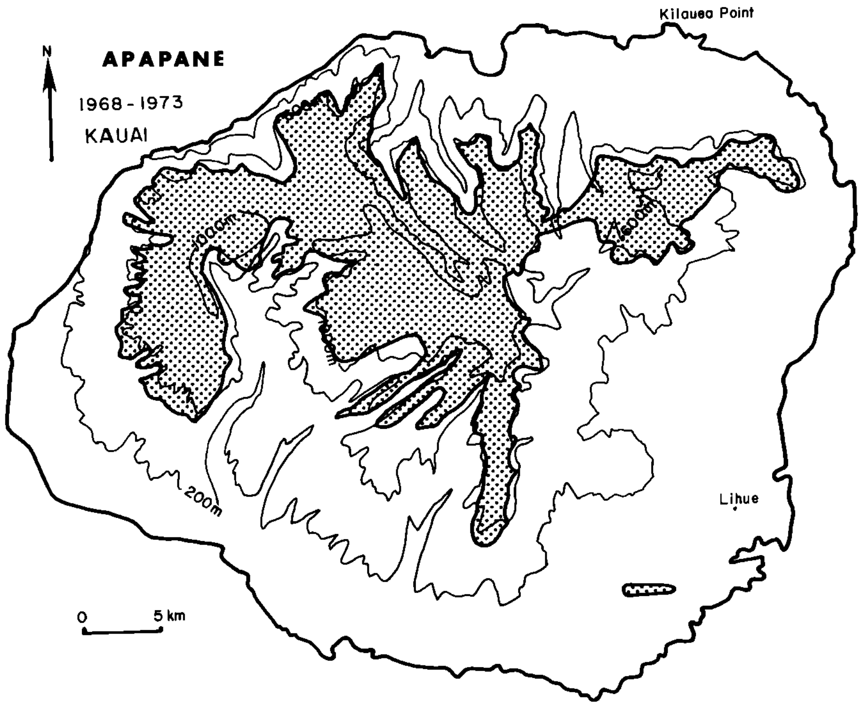


FIGURE 157. Range of the Apapane on Kauai, based on 1968–1973 survey (J. L. Sincock, unpub. data).

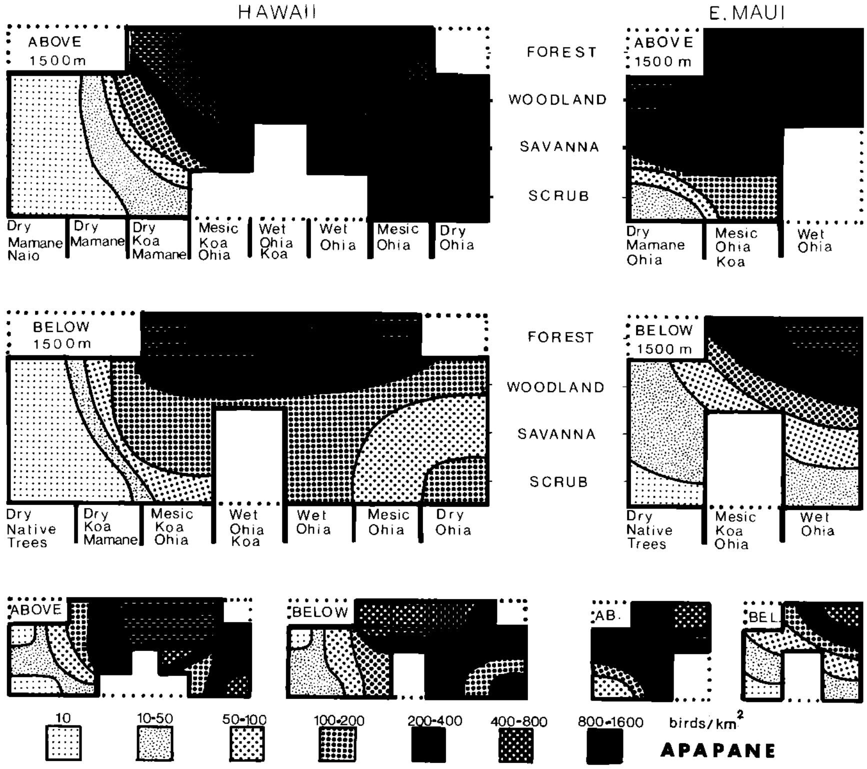


FIGURE 158. Habitat response graphs of the Apapane. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 32
Regression Models for Habitat Response of the Apapane[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Kohala	Maui	Molokai	Lanai	Kauai
R^2	0.33*	0.51*	0.56*	0.36*	0.43*	0.23*	0.50*	0.50*	0.07	0.23*
Moisture	2.5	···	−3.2	···	12.5*	X	3.0	···	···	X
Elevation	12.0*	17.7*	8.5*	···	···	5.4*	7.8*	···	···	···
(Elevation)^2	···	−13.2*	−6.6*	···	14.7*	···	−6.1*	3.4*	···	···
Tree biomass	···	···	···	···	−7.7*	···	5.7*	−2.3	2.2	4.8*
(Tree biomass)^2	8.1*	···	···	3.3	10.3*	···	···	5.6*	···	−4.1*
Crown cover	···	···	4.4*	2.3	···	···	···	···	···	···
Canopy height	−3.8*	···	4.4*	···	···	···	···	···	···	···
Koa	2.7	···	X	···	3.3	X	···	X	X	X
Ohia	···	4.3*	···	···	5.6*	···	8.3*	2.7	···	X
Naio	X	X	X	···	···	X	X	X	X	X
Mamane	X	···	···	···	···	X	−3.7*	X	X	X
Intro. trees	X	−2.1	···	X	−2.8	···	···	···	···	X
Shrub cover	···	6.3*	···	···	−3.4*	···	···	···	···	···
Ground cover	2.6	−4.1*	···	···	···	···	···	···	···	···
Native shrubs	···	···	···	···	5.6*	···	4.2*	···	···	···
Intro. shrubs	X	5.3*	···	···	···	···	−3.0	···	···	···
Ground ferns	X	X	···	···	3.0	···	···	···	X	···
Matted ferns	···	−4.6*	−4.5*	···	2.7	···	···	3.1	···	···
Tree ferns	···	X	2.3	X	···	···	···	−4.4*	X	···
Ieie	X	X	−3.2	X	−6.3*	X	4.8*	X	X	···
Passiflora	X	−2.8	X	X	···	···	···	X	X	···
Native herbs	X	X	···	−4.8*	−4.3*	···	···	···	X	···
Intro. herbs	X	X	−2.9	5.3*	···	2.9	4.7*	···	X	···
Native grasses	···	3.8*	6.6*	5.4*	5.8*	···	···	···	X	···
Intro. grasses	···	4.1*	−6.5*	···	−2.5	···	···	−3.9*	···	···
Ohia flowers	3.0	15.8*	···	···	9.9*	5.3*	4.6*	3.4*	···	···
Olapa fruit	−3.7*	···	···	···	···	···	···	···	···	···
Mamane flowers	X	X	X	···	X	X	···	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are *t* statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

POO-ULI
Melamprosops phaeosoma

Poo-uli (*Melamprosops phaeosoma*)

Poo-uli are rare, little-known birds discovered on East Maui in 1973 (Casey and Jacobi 1974). They feed on snails and insects gleaned from foliage and bark (Baldwin and Casey 1983). Two birds were recorded at a single station during our survey. This station was located at 1480 m elevation in wet ohia forest with about 60% crown

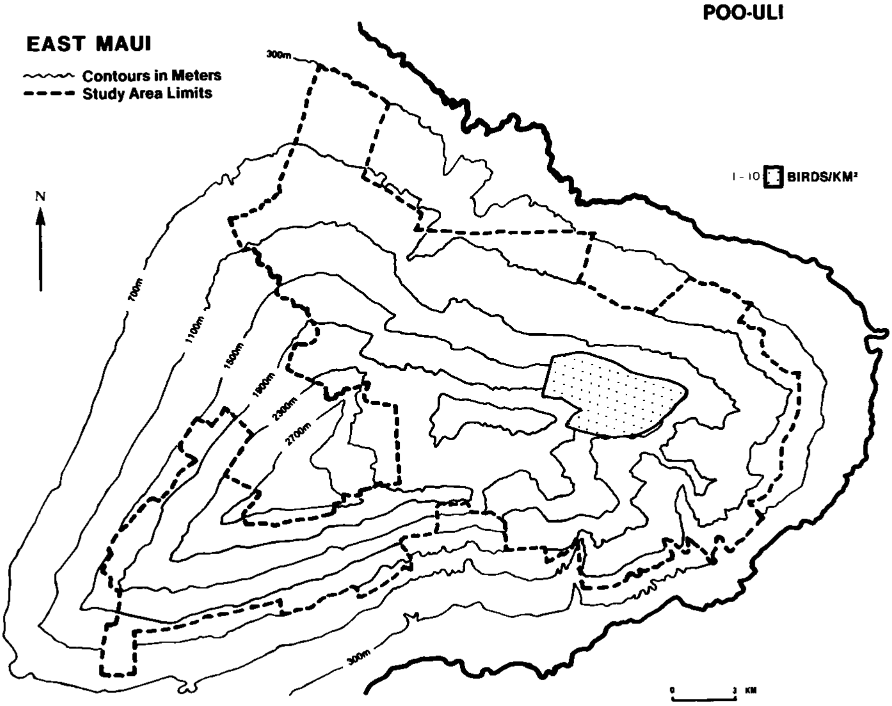


FIGURE 159. Distribution and abundance of the Poo-uli in the East Maui study area.

cover and a partially closed native understory dominated by graminoids, shrubs, and ground ferns. We also made incidental sightings of this species during the survey period. All known sightings have been on the northeast slopes of Haleakala from 1400 to 2050 m elevation in wet ohia forests with well-developed understories (Berger 1981, Conant 1981). Fossil records from Ulupalakua (S. L. Olson, pers. comm.) indicate that Poo-uli originally occupied a larger range that included dry to mesic habitat.

The total population of 140 ± 280 (95% CI) Poo-uli (Tables 11, 24) inhabits the upper Hanawi and Kuhiwa watersheds. The birds we found (0.03 birds/count period) within the species range in 1980 indicate about the same abundance as S. Mountainspring (unpub. data) found in 1981 in the upper Hanawi area (0.04 birds/count period). A decline in abundance was suggested by comparison with the upper Hanawi survey that T. L. C. Casey (unpub. data) conducted in 1976 (0.18 birds/count period). Incidental observations over the 1974–1983 period also suggest fewer Poo-uli now than a decade ago (T. L. C. Casey, pers. comm.). Correlated with this trend was an increase in pig damage to the understory of the upper Hanawi watershed (S. Mountainspring, pers. observ.).

Areas in Poo-uli range differ from nearby areas outside the range in the same elevational stratum and in the same general vegetation type. Whereas in-range areas have moderate pig damage and well-developed herb, ground fern, and moss layers, adjacent areas outside the range have significantly greater pig damage and less ground cover (S. Mountainspring, pers. observ.). Poo-uli appear to be adversely impacted by pig activity, possibly because pigs destroy microhabitat sites critical to the life cycle of the land snails and other invertebrates that species eats. Pigs are thus one probable cause of the apparent decline of Poo-uli over the past decade. The restriction of Poo-uli and Nukupuu to the wet ohia forests of the upper Hanawi watershed (Figs. 112, 159) suggests that these birds are in extreme danger of extinction. It seems imperative to remove pigs permanently from this and adjacent areas to ensure the survival of these species.

INTRODUCED SPECIES ACCOUNTS

General notes on format of the species accounts are given at the beginning of the native species section. Often only a few of the many individuals in a flock were detected for species such as Erckel's Francolin, Gray Francolin, Chukar, Wild Turkey, California Quail, House Finch, and Nutmeg Mannikin. Moreover, calling rates of gamebirds fell sharply within an hour after sunrise. For gallinaceous birds in particular, density and population estimates are therefore best interpreted as relative indices of abundance. It should be noted that as a result of our sampling design, many introduced species entered the study areas only at the periphery of their range.

BLACK FRANCOLIN
(*Francolinus francolinus*)

Black Francolins were introduced from India in 1959 (Berger 1981). They presently occur on Hawaii, Maui, Molokai, and Kauai. Black Francolins feed on plants, insects, and seeds.

We found this species in five study areas (Tables 33–35). The distribution patterns indicated that we sampled at the periphery of the range. An estimated 230 ± 40 (95% CI) birds occupy the Kona study area, mainly at low elevations on the north slope of Hualalai (near the initial release site on Puu Waawaa [Lewin 1971]) and at higher elevations in the area from Puu Lehua to Devil Country (Fig. 160). On Hawaii, Black Francolins occur from sea level to 2300 m elevation (Table 35). They occur below 2200 m in the Mauna Kea study area and are common along the Saddle Road west of Mauna Kea State Park. We consider the one bird recorded in the Kohala study area to be an extralimital record. The species is common at lower elevations on the leeward side of Kohala Mountain and Mauna Kea.

In the East Maui study area an estimated 8 ± 6 (95% CI) birds occur below 1300 m elevation in dry areas. As on Hawaii, they are more common below the study area. On Molokai 150 ± 60 birds inhabit the study area (Table 34, Fig. 161). Here they are very widespread in dry areas on lower slopes, but also penetrate closed-canopy forests along roads, jeep trails, clearings, and grassy areas.

Highest densities occur in dry scrubland and savanna (often scrubby pasturelands) at lower elevations, with occasional birds in mesic to wet areas and in open woodlands (Table 36, Fig. 162). Most tree species have negative terms in the regression models and little response appears to understory elements. The strong tendency of this species to wander, however, makes it a potential dispersal agent for banana poka (Warshauer et al. 1983).

In the Kohala area Black Francolins typically inhabit the perimeters of sugar cane fields, irrigation ditches, and drier pasture areas where mesquite and lantana are common (Lewin 1971). These habitats are similar to areas occupied within the native range in India: dry grasslands, open brushlands, and cultivated areas with available water and cover for feeding (Ali and Ripley 1969).

TABLE 33
SUMMARY STATISTICS FOR INTRODUCED BIRDS IN THE STUDY AREAS ON HAWAII

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Black Francolin							
Range (km^2)	...	...	...	...	275	97	12
Stations in range	...	...	...	...	605	234	19
Stations occupied	...	...	...	...	178	1	1
Birds recorded	...	...	...	...	487	1	1
Total population	...	...	...	...	230	6	1
SE	...	...	...	...	18	6	1
Pop. by habitat type							
Ohia	...	...	...	...	159	...	1
Koa-ohia	...	...	...	...	1	...	...
Mamane-naio	...	...	...	...	11	...	...
Mamane	...	...	...	...	30	6	...
Other natives	...	...	...	...	21	...	...
Intro. trees	...	...	...	...	8	...	...
Erckel's Francolin							
Range (km^2)	...	4	42	45	325	97	...
Stations in range	...	10	75	73	820	234	...
Stations occupied	...	1	58	22	421	53	...
Birds recorded	...	1	244	72	2047	100	...
Total population	...	1	287	43	1137	326	...
SE	...	1	25	6	47	48	...
Pop. by habitat type							
Ohia	...	...	287	...	669	...	...
Koa-ohia	...	...	...	39	110	...	...
Koa-mamane	...	...	...	4	2	...	...
Mamane-naio	...	...	...	...	28	253	...
Mamane	...	...	...	...	144	74	...
Other natives	...	1	...	...	97	...	...
Intro. trees	...	...	...	...	88	...	...
Gray Francolin							
Stations occupied	...	...	...	...	2	...	...
Birds recorded	...	...	...	...	2	...	...
Chukar							
Range (km^2)	...	14	...	127	242	139	...
Stations in range	...	27	...	157	608	317	...
Stations occupied	...	11	...	43	105	66	...
Birds recorded	...	21	...	67	194	165	...
Total population	...	239	...	227	777	4243	...
SE	...	52	...	45	84	655	...
Pop. by habitat type							
Ohia	...	...	...	208	405	...	...
Koa-ohia	...	...	...	...	26	...	...
Koa-mamane	...	219	...	9	11	...	...
Mamane-naio	...	...	...	...	24	1620	...
Mamane	...	...	...	...	239	2666	...
Other natives	...	20	...	2	3	...	...
Intro. trees	...	...	...	...	2	...	...
Treeless	...	...	...	8	67	...	...
Japanese Quail							
Range (km^2)	20	17	...	32	...	97	...
Stations in range	25	17	...	35	...	234	...
Stations occupied	1	3	...	3	...	2	...
Birds recorded	1	23	...	15	...	2	...
Total population	33	31	...	52	...	17	...
SE	33	21	...	23	...	11	...

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Pop. by habitat type							
Ohia	33	24	...	18	...	...	...
Koa-mamane	...	...	...	13	...	...	...
Mamane	...	...	...	...	...	17	...
Other natives	...	8	...	21	...	...	...
Kalij Pheasant							
Range (km²)	...	67	...	28	758	...	...
Stations in range	...	178	...	36	1760	...	...
Stations occupied	...	6	...	2	253	...	...
Birds recorded	...	8	...	3	432	...	...
Total population	...	174	...	23	5499	...	...
SE	...	83	...	20	461	...	...
Pop. by habitat type							
Ohia	...	80	...	3	2196	...	...
Koa-ohia	...	82	...	20	2116	...	...
Koa-mamane	...	...	...	...	527	...	...
Mamane-naio	...	...	...	...	8	...	...
Mamane	...	...	...	...	272	...	...
Other natives	...	...	...	...	3	...	...
Intro. trees	...	13	...	...	377	...	...
Red Junglefowl (Moa)							
Range (km²)	...	...	32	...	...	...	...
Stations in range	...	...	70	...	...	...	...
Stations occupied	...	...	11	...	...	...	...
Birds recorded	...	...	21	...	...	...	...
Total population	...	...	3	...	...	...	...
SE	...	...	1	...	...	...	...
Pop. by habitat type							
Ohia	...	...	3	...	...	...	...
Ring-necked Pheasant							
Range (km²)	71	354	81	271	933	139	19
Stations in range	156	740	219	458	2201	317	38
Stations occupied	44	185	45	265	1075	13	5
Birds recorded	101	556	110	1196	3578	17	8
Total population	1147	2088	270	2250	7452	657	45
SE	297	144	45	99	207	225	27
Pop. by habitat type							
Ohia	1142	666	252	927	3294	...	45
Koa-ohia	5	918	...	801	1287	...	...
Koa-mamane	...	171	...	324	1422	...	...
Mamane-naio	...	...	...	...	9	54	...
Mamane	...	...	...	...	1071	603	...
Other natives	...	333	...	189	81	...	...
Intro. trees	...	...	...	...	225	...	...
Treeless	...	...	18	...	54	...	...
Common Peafowl							
Range (km²)	...	...	...	...	239	...	...
Stations in range	...	...	...	...	545	...	...
Stations occupied	...	...	...	...	175	...	...
Birds recorded	...	...	...	...	953	...	...
Total population	...	...	...	...	83	...	...
SE	...	...	...	...	5	...	...
Pop. by habitat type							
Ohia	...	...	...	...	31	...	...
Koa-ohia	...	...	...	...	21	...	...

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Mamane	...	...	...	...	17	...	...
Other natives	...	...	...	...	6	...	...
Intro. trees	...	...	...	...	8	...	...
Wild Turkey							
Range (km²)	11	157	...	...	834	139	...
Stations in range	18	319	...	...	1960	317	...
Stations occupied	1	73	...	...	920	13	...
Birds recorded	1	222	...	...	3117	21	...
Total population	4	322	...	...	1616	42	...
SE	4	32	...	...	65	13	...
Pop. by habitat type							
Ohia	4	...	...	...	644	...	...
Koa-ohia	...	224	...	...	347	...	...
Koa-mamane	...	13	...	...	350	...	...
Mamane-naio	...	...	...	...	3	7	...
Mamane	...	...	...	...	231	35	...
Other natives	...	77	...	...	13	...	...
Intro. trees	...	8	...	...	27	...	...
Treeless	...	...	...	...	1	...	...
California Quail							
Range (km²)	...	65	34	220	465	139	...
Stations in range	...	151	71	361	1101	317	...
Stations occupied	...	24	9	151	333	84	...
Birds recorded	...	69	15	545	863	372	...
Total population	...	36	49	457	820	1408	...
SE	...	9	19	30	69	337	...
Pop. by habitat type							
Ohia	...	14	47	189	287	...	...
Koa-ohia	...	13	...	74	6	...	...
Koa-mamane	...	1	...	112	219	...	...
Mamane-naio	...	...	...	...	7	745	...
Mamane	...	...	...	...	274	663	...
Other natives	...	7	...	83	14	...	...
Intro. trees	...	...	...	...	13	...	...
Treeless	...	...	2	...	...	...	...
Spotted Dove							
Range (km²)	9	70	126	16	299	...	30
Stations in range	22	180	295	10	731	...	53
Stations occupied	9	16	60	6	145	...	2
Birds recorded	21	30	193	9	328	...	2
Total population	95	39	258	7	296	...	8
SE	35	8	35	2	24	...	6
Pop. by habitat type							
Ohia	80	10	256	7	132	...	2
Koa-ohia	15	5	...	...	58	...	...
Koa-mamane	...	...	...	...	1	...	...
Mamane	...	...	...	...	3	...	...
Other natives	...	19	...	...	4	...	...
Intro. trees	...	5	...	...	95	...	...
Treeless	...	...	2	...	2	...	6
Zebra Dove							
Range (km²)	...	37	...	64	515	...	...
Stations in range	...	97	...	42	1235	...	...
Stations occupied	...	7	...	5	342	...	...
Birds recorded	...	16	...	14	936	...	...
Total population	...	41	...	11	1114	...	...
SE	...	13	...	3	73	...	...

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Pop. by habitat type							
Ohia	...	19	...	3	554	...	...
Koa-ohia	...	22	...	3	139	...	...
Koa-mamane	...	...	...	...	147	...	...
Mamane	...	...	...	...	90	...	...
Other natives	...	...	...	4	29	...	...
Intro. trees	...	...	...	...	148	...	...
Treeless	...	...	...	...	6	...	...
Mourning Dove							
Range (km^2)	...	...	...	...	75	...	...
Stations in range	...	...	...	...	203	...	...
Stations occupied	...	...	...	...	12	...	...
Birds recorded	...	...	...	...	12	...	...
Total population	...	...	...	...	8	...	...
SE	...	...	...	...	3	...	...
Pop. by habitat type							
Ohia	...	...	...	...	7	...	...
Koa-mamane	...	...	...	...	2	...	...
Common Barn-Owl							
Stations occupied	...	1	...	...	1	...	1
Birds recorded	...	1	...	...	1	...	1
Eurasian Skylark							
Range (km^2)	7	103	15	177	663	139	...
Stations in range	19	192	54	268	1571	317	...
Stations occupied	1	57	1	65	653	160	1
Birds recorded	1	124	1	186	1958	421	1
Total population	19	395	1	445	4678	4461	...
SE	19	52	1	46	161	342	...
Pop. by habitat type							
Ohia	19	17	1	168	1183	...	...
Koa-ohia	...	114	...	95	401	...	...
Koa-mamane	...	109	...	51	1240	...	...
Mamane-naio	...	...	...	...	5	724	...
Mamane	...	...	...	...	1516	3737	...
Other natives	...	154	...	131	148	...	...
Intro. trees	...	...	...	...	94	...	...
Treeless	...	...	...	...	92	...	...
Melodious Laughing-thrush							
Range (km^2)	...	896	246	5	61	97	110
Stations in range	...	2131	621	28	120	234	207
Stations occupied	...	661	355	1	9	28	109
Birds recorded	...	1412	1102	1	23	44	310
Total population	...	5406	3146	1	12	284	1445
SE	...	203	127	1	4	58	121
Pop. by habitat type							
Ohia	...	2323	3146	...	12	...	1405
Koa-ohia	...	2682	...	...	...	...	...
Koa-mamane	...	...	...	1	...	...	...
Mamane-naio	...	...	...	...	...	284	...
Other natives	...	8	...	...	...	...	...
Intro. trees	...	385	...	...	...	...	40
Treeless	...	8	...	...	...	...	...
Red-billed Leiothrix							
Range (km^2)	278	973	8	63	712	139	111
Stations in range	793	2187	15	134	1636	317	204
Stations occupied	418	1260	2	24	518	44	142

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Birds recorded	1064	4452	3	43	1681	81	550
Total population	15,398	60,547	30	582	11,289	1807	8233
SE	658	1417	21	86	474	299	624
Pop. by habitat type							
Ohia	9275	32,329	30	102	4810	...	7670
Koa-ohia	6123	26,961	...	245	3859	...	...
Koa-mamane	...	3	...	53	937	...	...
Mamane-naio	...	...	...	...	4	1709	...
Mamane	...	...	...	...	1217	98	...
Other natives	...	88	...	19	83	...	...
Intro. trees	...	1165	...	...	379	...	563
Treeless	...	2	...	162	...	...	...
Northern Mockingbird							
Range (km^2)	...	...	...	...	10	97	...
Stations in range	...	...	...	...	20	234	...
Stations occupied	...	...	...	...	5	34	...
Birds recorded	...	...	...	...	8	38	...
Total population	...	...	...	...	32	439	...
SE	...	...	...	...	13	85	...
Pop. by habitat type							
Ohia	...	...	...	...	32	...	...
Mamane-naio	...	...	...	...	...	371	...
Mamane	...	...	...	...	...	68	...
Common Myna							
Range (km^2)	9	138	35	72	355	97	...
Stations in range	11	307	75	136	828	234	...
Stations occupied	2	83	21	31	265	2	...
Birds recorded	9	335	71	101	1069	9	...
Total population	39	1170	337	171	2652	90	...
SE	19	117	69	23	164	63	...
Pop. by habitat type							
Ohia	39	312	337	56	712	...	...
Koa-ohia	...	355	...	25	1168	...	...
Koa-mamane	...	191	...	40	556	...	...
Mamane-naio	...	...	...	...	2	90	...
Mamane	...	...	...	...	76	...	...
Other natives	...	311	...	49	51	...	...
Intro. trees	...	...	...	...	87	...	...
Japanese White-eye							
Range (km^2)	329	1095	269	276	1228	139	121
Stations in range	868	2426	668	462	2832	317	215
Stations occupied	573	2150	643	234	2251	178	156
Birds recorded	2308	11,635	4254	1041	11,069	484	742
Total population	129,598	638,018	158,182	26,414	302,235	34,614	48,038
SE	4254	8958	3249	1259	5402	2420	2549
Pop. by habitat type							
Ohia	107,028	303,006	155,678	8769	167,170	...	46,705
Koa-ohia	22,570	300,711	...	14,261	73,416	...	...
Koa-mamane	...	3579	...	2425	18,144	...	...
Mamane-naio	...	...	...	...	650	26,671	...
Mamane	...	...	...	...	9242	7943	...
Other natives	...	9685	...	866	3402	...	...
Intro. trees	...	20,503	...	...	28,332	...	1332
Treeless	...	355	2504	93	1879	...	...
Northern Cardinal							
Range (km^2)	140	829	259	142	1232	97	81

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
Stations in range	375	1944	632	275	2849	234	176
Stations occupied	68	574	346	140	2207	29	40
Birds recorded	143	1188	1030	426	7617	43	81
Total population	1359	9413	6044	1360	28,445	493	604
SE	231	419	286	85	498	94	92
Pop. by habitat type							
Ohia	1041	2269	6044	247	12,422	···	539
Koa-ohia	318	6343	···	808	7129	···	···
Koa-mamane	···	···	···	205	3696	···	···
Mamane-naio	···	···	···	···	81	436	···
Mamane	···	···	···	···	1869	57	···
Other natives	···	51	···	99	332	···	···
Intro. trees	···	751	···	···	2582	···	65
Treeless	···	···	···	1	335	···	···
Saffron Finch							
Range (km²)	···	···	···	···	123	···	···
Stations in range	···	···	···	···	307	···	···
Stations occupied	···	···	···	···	70	···	···
Birds recorded	···	···	···	···	156	···	···
Total population	···	···	···	···	2388	···	···
SE	···	···	···	···	294	···	···
Pop. by habitat type							
Ohia	···	···	···	···	1035	···	···
Koa-ohia	···	···	···	···	80	···	···
Mamane	···	···	···	···	574	···	···
Other natives	···	···	···	···	71	···	···
Intro. trees	···	···	···	···	629	···	···
House Finch							
Range (km²)	25	348	229	261	1181	139	61
Stations in range	36	676	554	471	2773	317	151
Stations occupied	1	214	130	246	1600	196	10
Birds recorded	1	1495	473	923	7037	735	12
Total population	47	21,898	7301	8111	65,743	23,742	253
SE	42	2201	610	533	1622	2299	83
Pop. by habitat type							
Ohia	47	2232	6901	4050	35,600	···	245
Koa-ohia	···	11,008	···	2928	12,153	···	···
Koa-mamane	···	1523	···	630	5181	···	···
Mamane-naio	···	···	···	···	351	14,482	···
Mamane	···	···	···	···	5964	9261	···
Other natives	···	6466	···	500	2241	···	···
Intro. trees	···	668	···	···	3688	···	9
Treeless	···	···	400	3	565	···	···
Yellow-fronted Canary							
Range (km²)	···	···	···	···	134	···	···
Stations in range	···	···	···	···	301	···	···
Stations occupied	···	···	···	···	76	···	···
Birds recorded	···	···	···	···	286	···	···
Total population	···	···	···	···	4464	···	···
SE	···	···	···	···	418	···	···
Pop. by habitat type		···	···	···		···	···
Ohia	···	···	···	···	3716	···	···
Koa-ohia	···	···	···	···	398	···	···
Mamane	···	···	···	···	64	···	···
Other natives	···	···	···	···	130	···	···
Intro. trees	···	···	···	···	157	···	···

TABLE 33
CONTINUED

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala
House Sparrow							
Stations occupied	...	3	2	...	2	6	...
Birds recorded	...	8	4	...	4	305	...
Red-cheeked Cordonbleu							
Range (km²)	...	...	...	...	22	...	...
Stations in range	...	...	...	...	54	...	...
Stations occupied	...	...	...	...	2	...	...
Birds recorded	...	...	...	...	3	...	...
Total population	...	...	...	...	32	...	...
SE	...	...	...	...	23	...	...
Pop. by habitat type							
Ohia	...	...	...	...	18	...	...
Other natives	...	...	...	...	14	...	...
Lavender Waxbill							
Range (km²)	...	...	...	...	20	...	...
Stations in range	...	...	...	...	46	...	...
Stations occupied	...	...	...	...	5	...	...
Birds recorded	...	...	...	...	9	...	...
Total population	...	...	...	...	234	...	...
SE	...	...	...	...	60	...	...
Pop. by habitat type							
Ohia	...	...	...	...	19	...	...
Other natives	...	...	...	...	18	...	...
Intro. trees	...	...	...	...	197	...	...
Warbling Silverbill							
Range (km²)	...	...	...	...	157	97	...
Stations in range	...	...	...	...	375	234	...
Stations occupied	...	...	...	...	72	1	...
Birds recorded	...	...	...	...	127	4	...
Total population	...	...	...	...	3536	486	...
SE	...	...	...	...	669	486	...
Pop. by habitat type							
Ohia	...	...	...	...	2542	...	...
Koa-ohia	...	...	...	...	13	...	...
Mamane-naio	...	...	...	...	21	486	...
Mamane	...	...	...	...	58	...	...
Other natives	...	...	...	...	604	...	...
Intro. trees	...	...	...	...	299	...	...
Nutmeg Mannikin							
Range (km²)	...	375	150	40	307	139	44
Stations in range	...	890	373	41	800	317	100
Stations occupied	...	61	31	11	86	4	12
Birds recorded	...	151	52	23	197	29	21
Total population	...	10,316	2449	657	6367	3703	1353
SE	...	1151	519	226	1007	2078	295
Pop. by habitat type							
Ohia	...	3181	2449	...	3538	...	1353
Koa-ohia	...	2635	...	648	806	...	...
Mamane-naio	...	...	...	...	...	3301	...
Mamane	...	...	...	...	281	402	...
Other natives	...	326	...	9	161	...	...
Intro. trees	...	4174	...	...	1582	...	...

TABLE 34

SUMMARY STATISTICS FOR INTRODUCED BIRDS IN THE STUDY AREAS ON MAUI, MOLOKAI, LANAI, AND KAUAI

	East Maui	West Maui	Molokai	Lanai	Kauai
Black Francolin					
Range (km²)	4	...	67	...	...
Stations in range	15	...	313	...	...
Stations occupied	5	...	85	...	...
Birds recorded	24	...	246	...	...
Total population	8	...	151	...	...
SE	3	...	28	...	...
Pop. by habitat type					
Ohia	...	...	25	...	...
Other natives	8	...	60	...	...
Intro. trees	...	...	67	...	...
Erckel's Francolin					
Range (km²)	4	...	14	20	25
Stations in range	19	...	74	77	140
Stations occupied	3	...	13	41	4
Birds recorded	4	...	19	108	5
Total population	2	...	10	44	4
SE	2	...	3	7	2
Pop. by habitat type					
Ohia	...	...	5	...	4
Koa-ohia	1	...	...	...	...
Other natives	1	...	4	10	...
Intro. trees	...	...	1	27	...
Treeless	...	...	...	7	...
Gray Francolin					
Range (km²)	31	0.2	4	20	...
Stations in range	82	8	7	77	...
Stations occupied	22	2	2	4	...
Birds recorded	41	5	2	8	...
Total population	39	1	1	4	...
SE	9	1	1	3	...
Pop. by habitat type					
Ohia	...	1	...	...	...
Koa-ohia	1	...	...	...	...
Other natives	38	...	1	3	...
Intro. trees	1	...	...	1	
Chukar					
Range (km²)	46	0.2	14	...	...
Stations in range	262	8	56	...	...
Stations occupied	121	1	14	...	...
Birds recorded	549	1	30	...	...
Total population	1716	1	249	...	...
SE	203	1	79	...	...
Pop. by habitat type					
Ohia	31	1	239	...	...
Koa-ohia	15	...	...	...	...
Mamane	151	...	...	...	...
Other natives	617	...	10	...	...
Intro. trees	18	...	...	...	...
Treeless	883	...	...	...	...
Japanese Quail					
Range (km²)	9	...	...	...	...
Stations in range	29	...	...	...	...
Stations occupied	9	...	...	...	...
Birds recorded	29	...	...	...	...
Total population	133	...	...	...	...
SE	63	...	...	...	...

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Pop. by habitat type					
Koa-ohia	17	...	...	...	...
Other natives	115	...	...	...	...
Intro. trees	1	...	...	...	...
Red Junglefowl (Moa)					
Range (km²)	...	...	...	...	25
Stations in range	...	...	...	...	140
Stations occupied	...	...	...	...	24
Birds recorded	...	...	...	...	63
Total population	...	...	...	...	4
SE	...	...	...	...	1
Pop. by habitat type					
Ohia	...	...	...	...	4
Ring-necked Pheasant					
Range (km²)	153	...	14	20	25
Stations in range	425	...	80	77	140
Stations occupied	244	...	6	31	1
Birds recorded	1258	...	7	76	1
Total population	1728	...	9	162	9
SE	90	...	9	27	9
Pop. by habitat type					
Ohia	99	...	9	...	9
Koa-ohia	171	...	...	...	...
Mamane	54	...	...	...	...
Other natives	729	...	...	63	...
Intro. trees	54	...	...	63	...
Treeless	18	...	...	27	...
Common Peafowl					
Range (km²)	25	...	...	...	...
Stations in range	62	...	...	...	...
Stations occupied	21	...	...	...	...
Birds recorded	107	...	...	...	...
Total population	8	...	...	...	...
SE	1	...	...	...	...
Pop. by habitat type					
Koa-ohia	1	...	...	...	...
Other natives	7	...	...	...	...
Wild Turkey					
Range (km²)	9	...	...	...	...
Stations in range	24	...	...	...	...
Stations occupied	3	...	...	...	...
Birds recorded	4	...	...	...	...
Total population	2	...	...	...	...
SE	1	...	...	...	...
Pop. by habitat type					
Other natives	2	...	...	...	...
California Quail					
Range (km²)	37	...	...	20	...
Stations in range	81	...	...	77	...
Stations occupied	25	...	...	1	...
Birds recorded	56	...	...	3	...
Total population	50	...	...	7	...
SE	10	...	...	1	...
Pop. by habitat type					
Other natives	50	...	...	7	...

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Rock Dove					
Stations occupied	...	2	1	...	...
Birds recorded	...	8	2	...	...
Spotted Dove					
Range (km^2)	85	13	86	20	25
Stations in range	70	84	438	77	140
Stations occupied	44	7	148	10	14
Birds recorded	96	12	375	16	23
Total population	65	4	309	15	15
SE	9	1	29	5	5
Pop. by habitat type					
Ohia	17	4	165	...	15
Koa-ohia	2	...	...	...	...
Other natives	27	...	51	3	...
Intro. trees	18	...	93	13	...
Zebra Dove					
Range (km^2)	7	...	19	20	...
Stations in range	19	...	90	77	...
Stations occupied	15	...	22	5	...
Birds recorded	43	...	41	8	...
Total population	35	...	91	3	...
SE	4	...	32	2	...
Pop. by habitat type					
Ohia	...	...	1	...	...
Other natives	35	...	16	2	...
Intro. trees	...	...	74	1	...
Common Barn-Owl					
Stations occupied	...	...	1	...	...
Birds recorded	...	...	1	...	...
Eurasian Skylark					
Range (km^2)	87	...	...	...	...
Stations in range	220	...	...	...	...
Stations occupied	67	...	...	...	...
Birds recorded	172	...	...	...	...
Total population	381	...	...	...	...
SE	49	...	...	...	...
Pop. by habitat type					
Koa-ohia	14	...	...	...	...
Mamane	33	...	...	...	...
Other natives	274	...	...	...	...
Intro. trees	7	...	...	...	...
Treeless	2	...	...	...	...
Japanese Bush-Warbler					
Range (km^2)	17	...	27	...	...
Stations in range	48	...	172	...	...
Stations occupied	1	...	43	...	...
Birds recorded	1	...	164	...	...
Total population	5	...	202	...	...
SE	5	...	40	...	...
Pop. by habitat type					
Ohia	5	...	202	...	...
White-rumped Shama					
Range (km^2)	...	...	...	...	25
Stations in range	...	...	...	...	140

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Stations occupied	...	...	...	...	8
Birds recorded	...	...	...	...	15
Total population	...	...	...	...	45
SE	...	...	...	...	18
Pop. by habitat type					
Ohia	...	...	...	...	45
Melodious Laughing-thrush					
Range (km²)	290	19	...	...	25
Stations in range	863	135	...	...	140
Stations occupied	299	23	...	...	108
Birds recorded	724	47	...	...	450
Total population	2078	43	...	...	445
SE	138	11	...	...	37
Pop. by habitat type					
Ohia	1236	42	...	...	445
Koa-ohia	409	...	...	...	...
Mamane	2	...	...	...	...
Other natives	31	...	...	...	...
Intro. trees	370	1	...	...	...
Treeless	29	...	...	...	...
Red-billed Leiothrix					
Range (km²)	332	28	63	...	...
Stations in range	1005	135	358	...	...
Stations occupied	674	60	150	...	...
Birds recorded	2858	143	759	...	...
Total population	18,652	755	1836	...	...
SE	607	116	114	...	...
Pop. by habitat type					
Ohia	11,391	755	1831	...	...
Koa-ohia	3115	...	...	...	...
Mamane	1	...	...	...	...
Other natives	1199	...	...	...	...
Intro. trees	2686	...	5	...	...
Treeless	260	...	...	...	...
Northern Mockingbird					
Range (km²)	99	0.5	15	...	...
Stations in range	251	4	68	...	...
Stations occupied	147	2	13	...	...
Birds recorded	563	2	24	...	...
Total population	1122	1	69	...	...
SE	77	1	25	...	...
Pop. by habitat type					
Ohia	...	1	...	...	...
Koa-ohia	2	...	...	...	...
Mamane	12	...	...	...	...
Other nataives	939	...	38	...	...
Intro. trees	7	...	31	...	...
Treeless	162	...	...	...	...
Common Myna					
Range (km²)	24	...	11	20	...
Stations in range	63	...	46	77	...
Stations occupied	26	...	9	3	...
Birds recorded	94	...	25	3	...
Total population	185	...	136	22	...
SE	45	...	76	11	...

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Pop. by habitat type					
Koa-ohia	33	...	...	...	...
Other natives	136	...	57	6	...
Intro. trees	17	...	79	16	...
Japanese White-eye					
Range (km²)	384	43	125	20	25
Stations in range	1091	203	573	77	140
Stations occupied	818	178	554	72	138
Birds recorded	3727	773	4213	508	1471
Total population	113,968	19,230	119,092	11,380	15,231
SE	3767	1323	4518	1887	721
Pop. by habitat type					
Ohia	64,277	18,864	74,785	...	15,218
Koa-ohia	18,904	...	...	...	...
Mamane	82	...	...	...	...
Other natives	12,744	...	9751	4156	...
Intro. trees	13,666	65	34,463	5711	...
Treeless	4297	301	93	1513	12
Northern Cardinal					
Range (km²)	311	21	116	20	25
Stations in range	896	121	488	77	140
Stations occupied	242	16	163	65	37
Birds recorded	697	31	305	304	68
Total population	2937	55	1741	1116	111
SE	187	16	142	152	20
Pop. by habitat type					
Ohia	1120	54	671	...	111
Koa-ohia	385	...	...	...	...
Mamane	1	...	...	...	...
Other natives	660	...	110	268	...
Intro. trees	713	2	959	704	...
Treeless	59	...	1	144	...
House Finch					
Range (km²)	134	21	112	20	25
Stations in range	417	111	496	77	140
Stations occupied	157	9	174	9	1
Birds recorded	862	16	416	23	2
Total population	7635	123	5321	614	22
SE	500	68	652	202	22
Pop. by habitat type					
Ohia	11	116	2131	...	22
Koa-ohia	1013	...	...	...	...
Mamane	3	...	...	...	...
Other natives	3753	...	717	46	...
Intro. trees	2733	2	2470	332	...
Treeless	123	4	3	236	...
House Sparrow					
Stations occupied	5	...	...	...	...
Birds recorded	11	...	...	...	...
Nutmeg Mannikin					
Range (km²)	113	26	97	...	25
Stations in range	116	122	421	...	140
Stations occupied	64	21	94	...	1
Birds recorded	190	106	444	...	4
Total population	8192	3290	10,619	...	128
SE	1507	1117	1851	...	128

TABLE 34
CONTINUED

	East Maui	West Maui	Molokai	Lanai	Kauai
Pop. by habitat type					
Ohia	2051	3290	3077	···	128
Koa-ohia	1626	···	···	···	···
Other natives	3242	···	1188	···	···
Intro. trees	1253	···	5868	···	···
Treeless	19	···	485	···	···

TABLE 35
DENSITY [MEAN (SE)] OF THE BLACK FRANCOLIN AND GRAY FRANCOLIN BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Black Francolin					Gray Francolin			
	Kona	Mauna Kea	Kohala	East Maui	Molokai	East Maui	West Maui	Molokai	Lanai
Elevation									
100–300 m	···	···	···	···	0	···	···	0	···
300–500 m	+ (+)	···	0	0	+ (+)	0	···	0	···
500–700 m	1 (+)	···	0	0	3 (1)	0	0	0	+ (+)
700–900 m	1 (+)	···	0	4 (2)	3 (1)	3 (2)	4 (4)	1 (+)	+ (+)
900–1100 m	+ (+)	···	+ (+)	2 (1)	2 (+)	2 (1)	+	+ (+)	1(1)
1100–1300 m	2 (+)	···	+ (+)	+ (+)	+ (+)	5 (1)	+	0	···
1300–1500 m	1 (+)	···	0	0	+ (+)	1 (+)	0	0	···
1500–1700 m	1 (+)	···	0	0	···	+ (+)	0	···	···
1700–1900 m	+ (+)	···	···	0	···	+ (+)	0	···	···
1900–2100 m	+ (+)	+ (+)	···	0	···	1 (1)	···	···	···
2100–2300 m	+ (+)	+ (+)	···	0	···	+ (+)	···	···	···
2300–2500 m	0	0	···	0	···	+ (+)	···	···	···
2500–2700 m	···	0	···	0	···	+ (+)	···	···	···
2700–2900 m	···	0	···	0	···	+ (+)	···	···	···
2900–3100 m	···	0	···	···	···	···	···	···	···
Habitat									
Ohia	1 (+)	···	+ (+)	0	1 (+)	0	+ (+)	0	···
Koa-ohia	+ (+)	···	···	0	···	+ (+)	···	···	···
Koa-mamane	*	···	···	···	···	···	···	···	···
Mamane-naio	2 (+)	+ (+)	···	···	···	···	···	···	···
Mamane	1 (+)	+ (+)	···	0	···	0	···	···	···
Other natives	2 (+)	···	···	2 (1)	4 (1)	2 (1)	···	+ (+)	1 (+)
Intro. trees	1 (1)	···	+ (+)	0	4 (1)	1 (1)	0	+ (+)	+ (+)
Treeless	+ (+)		+		+ (+)	+ (+)	0	0	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area, * indicates stratum was not sampled in range but was sampled elsewhere in study area.

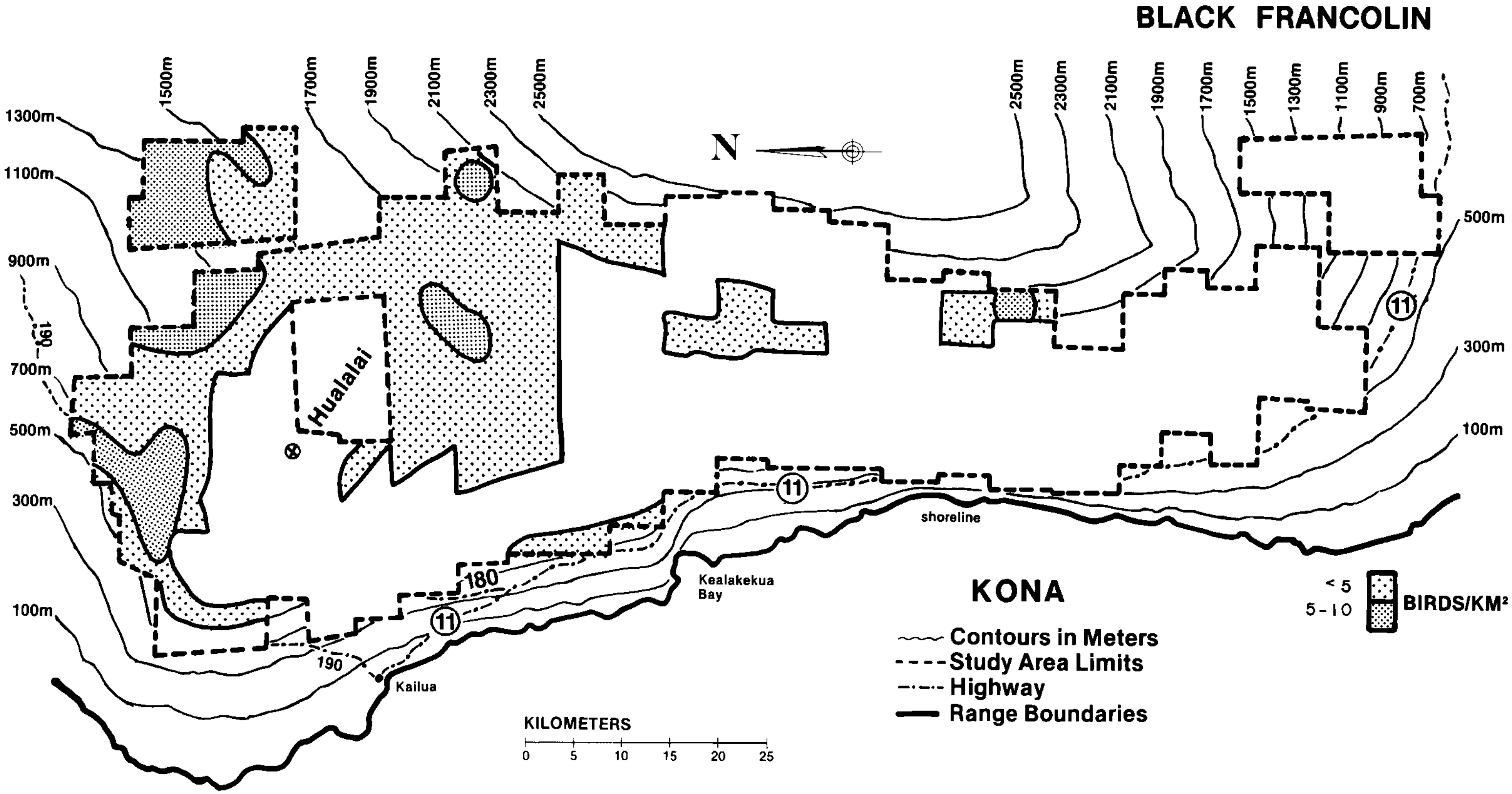


FIGURE 160. Distribution and abundance of the Black Francolin in the Kona study area.

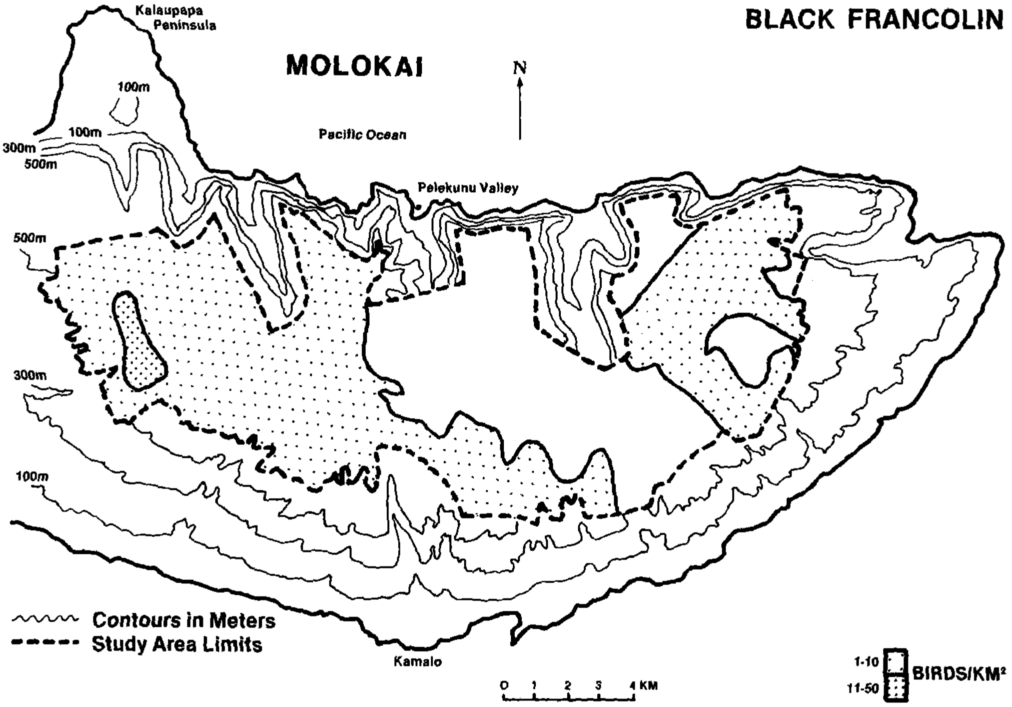


FIGURE 161. Distribution and abundance of the Black Francolin in the Molokai study area.

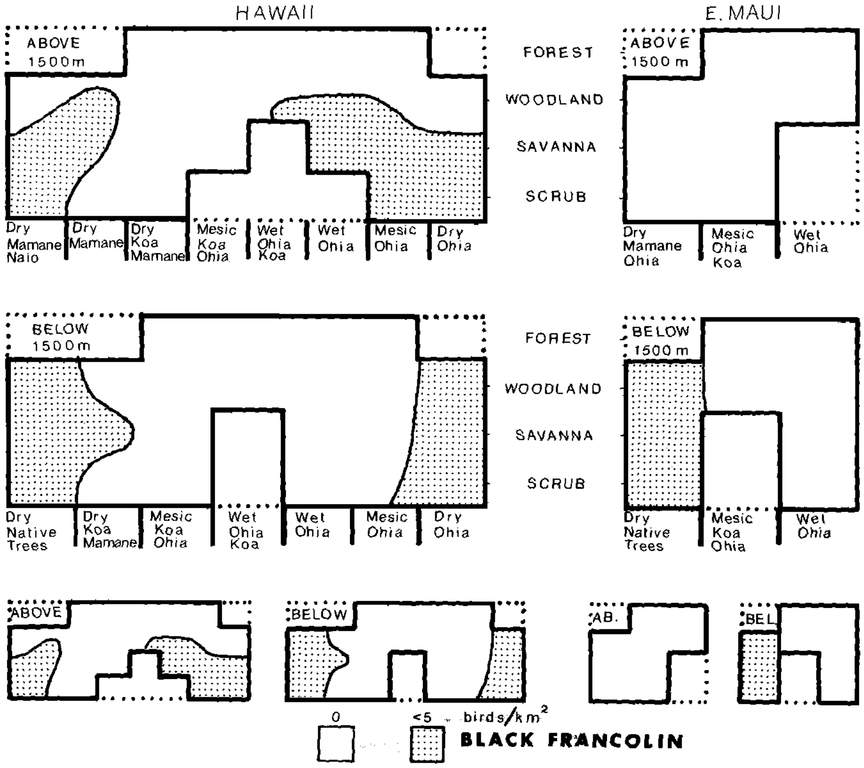


FIGURE 162. Habitat response graphs of the Black Francolin. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 36

Regression Models for Habitat Response of the Black Francolin, Erckel's Francolin, and Gray Francolin[a]

	Black Francolin		Erckel's Francolin				Gray Francolin	
	Kona	Molokai	Puna	Kipukas	Kona	Mauna Kea	Maui	Lanai
R^2	0.10*	0.23*	0.60*	0.32*	0.26*	0.07*	0.24*	0.18
Moisture	−9.1*	−7.7*	−7.6*	−4.9*	−16.5*	X	−8.5*	−3.4
Elevation	4.0*	4.8*	6.5*	−11.2*	···	−2.2	···	···
(Elevation)^2	−5.6*	−4.2*	−6.6*	10.7*	−20.2*	···	−5.9*	···
Tree biomass	···	···	···	3.6*	3.5*	···	4.8*	···
(Tree biomass)^2	···	···	7.6*	···	−4.4*	···	···	···
Crown cover	···	···	−3.9*	−3.2	···	···	−3.8*	2.6
Canopy height	5.4*	···	−4.0*	···	3.9*	3.3	···	···
Koa	−5.1*	X	X	3.2	···	X	···	X
Ohia	−6.4*	···	6.9*	···	−3.3*	X	···	···
Naio	···	X	X	···	−4.6*	···	X	X
Mamane	−4.1*	X	···	···	···	···	−2.6	X
Intro. trees	−2.3	3.1	···	X	3.6*	X	−2.7	···
Shrub cover	3.9*	···	2.6	···	···	···	−7.7*	···
Ground cover	···	···	···	···	6.8*	···	6.1*	···
Native shrubs	···	···	6.0*	···	···	X	···	···
Intro. shrubs	···	···	···	···	−5.1*	X	···	···
Ground ferns	···	···	−3.8*	···	···	X	···	X
Matted ferns	···	···	···	···	···	X	···	···
Tree ferns	···	···	−6.1*	X	···	X	···	X
Ieie	···	X	···	X	···	X	···	X
Passiflora	···	X	X	X	6.7*	X	11.2*	X
Native herbs	···	···	···	···	···	X	···	X
Intro. herbs	···	···	2.7	−3.0	···	···	···	X
Native grasses	···	···	−3.4*	···	4.1*	···	···	X
Intro. grasses	3.4*	···	···	···	···	···	···	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

ERCKEL'S FRANCOLIN (*Francolinus erckelii*)

Erckel's Francolins were introduced to all major islands between 1957 and 1962 (R. L. Walker, pers. comm.) and are native to northeast Africa (Berger 1981). They occur alone or in flocks, and feed on grass shoots, insects, and seeds; drinking water may also be a requirement (Mackworth-Praed and Grant 1957). In their native range, they occur in high-elevation semi-arid open scrub and open woodlands (Bohl 1972).

We found this species in all but three study areas (Tables 33, 34, 37; Figs. 163–167). On Hawaii 1800 ± 150 (95% CI) birds inhabit the study areas. Populations are well established in the Mauna Kea mamane-naio woodland, on the north slope of Hualalai, in the Puu Lehua/Devil Country area south of Hualalai, on the Kahuku Tract, on the Kapapala Tract, and along the east margin of the Kau Desert. Their range is probably still expanding on Hawaii. On Maui an estimated 2 ± 4 birds occur on the northwest slopes of Haleakala. On Molokai 10 ± 6 birds occur in the dry scrublands in the southwest part of the study area. On Lanai 45 ± 15 birds occur throughout the study area. On Kauai, birds occur occasionally in forest clearings along trails, particularly near the tops of dry canyons. Well established populations occur on all these islands outside the study areas.

Highest densities occur in dry open woodlands at lower elevations (Table 36, Fig. 168). They are strongly associated with passiflora and are probable dispersal agents of banana poka (Warshauer et al. 1983). No variable meets the entry criteria in the Lanai regression model.

Erckel's Francolins primarily occur in dry areas. Even in the Kipukas, the driest study area, a negative relation to moisture occurs. The Kipukas model shows a curious bimodal relation for elevation that reflects the distribution of birds at the tops and bottoms of certain transects, but not in the middle. This separation may represent birds arriving at lower elevations from the population in Puna and birds arriving independently from the high elevation population. Future dispersal may close the hiatus.

In Kona, Erckel's Francolins are associated with

TABLE 37
DENSITY [MEAN (SE)] OF THE ERCKEL'S FRANCOLIN BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	East Maui	Molokai	Lanai	Kauai
Elevation									
100–300 m	···	···	···	···	···	···	0	···	···
300–500 m	0	0	···	0	···	0	0	···	···
500–700 m	0	+ (+)	···	7 (1)	···	0	0	4 (1)	···
700–900 m	0	17 (2)	···	9 (1)	···	1 (1)	+ (+)	3 (1)	···
900–1100 m	0	8 (1)	···	7 (1)	···	+ (+)	1 (+)	3 (1)	···
1100–1300 m	0	+ (+)	5 (1)	5 (1)	···	+ (+)	2 (1)	···	+ (+)
1300–1500 m	0	···	+ (+)	4 (+)	···	*	0	···	+ (+)
1500–1700 m	0	···	+ (+)	1 (+)	···	1 (1)	···	···	···
1700–1900 m	+ (+)	···	1 (1)	1 (+)	···	0	···	···	···
1900–2100 m	0	···	+ (+)	1 (+)	4 (1)	0	···	···	···
2100–2300 m	0	···	0	+ (+)	5 (2)	0	···	···	···
2300–2500 m	···	···	···	+ (+)	4 (2)	0	···	···	···
2500–2700 m	···	···	···	···	2 (1)	0	···	···	···
2700–2900 m	···	···	···	···	3 (1)	0	···	···	···
2900–3100 m	···	···	···	···	+ (+)	···	···	···	···
Habitat									
Ohia	0	10 (1)	+ (+)	3 (+)	···	0	2 (1)	···	+ (+)
Koa-ohia	+ (+)	···	2 (+)	4 (1)	···	2 (2)	···	···	···
Koa-mamane	+ (+)	···	1 (+)	+ (+)	···	···	···	···	···
Mamane-naio	···	···	···	5 (1)	4 (1)	···	···	···	···
Mamane	···	···	···	4 (1)	3 (1)	0	···	···	···
Other natives	+ (+)	···	+ (+)	6 (1)	···	+ (+)	1 (+)	1 (1)	···
Intro. trees	+ (+)	···	···	7 (1)	···	+ (+)	+ (+)	4 (1)	···
Treeless	0	+ (+)	+ (+)	+ (+)	···	0	+ (+)	2 (1)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area, * indicates stratum was not sampled in range but was sampled elsewhere in study area.

sparse woodland and scattered high trees. Some response to individual tree species also occurs in the regression models. Ohia generates a positive response in Puna, where birds frequent spindly open ohia groves on recent substrates in drier areas. The negative tree fern term for Puna represents absence in rainforest interiors. In Kona lower densities are associated with naio and higher ones with introduced trees.

Erckel's Francolins also respond to some understory components. In Puna they are associated with dry native shrubs on recent substrates. In Kona low densities occur in dense shrub thickets of guava and Christmas-berry at lower elevations. The strong response to passiflora in Kona is paralleled by their occurrence in Hamakua and on Maui at passiflora infestations. Little response to herbs or grasses occurs. The difference in signs for native grasses in Puna and Kona results from the distribution of native graminoids in wet forest interiors in Puna where birds are absent, and in dry grassy woodlands in Kona where birds are common. Native grasses thus indicate different habitat types in these two study areas.

GRAY FRANCOLIN
(*Francolinus pondicerianus*)

Gray Francolins were introduced in 1958 (R. L. Walker, pers. comm.) and are native to India (Berger 1981). There they inhabit dry open grasslands and xerophytic thorn-scrub (Ali and Ripley 1969) and feed extensively on plants and insects (Bump 1970).

We found Gray Francolins in the Kona, East Maui, West Maui, Molokai, and Lanai study areas (Tables 33–35, Fig. 169). Although rare on Oahu (R. L. Walker, pers. comm.), Gray Francolins are well established in the drier lowland areas of all the major islands, especially from sea level to 1000 m elevation (Lewin 1971). Only the extreme upper elevations of the range of this species fall in our study areas. We considered the two birds recorded near the lower study boundary at Puu Waawaa to be extralimital.

Gray Francolins are associated with scrublands and sparse woodlands in dry low-elevation areas, but appear to avoid brushy understories (Table 36, Fig. 170). Although we had too few observations to construct a habitat response graph, the areas inhabited on Hawaii are similar

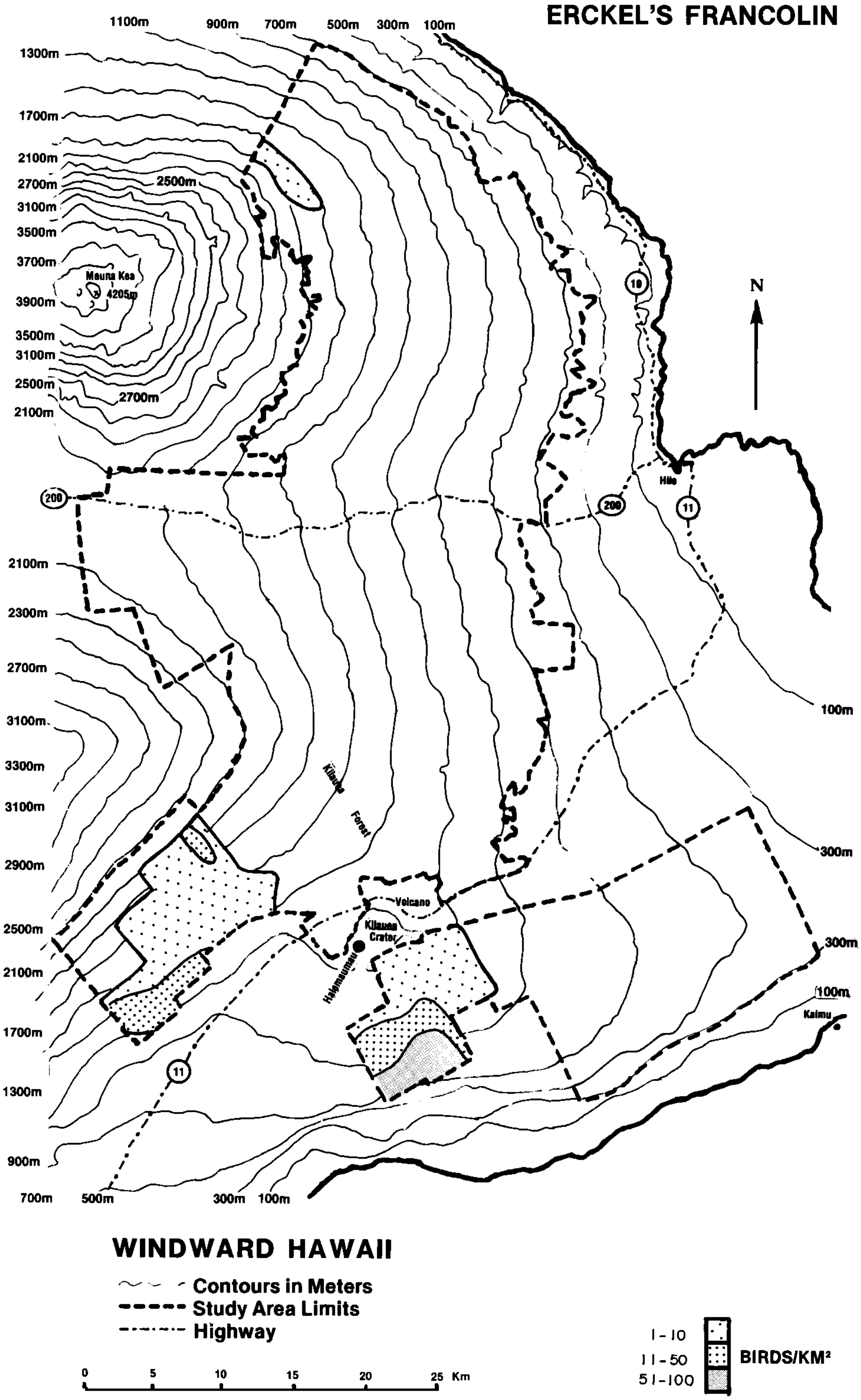


FIGURE 163. Distribution and abundance of the Erckel's Francolin in the windward Hawaii study areas.

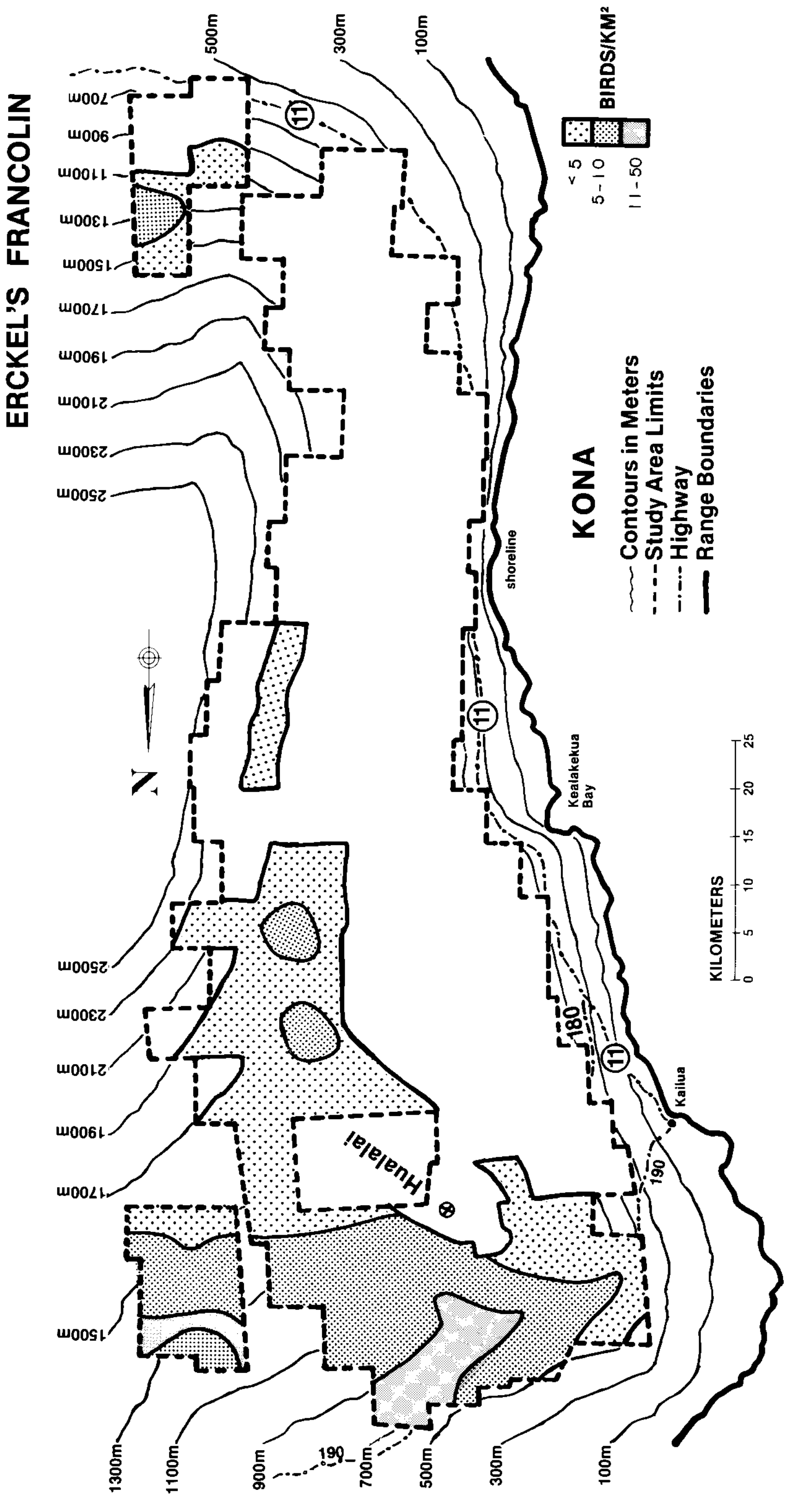


FIGURE 164. Distribution and abundance of the Erckel's Francolin in the Kona study area.

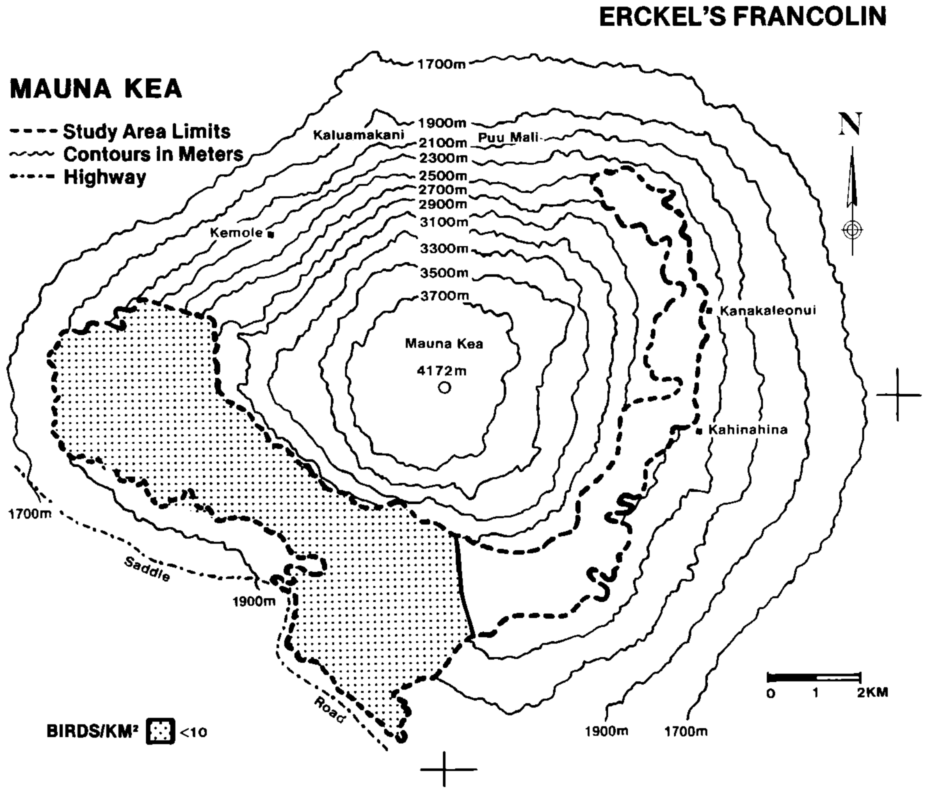


FIGURE 165. Distribution and abundance of the Erckel's Francolin in the Mauna Kea study area.

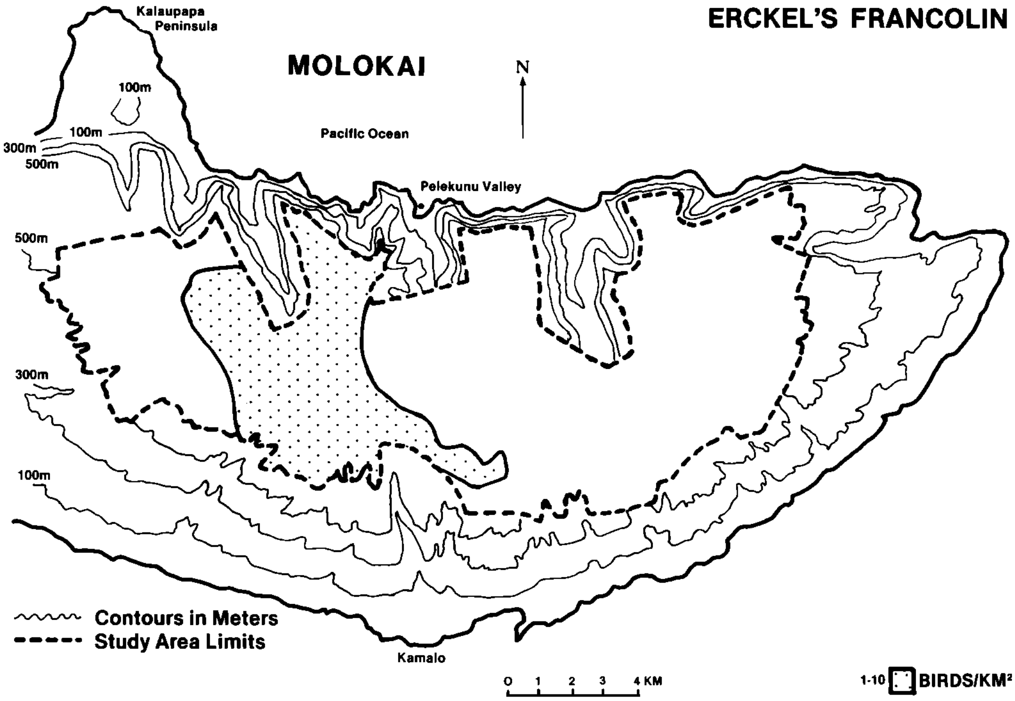


FIGURE 166. Distribution and abundance of the Erckel's Francolin in the Molokai study area.

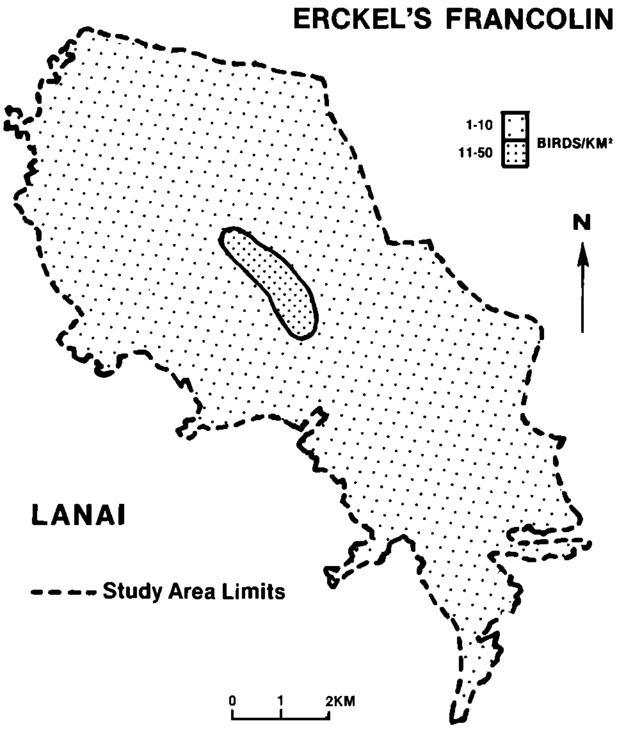
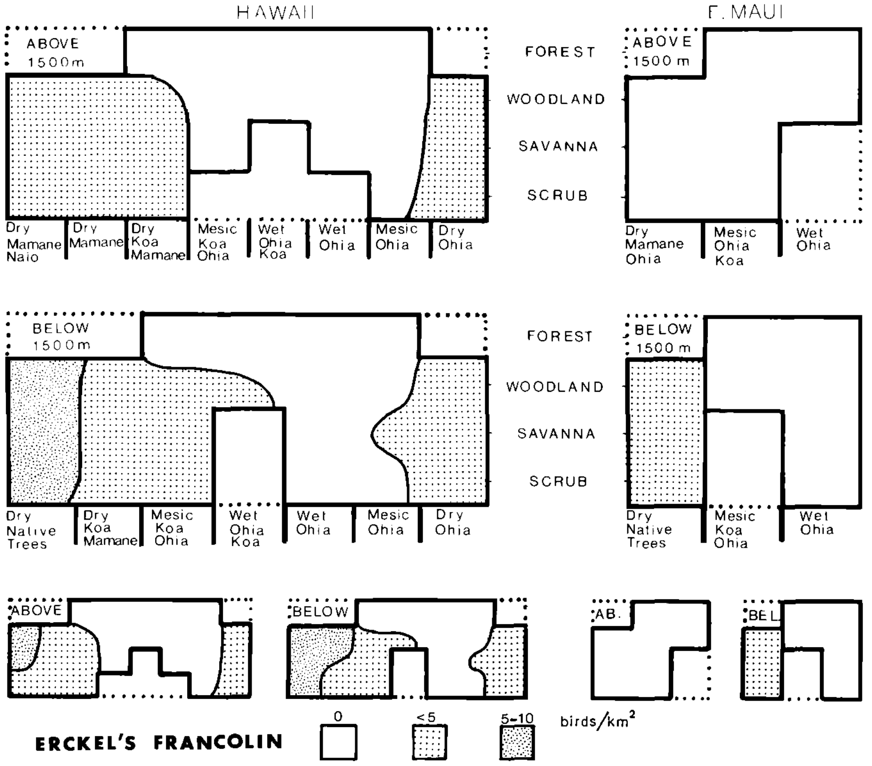


FIGURE 167. Distribution and abundance of the Erckel's Francolin in the Lanai study area.



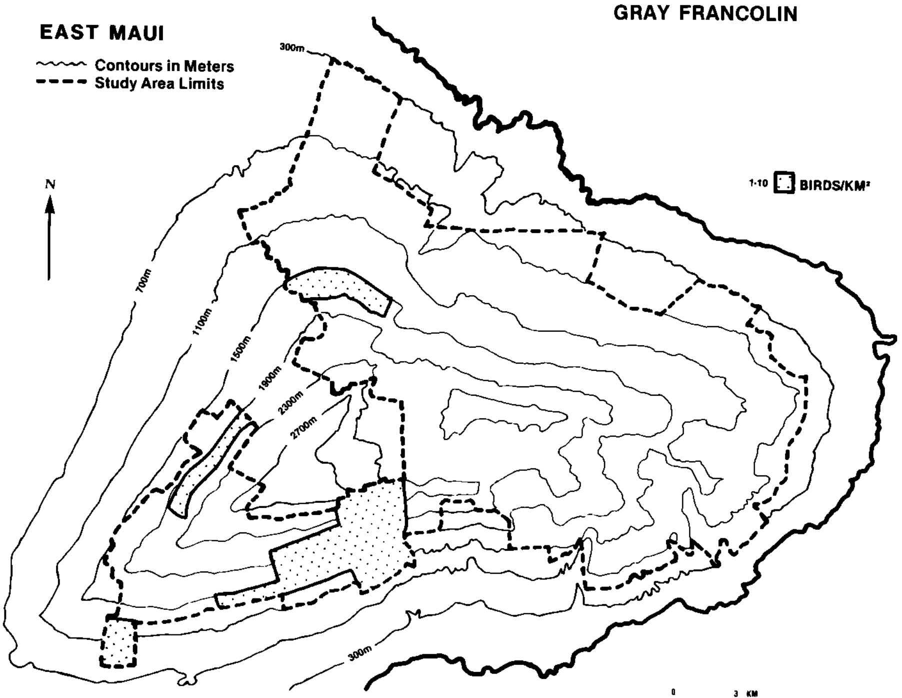


FIGURE 169. Distribution and abundance of the Gray Francolin in the East Maui study area.

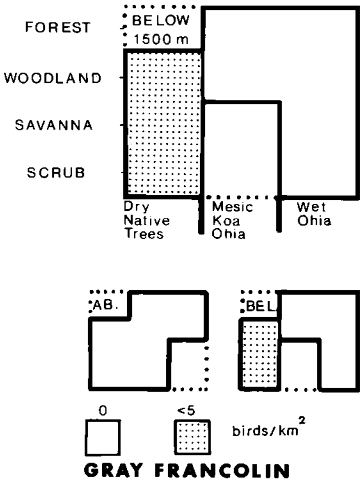


FIGURE 170. Habitat response graphs of the Gray Francolin. (Graphs give mean density below 1500 m elevation for East Maui; half-size graphs give standard deviation.)

←

FIGURE 168. Habitat response graphs of the Erckel's Francolin. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

to those shown for Maui. Gray Francolins are common in open mesquite woodland in lowland leeward Hawaii (Lewin 1971). The preference for passiflora is biologically significant, because Gray Francolins are possible dispersal agents for banana poka (Warshauer et al. 1983).

CHUKAR (*Alectoris chukar*)

Chukar were first introduced to the Hawaiian Islands in 1923 (Caum 1933) and are native to southern Eurasia. During their survey, Schwartz and Schwartz (1949) found very low numbers on Molokai and Lanai. Berger (1981) considered Chukar to be well established on all the main islands, although they may be absent from Oahu now, as there have been no game reports since 1979 (R. L. Walker, unpub. data). Chukar feed on grass, weeds, seeds, leaves, bulbs, fruits, berries, and insects (Bohl 1971). Because Chukar flock and we had no independent estimates of flock size, our sampling design did not yield unbiased density estimates.

Chukar have greatly increased since 1949 due to introduction. We found them well established in dry upland habitats on all study areas except Lanai (Tables 33, 34, 38, Figs. 171–175). On Hawaii 5500 ± 1300 (95% CI) birds occupy four study areas. They are best established on the upper slopes of Mauna Kea where 4200 ± 1100 birds occur. From release sites there and on Puu Waawaa, Chukar have spread across Hualalai and the upper elevations of windward Hawaii. On East Maui 1700 ± 400 birds are well established in Haleakala Crater and on the leeward side; these birds may compete with Hawaiian Geese for browse. On Molokai 250 ± 150 birds occur sparsely in dry open habitat. Although we failed to find Chukar on Lanai, Hirai (1978) reported birds at lower elevations near release sites.

The habitat response graphs (Fig. 176) and regression models (Table 39) show that Chukar occur at high elevations in dry areas with sparse tree and ground cover. Mamane is characteristic of this habitat configuration and usually has high Chukar densities.

Rocky slopes and water are two important habitat requirements for Chukar that were not examined as variables. Rocky slopes, including talus, bluffs, or rimrock, are essential to good Chukar habitat for escape routes and roosting sites, as is the presence of drinking water within 1 km (Johnsgaard 1973). In most areas where we

TABLE 38

DENSITY [MEAN (SE)] OF THE CHUKAR AND RED JUNGLEFOWL BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Chukar							Red Junglefowl	
	Hamakua	Kipukas	Kona	Mauna Kea	East Maui	West Maui	Molokai	Puna	Kauai
Elevation									
100–300 m	···	···	···	···	···	···	0	···	···
300–500 m	0	···	0	···	0	···	0	0	···
500–700 m	0	···	0	···	0	0	0	0	···
700–900 m	0	···	0	···	0	+ (+)	44 (4)	+ (+)	···
900–1100 m	0	···	15 (5)	···	0	2 (2)	30 (15)	+ (+)	···
1100–1300 m	0	0	39 (39)	···	30 (17)	+ (+)	17 (6)	+ (+)	+ (+)
1300–1500 m	0	0	3 (1)	···	15 (15)	0	0	···	+ (+)
1500–1700 m	3 (3)	+ (+)	2 (+)	···	16 (6)	0	···	···	···
1700–1900 m	6 (4)	4 (1)	2 (1)	···	9 (3)	0	···	···	···
1900–2100 m	46 (11)	3 (1)	5 (1)	6 (4)	19 (4)	···	···	···	···
2100–2300 m	5 (5)	4 (2)	8 (2)	16 (7)	26 (7)	···	···	···	···
2300–2500 m	···	···	2 (1)	6 (3)	17 (5)	···	···	···	···
2500–2700 m	···	···	···	24 (7)	21 (9)	···	···	···	···
2700–2900 m	···	···	···	68 (14)	7 (1)	···	···	···	···
2900–3100 m	···	···	···	171 (82)	···	···	···	···	···
Habitat									
Ohia	0	3 (1)	4 (1)	···	5 (5)	1 (1)	28 (9)	+ (+)	+ (+)
Koa-ohia	+ (+)	+ (+)	4 (3)	···	8 (7)	···	···	···	···
Koa-mamane	29 (9)	3 (1)	1 (+)	···	···	···	···	···	···
Mamane-naio	···	···	4 (4)	24 (5)	···	···	···	···	···
Mamane	···	···	6 (1)	38 (9)	103 (48)	···	···	···	···
Other natives	5 (3)	3 (2)	1 (1)	···	23 (4)	···	1 (1)	···	···
Intro. trees	+ (+)	···	7 (7)	···	5 (2)	0	+ (+)	···	···
Treeless	0	11 (11)	7 (2)	···	19 (3)	0	+ (+)	+ (+)	+ (+)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

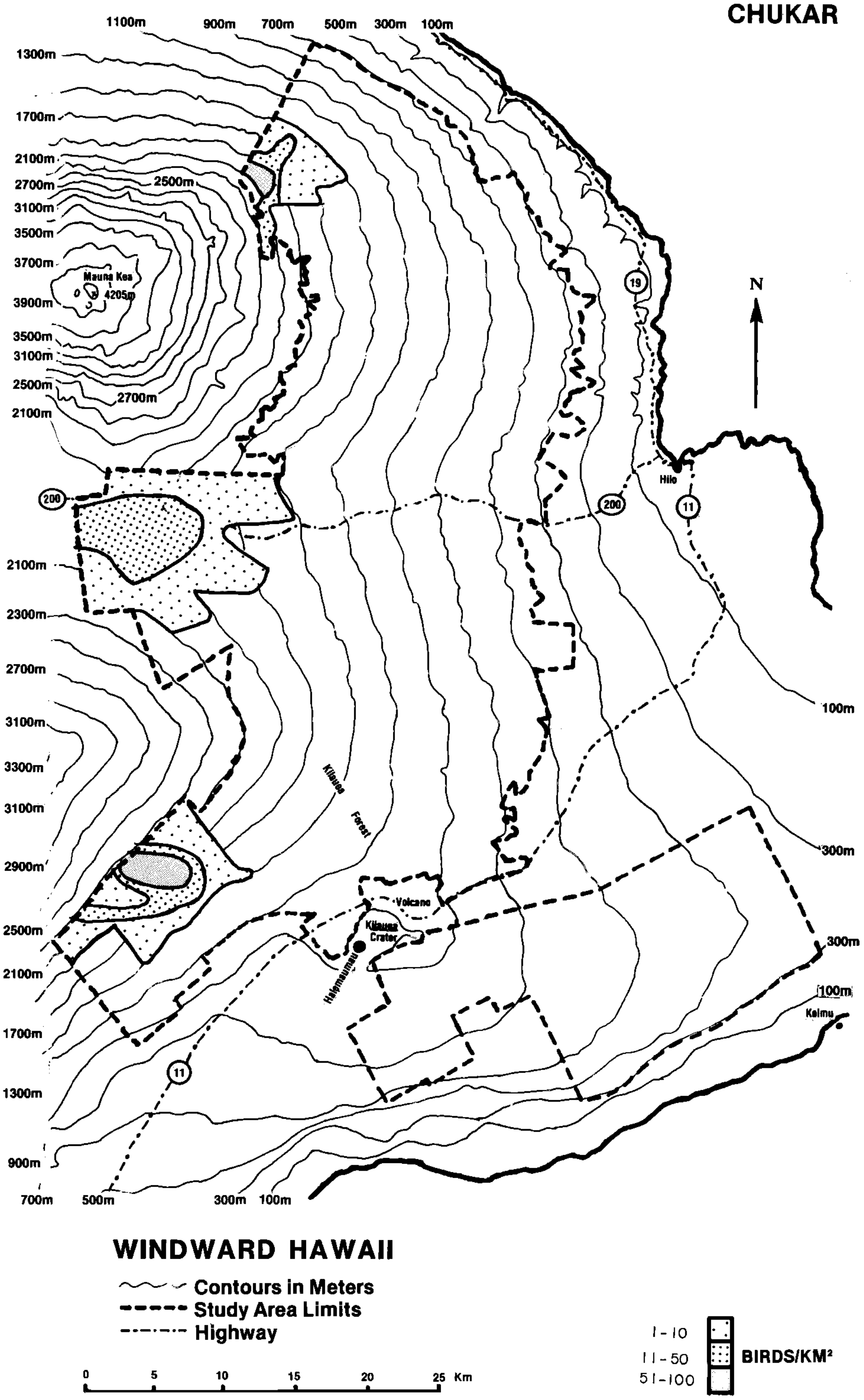


FIGURE 171. Distribution and abundance of the Chukar in the windward Hawaii study areas.

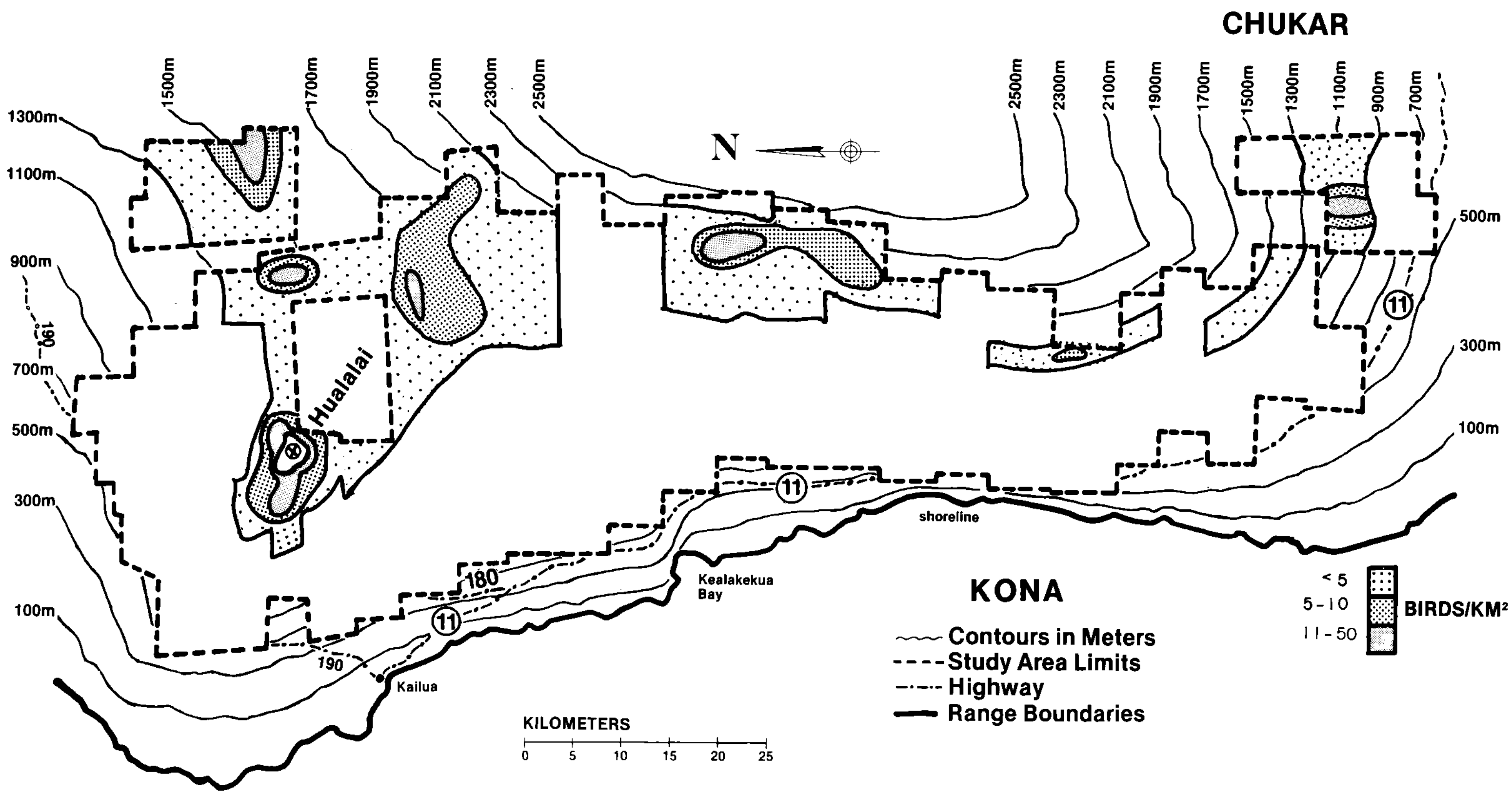


FIGURE 172. Distribution and abundance of the Chukar in the Kona study area.

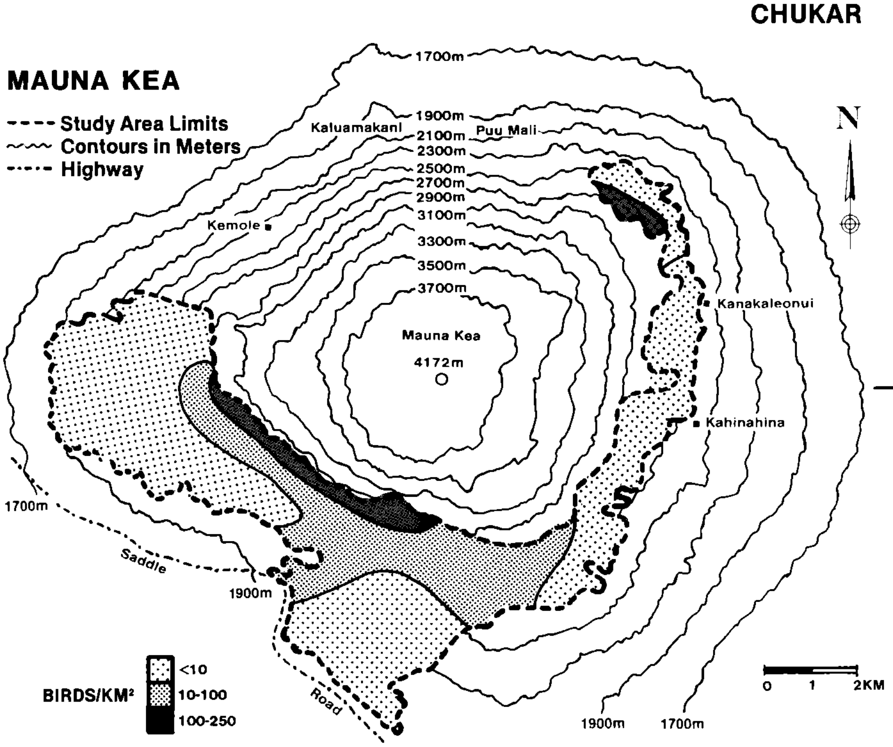


FIGURE 173. Distribution and abundance of the Chukar in the Mauna Kea study area.

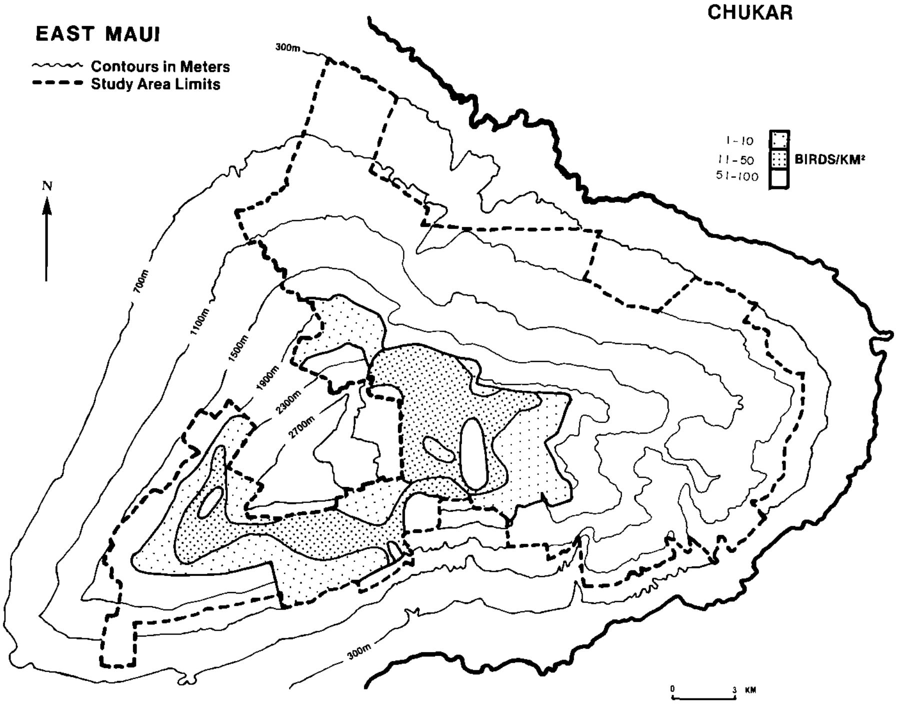


FIGURE 174. Distribution and abundance of the Chukar in the East Maui study area.

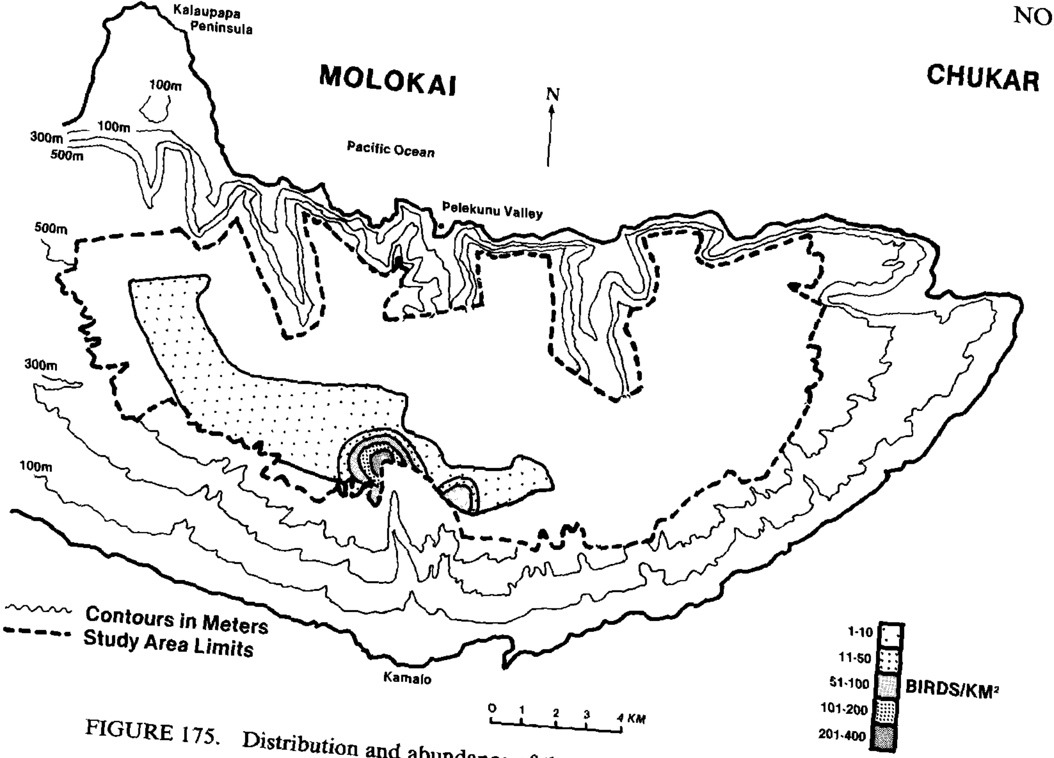


FIGURE 175. Distribution and abundance of the Chukar in the Molokai study area.

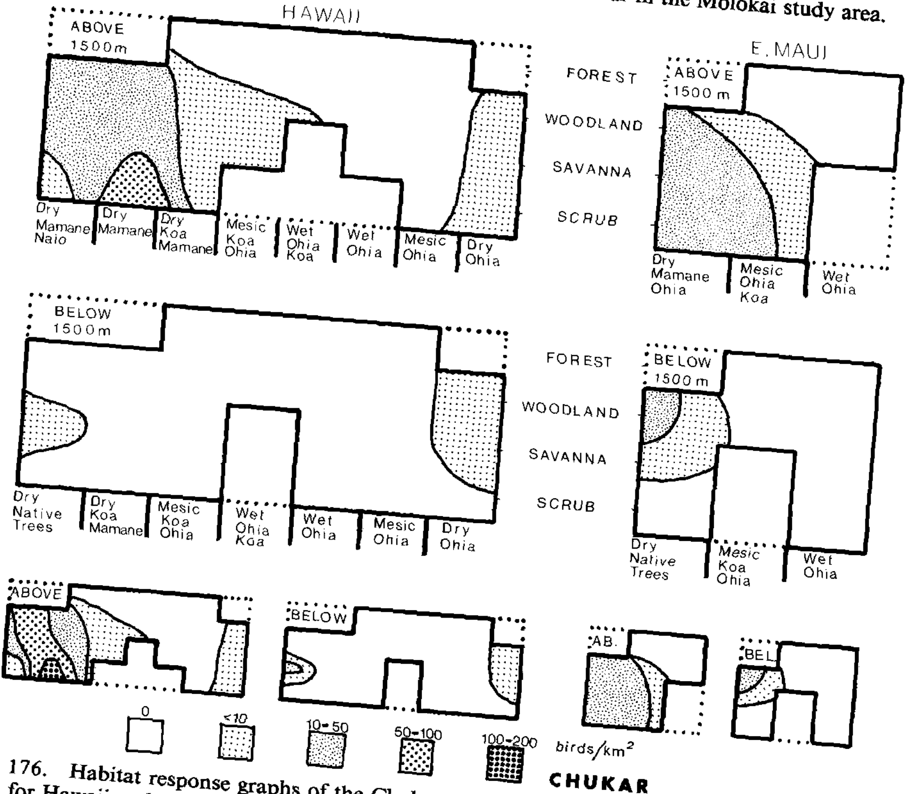


FIGURE 176. Habitat response graphs of the Chukar. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 39

REGRESSION MODELS FOR HABITAT RESPONSE OF THE CHUKAR, KALIJ PHEASANT, AND RED JUNGLEFOWL[a]

	Chukar					Kalij Pheasant		Red Junglefowl
	Hamakua	Kipukas	Kona	Mauna Kea	Maui	Hamakua	Kona	Kauai
R^2	0.21*	0.12*	0.08*	0.21*	0.32*	0.01*	0.08*	0.36*
Moisture	···	···	···	X	−5.8*	···	5.5*	X
Elevation	···	4.9*	−3.6*	−4.6*	···	···	4.1*	−3.1
(Elevation)^2	···	···	4.9*	5.1*	···	···	···	2.9
Tree biomass	···	···	−9.0*	···	−9.8*	···	3.1	X
(Tree biomass)^2	···	···	···	···	7.0*	···	···	···
Crown cover	···	···	···	···	···	···	···	···
Canopy height	···	···	···	2.5	···	···	−2.1	···
Koa	···	···	···	X	···	···	···	X
Ohia	···	···	···	X	···	···	···	X
Naio	X	···	···	···	···	X	···	X
Mamane	12.5*	···	···	···	7.0*	···	···	X
Intro. trees	···	X	···	X	−2.7	···	···	X
Shrub cover	−12.4*	···	3.0	···	···	···	···	···
Ground cover	−5.6*	−2.5	···	···	···	···	···	···
Native shrubs	···	−4.2*	···	X	···	···	···	···
Intro. shrubs	···	···	···	X	···	···	···	2.3
Ground ferns	X	−3.0	···	X	···	X	2.8	···
Matted ferns	−2.9	···	···	X	···	···	−2.5	···
Tree ferns	X	X	···	X	···	X	−4.6*	···
Ieie	X	X	···	X	···	X	···	3.5*
Passiflora	···	X	···	X	···	5.2*	9.0*	X
Native herbs	X	···	···	X	···	X	···	−2.3
Intro. herbs	X	···	−2.6	···	···	X	···	···
Native grasses	···	···	···	···	···	···	···	···
Intro. grasses	···	···	···	···	···	···	···	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

found Chukar, rocky slopes are frequent, and water is usually available from ranching or game management activities. On Mauna Kea special watering units are maintained to support high densities of Chukar and other gamebirds. The native habitat in India is similar to areas occupied in Hawaii—barren, stony hillsides with sparse shrub cover, boulder-strewn ravines, and the nearby presence of drinking water (Ali and Ripley 1969).

JAPANESE QUAIL (*Coturnix japonica*)

Japanese Quail were introduced to Maui and Lanai in 1921 (Caum 1933). Schwartz and Schwartz (1949) found them well established on all the islands except Oahu, in grasslands, pastures, and some agricultural fields. Native to China and Japan, this species feeds primarily on seeds and insects (Schwartz and Schwartz 1949).

We found the species only on Hawaii and Maui (Tables 33, 34, 40, Figs. 177–179), with a total population of 270 ± 150 (95% CI) birds in the study areas. The Kau population was not reported by Schwartz and Schwartz (1949), but by 1984 the species had become moderately common in the subalpine scrub (S. Mountainspring, pers. observ.). Japanese Quail occur in dry woodland, savanna, and scrub (Fig. 180). Highest densities occur outside the study areas in very open tall grass pastures on the northwest slopes of both Mauna Kea and Haleakala. Since we failed to sample much of the area indicated as within range by earlier workers on Maui, we cannot state whether the abundance and range changed since 1948.

KALIJ PHEASANT (*Lophura leucomelana*)

Kalij Pheasant, native to the Himalayan foothills and northern southeast Asia, were introduced in 1962 (Lewin 1971). In the Hawaiian Islands they have been introduced only to Hawaii where the range is still expanding. The diet includes seeds, fleshy fruit, leaves, and insects (Bohl 1971).

As late as 1972 this species was listed as "possibly" established on Puu Waawaa on northwest Hawaii (Berger 1972). During the 1970s, however, Kalij Pheasant became well established throughout the wetter forests of Kona and invaded the upper-elevation forests of Hamakua

TABLE 40

DENSITY [MEAN (SE)] OF THE JAPANESE QUAIL AND KALIJ PHEASANT BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Japanese Quail					Kalij Pheasant		
	Kau	Hamakua	Kipukas	Mauna Kea	East Maui	Hamakua	Kipukas	Kona
Elevation								
100–300 m	···	···	···	···	···	···	···	···
300–500 m	···	0	···	···	0	0	···	3 (3)
500–700 m	0	0	···	···	0	0	···	5 (2)
700–900 m	0	0	···	···	0	0	···	7 (1)
900–1100 m	0	0	···	···	2 (2)	0	···	13 (4)
1100–1300 m	0	0	6 (6)	···	24 (13)	8 (8)	0	12 (2)
1300–1500 m	0	+ (+)	5 (2)	···	36 (12)	3 (2)	0	8 (2)
1500–1700 m	26 (26)	2 (1)	2 (2)	···	19 (16)	2 (2)	0	7 (1)
1700–1900 m	+ (+)	2 (2)	0	···	0	3 (3)	3 (1)	7 (2)
1900–2100 m	+ (+)	0	0	+ (+)	0	0	0	4 (1)
2100–2300 m	0	0	0	1 (+)	0	0	0	2 (1)
2300–2500 m	···	···	···	+ (+)	0	···	···	7 (7)
2500–2700 m	···	···	···	+ (+)	0	···	···	···
2700–2900 m	···	···	···	0	0	···	···	···
2900–3100 m	···	···	···	0	···	···	···	···
Habitat								
Ohia	7 (7)	2 (+)	6 (6)	···	0	2 (2)	1 (1)	5 (1)
Koa-ohia	0	+ (+)	+ (+)	···	34 (14)	3 (2)	13 (13)	13 (2)
Koa-mamane	···	0	3 (3)	···	···	+ (+)	0	6 (2)
Mamane-naio	···	···	···	+ (+)	···	···	···	22 (22)
Mamane	···	···	···	1 (+)	0	···	···	5 (2)
Other natives	···	3 (1)	3 (1)	···	15 (8)	+ (+)	+ (+)	25 (5)
Intro. trees	···	0	···	···	4 (4)	3 (3)	···	15 (+)
Treeless	0	+ (+)	0	···	0	0	0	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

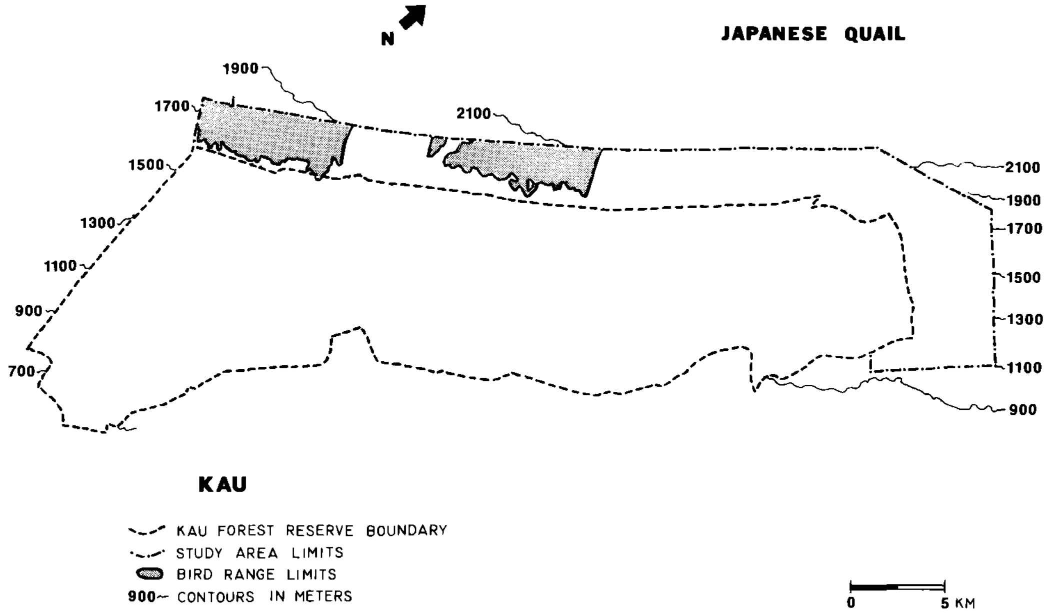


FIGURE 177. Distribution and abundance of the Japanese Quail in the Kau study area. (Density within range is less than 10 birds/km^2.)

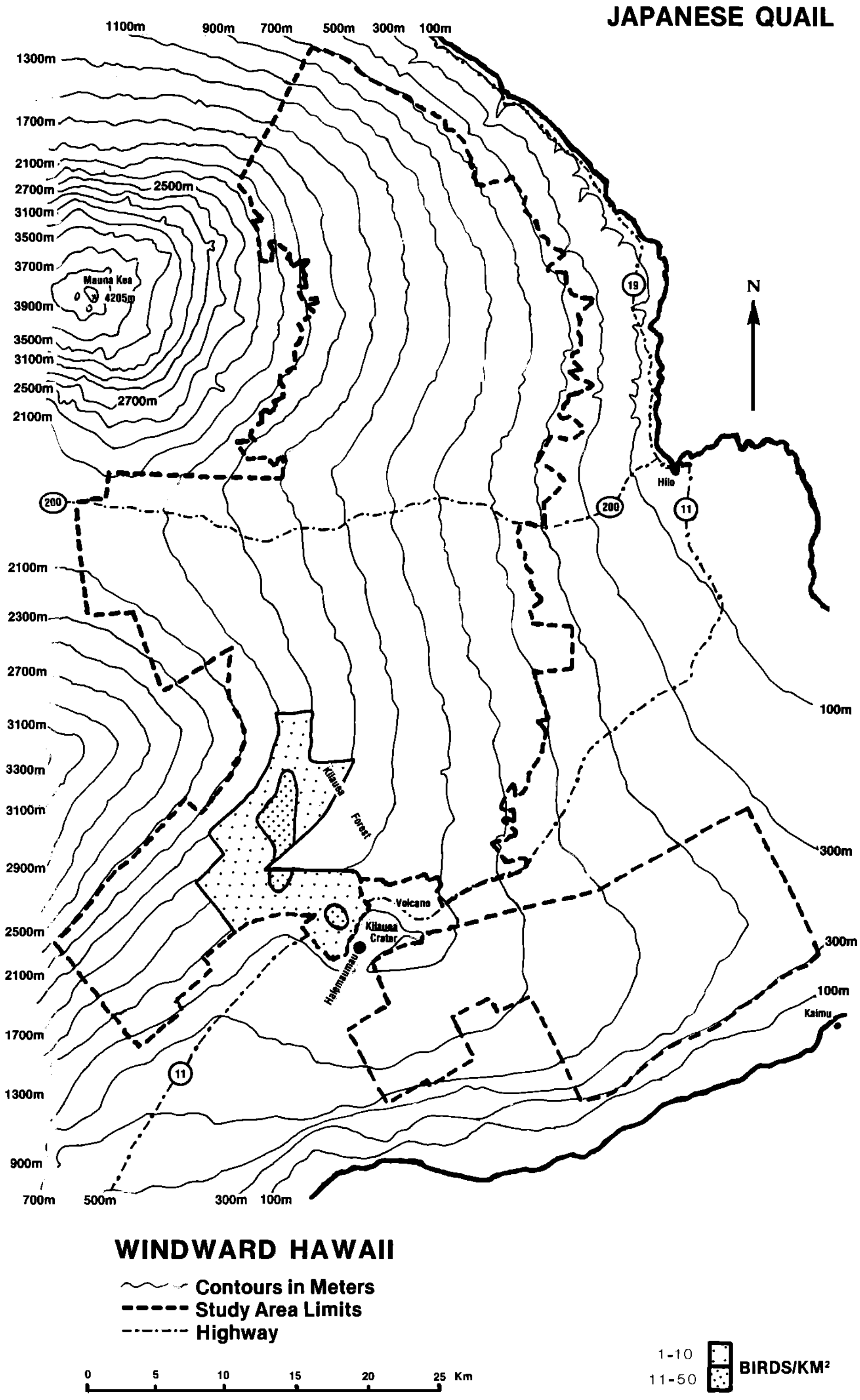


FIGURE 178. Distribution and abundance of the Japanese Quail in the windward Hawaii study areas.

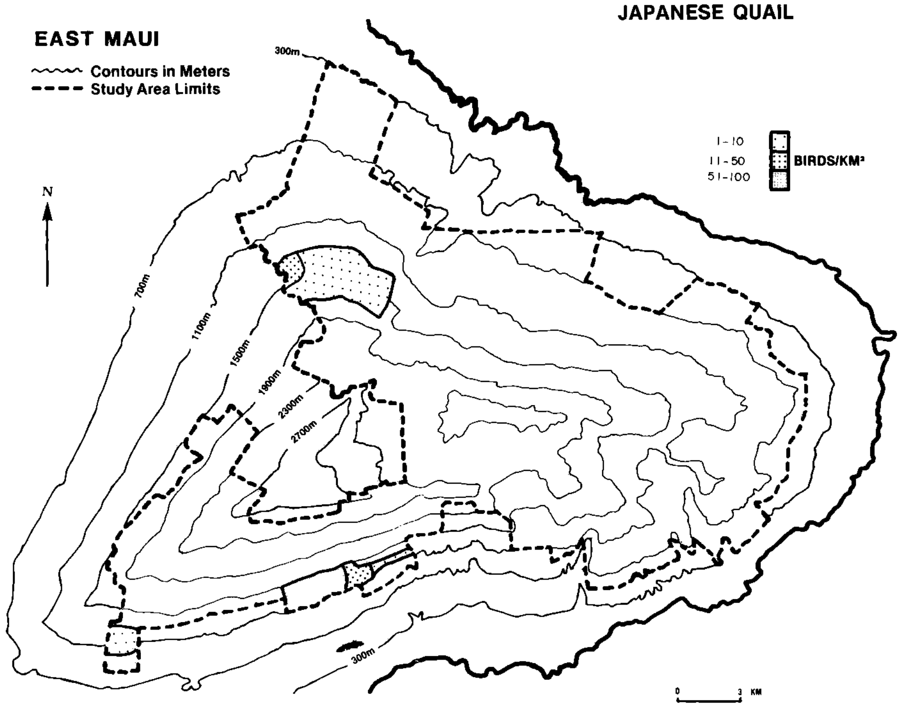


FIGURE 179. Distribution and abundance of the Japanese Quail in the East Maui study area.

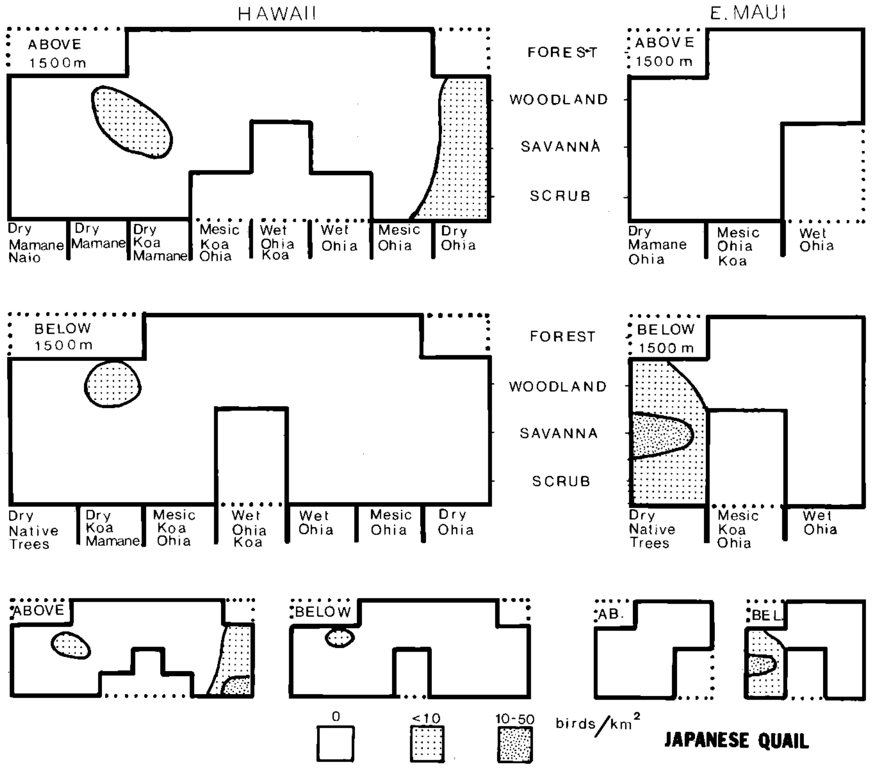


FIGURE 180. Habitat response graphs of the Japanese Quail. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

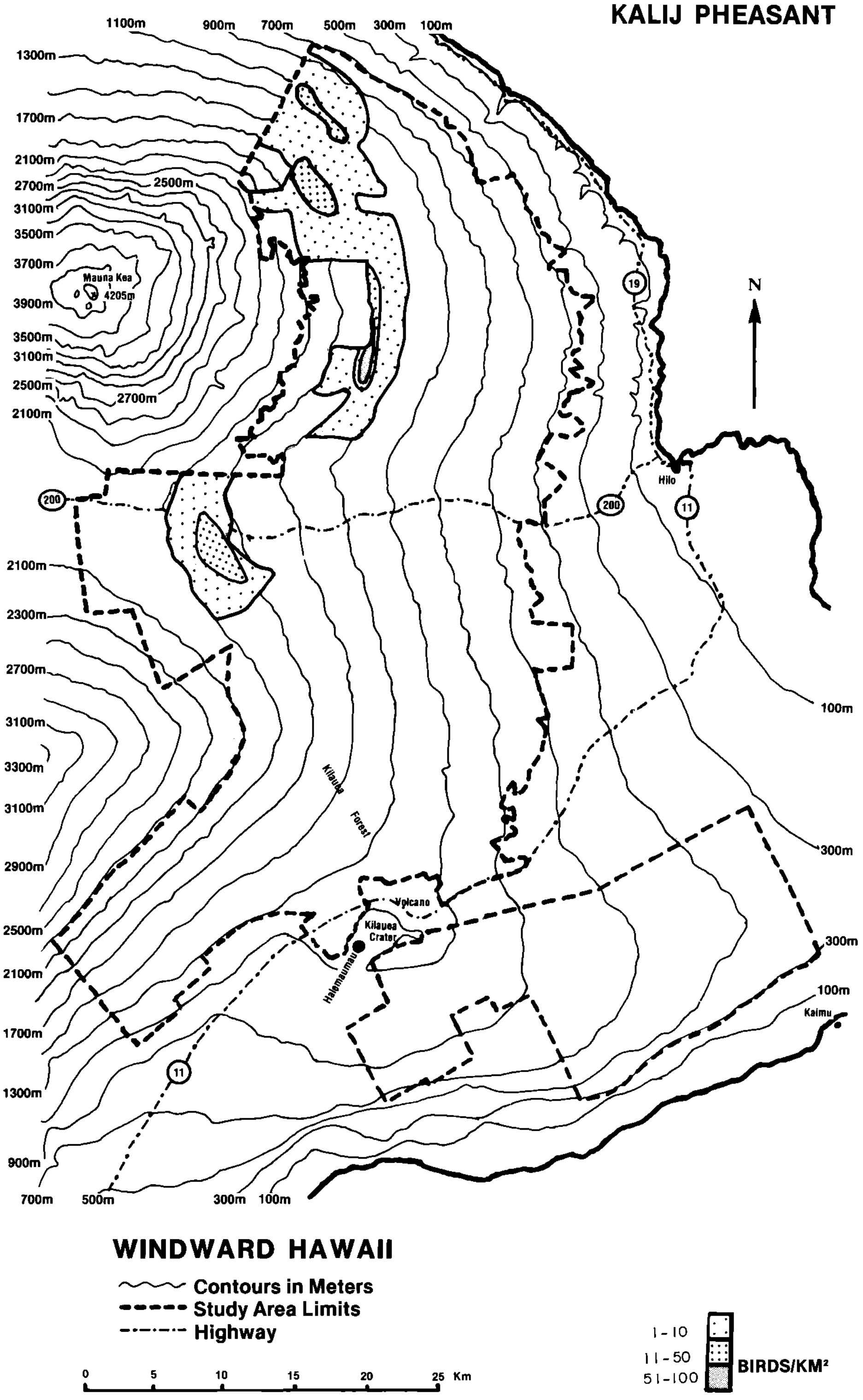


FIGURE 181. Distribution and abundance of the Kalij Pheasant in the windward Hawaii study areas.

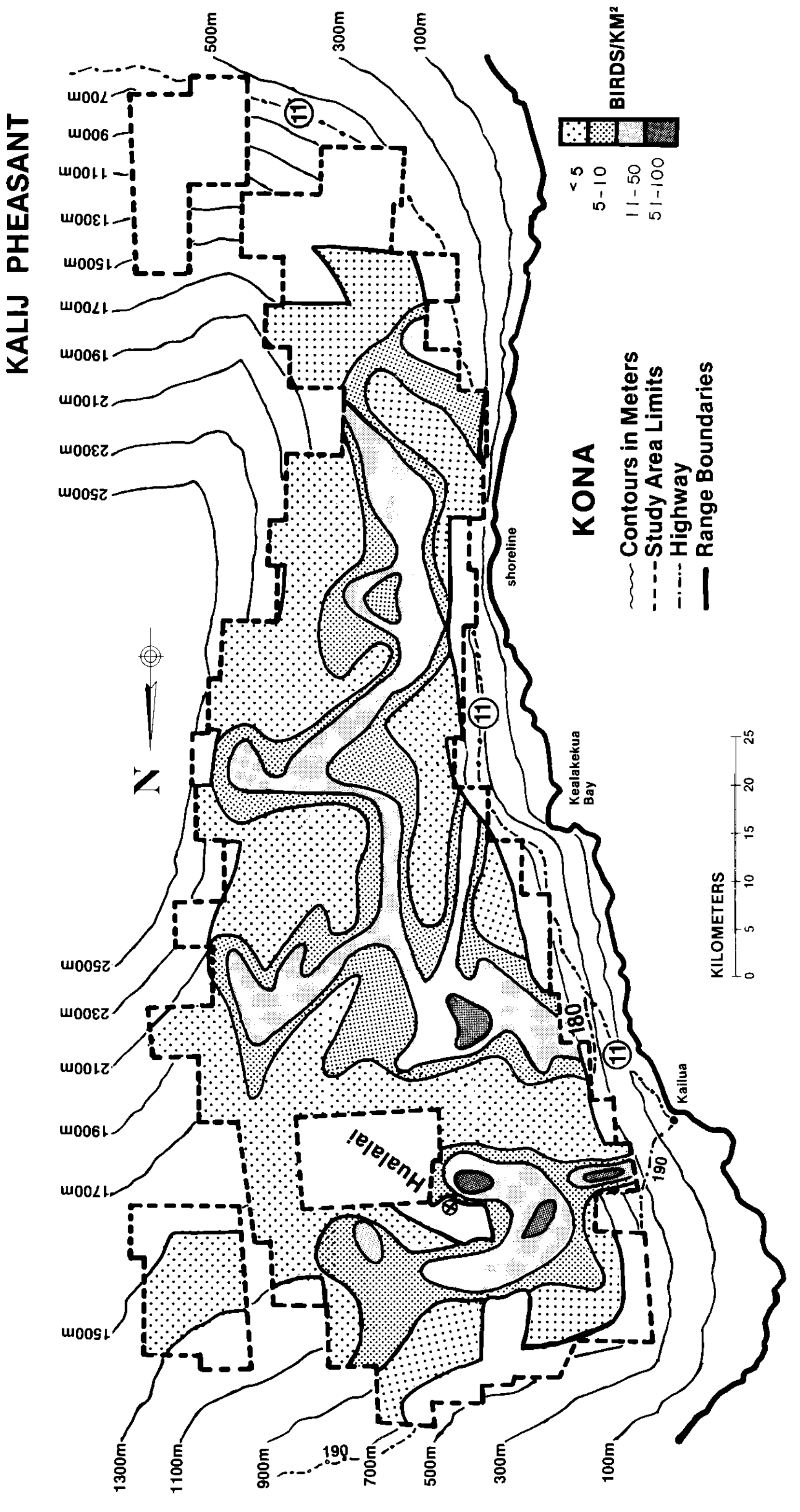


FIGURE 182. Distribution and abundance of the Kalij Pheasant in the Kona study area.

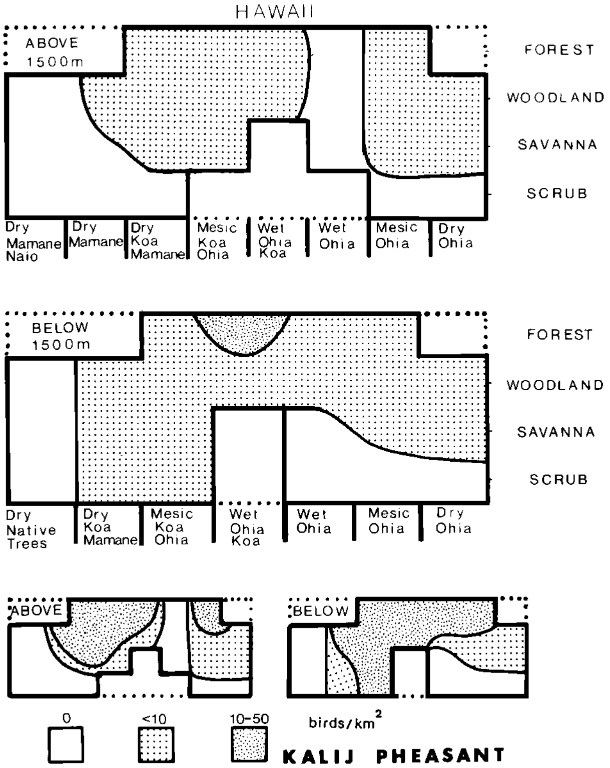


FIGURE 183. Habitat response graph of Kalij Pheasant. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

(Berger 1981; Tables 33, 40, Figs. 181, 182). We estimated 5700 ± 900 (95% CI) birds in our study areas; 97% were in Kona. Although in Kau we failed to find birds during count periods, we saw one bird in 1976 at 1670 m elevation along a jeep trail in ohia forest between transects 2 and 3. In 1984 this species was fairly common in the Kau study area (U.S.F.W.S. data). Kalij were first recorded in the vicinity of Kilauea Crater in 1977 (Katahira 1978) and have been sighted with increasing frequency in Hawaii Volcanoes National Park since 1980, particularly in kipukas along the Mauna Loa Strip Road (S. Mountainspring, J. M. Scott, pers. observ.).

Kalij Pheasant occur from 300 to 2500 m elevation in a variety of habitat types, but most often in wet ohia-koa forests (Table 40, Fig. 183). Because the range was still expanding during our survey, the observed habitat responses may change somewhat as new areas are colonized.

The regression models for Hamakua and Kona (Table 39) show that Kalij Pheasant are especially associated with passiflora. Birds actively disperse the seeds of banana poka (Lewin and Lewin 1984). Kalij Pheasant occur in moderately dry to moderately wet forests at mid to high elevations; this resembles their foothill forest habitat in India (Ali and Ripley 1969). On Hawaii, Lewin (1971) found that Kalij often occupy dense stands of silky oak. Matted ferns are probably too dense for their activities, as reflected by the negative term in the Kona regression model.

Red Junglefowl (*Gallus gallus*)

Red Junglefowl, known as Moa by the Hawaiians, were introduced by the early Polynesians and are native to India and southeast Asia. They are most common on Kauai, although small populations occur on Hawaii and Niihau near human habitation (Berger 1981). The rarity or extinction on most islands has been attributed to predation by cats and mongooses, and to a lesser degree to excessive hunting, interbreeding with domestic stock, and forest destruction (Schwartz and Schwartz 1949, Berger 1981). Their ground nesting habits make them particularly vulnerable to predators. Red Junglefowl are omnivorous, taking seeds, fruits, insects, and other small invertebrates (Schwartz and Schwartz 1949).

During our survey we found Red Junglefowl

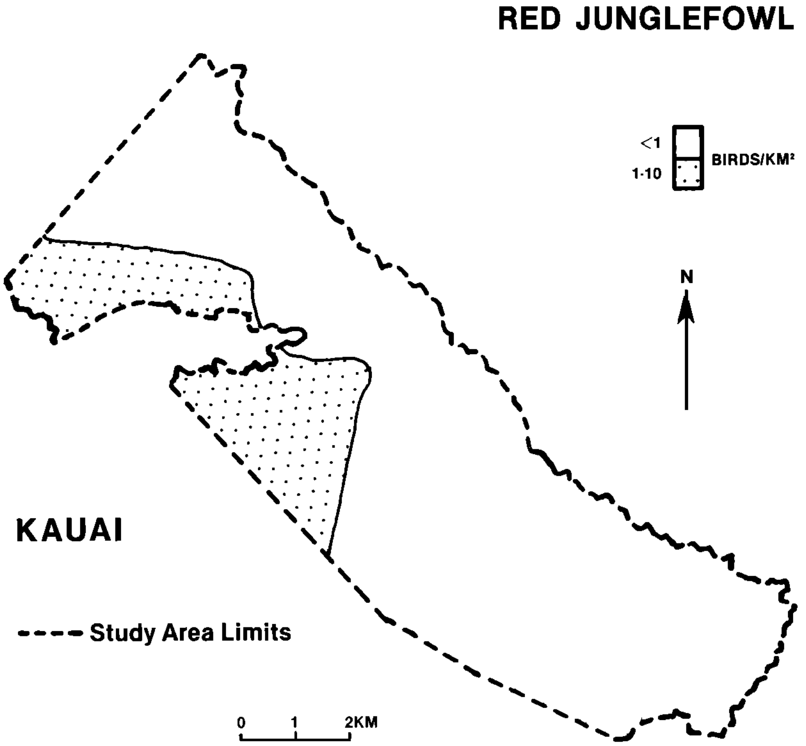


FIGURE 184. Distribution and abundance of the Red Junglefowl in the Kauai study area.

on Kauai, where they have penetrated the Alakai Swamp, and on Hawaii near Ainahou in Hawaii Volcanoes National Park (Tables 33, 34, 38, Fig. 184). We suspect that on Hawaii this species is maintained in the wild by escaped or released domestic birds. Van Riper (1973a) found a small population of birds at 600–900 m elevation on the southwest slopes of Hualalai. In native forests on Kauai, Sincock et al. (1984) found the species almost only in the Alakai Swamp and Kokee State Park area, estimated the population at 1000 ± 750 (95% CI) birds, but believed the total island population to be about 5000.

The regression model for Kauai (Table 39) is fairly inconclusive, although the positive term for ieie may reflect the large component of fruit in the diet. Schwartz and Schwartz (1949) described the habitat on Kauai as the periphery of rather mesic, partly open forests, usually of koa and ohia, although at lower elevations kukui (*Aleurites moluccana*) and guava stands are occupied. Forests that are very dense, wet, open, or dry are unoccupied. Typically the understory has a scattering of shrubs, ground ferns, matted ferns, and tree ferns. In India, Red Junglefowl usually occur in moist forests and scrub jungles interspersed with cultivated patches and clearings (Ali and Ripley 1969).

RING-NECKED PHEASANT
(*Phasianus colchicus*)

Ring-necked Pheasant, introduced to the Hawaiian Islands in 1875 (Caum 1933), are native to eastern Asia. Additional introductions have been made on all the major islands since that time. In 1948, pheasant were characterized as having low densities (1–25 birds/km^2) over most of our study areas (Schwartz and Schwartz 1949). Densities in Hawaii Volcanoes National Park appear to have increased over the 1940–1975 interval (Conant 1975, Banko and Banko 1980). The Green Pheasant of Japan, considered by some a distinct allospecies (*P. versicolor*), has recently been merged with *colchicus* (A.O.U. 1983).

In the Hawaiian Islands, Ring-necked Pheasant range from sea level to 3000 m elevation, from very dry to very wet habitat, and from grassland to forest (Schwartz and Schwartz 1949, 1951b). We found this species in all study areas (Tables 33, 34, 41, Figs. 185–192). An estimated 14,000 ± 1000 (95% CI) birds occupy our study areas on Hawaii; 1700 ± 200 on Maui; 10 ± 20 on Molokai; 320 ± 50 on Lanai; and 10 ± 20 on Kauai.

The distributional patterns we observed differ

TABLE 41
Density [mean (se)] of the Ring-necked Pheasant by Elevation, Habitat, and Study Area[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	Molokai	Lanai	Kauai
Elevation											
100–300 m	...	...	...	...	...	...	...	...	0	...	...
300–500 m	...	0	0	...	1 (1)	...	0	0	0	...	...
500–700 m	0	0	+ (+)	...	3 (1)	...	+ (+)	0	+ (+)	13 (5)	...
700–900 m	+ (+)	4 (1)	1 (+)	...	7 (1)	...	3 (2)	2 (1)	+ (+)	5 (1)	...
900–1100 m	2 (2)	+ (+)	13 (3)	...	8 (1)	...	+ (+)	12 (2)	+ (+)	9 (4)	...
1100–1300 m	3 (3)	8 (2)	5 (1)	27 (4)	10 (1)	...	2 (2)	18 (4)	4 (3)	...	+ (+)
1300–1500 m	+ (+)	4 (1)	...	20 (2)	9 (1)	...	0	28 (5)	0	...	+ (+)
1500–1700 m	2 (2)	3 (1)	...	19 (2)	11 (1)	...	0	23 (4)	...	...	...
1700–1900 m	15 (6)	8 (1)	...	9 (1)	8 (1)	...	...	9 (2)	...	...	...
1900–2100 m	17 (4)	13 (2)	...	3 (1)	10 (1)	4 (3)	...	8 (1)	...	...	...
2100–2300 m	18 (11)	17 (6)	...	+ (+)	5 (1)	19 (12)	...	14 (2)	...	...	...
2300–2500 m	...	...	...	...	+ (+)	4 (2)	...	7 (1)	...	...	...
2500–2700 m	...	...	...	...	...	4 (2)	...	15 (4)	...	...	...
2700–2900 m	...	...	...	...	...	+ (+)	...	0	...	...	...
2900–3100 m	...	...	...	...	...	+ (+)	...	...	...	...	...
Habitat											
Ohia	14 (3)	5 (1)	4 (1)	7 (1)	7 (+)	...	2 (1)	5 (1)	+ (+)	...	+ (+)
Koa-ohia	1 (1)	6 (1)	...	20 (2)	9 (+)	...	...	39 (8)	...	...	...
Koa-mamane	...	13 (2)	...	18 (2)	15 (1)	...	...	...	...	...	...
Mamane-naio	...	...	...	...	2 (1)	1 (1)	...	...	...	...	...
Mamane	...	...	...	...	14 (1)	9 (4)	...	30 (17)	...	...	...
Other natives	...	15 (2)	...	16 (4)	7 (1)	...	...	17 (2)	+ (+)	9 (3)	...
Intro. trees	...	2 (1)	...	...	7 (1)	...	2 (2)	6 (2)	+ (+)	7 (2)	...
Treeless	...	+ (+)	4 (2)	+ (+)	4 (1)	...	...	11 (1)	+ (+)	9 (4)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

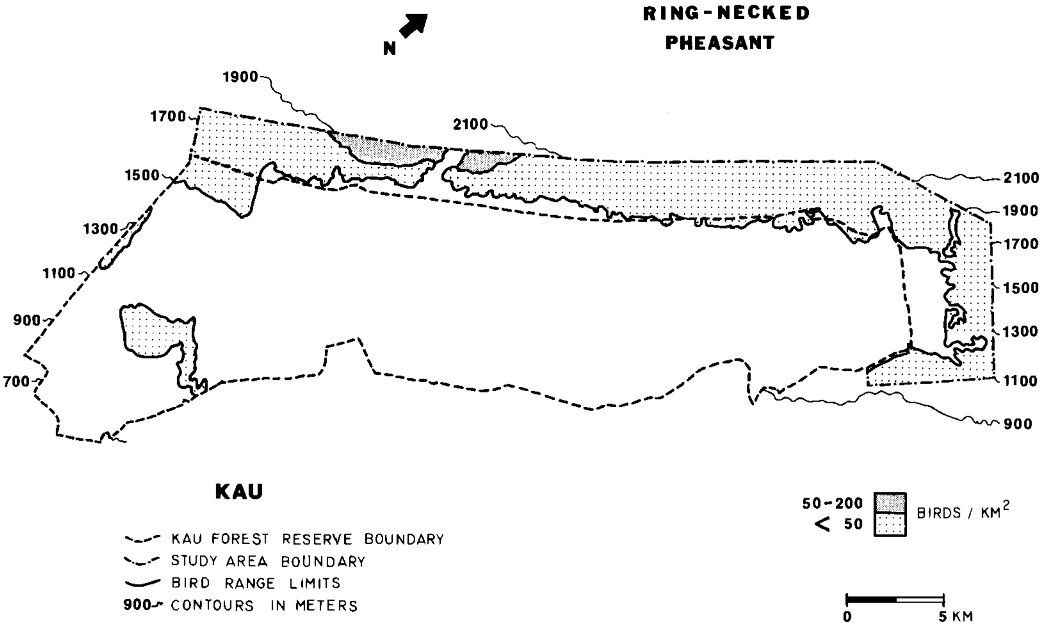


FIGURE 185. Distribution and abundance of the Ring-necked Pheasant in the Kau study area.

TABLE 42
REGRESSION MODELS FOR HABITAT RESPONSE OF THE RING-NECKED PHEASANT AND COMMON PEAFOWL[a]

	Ring-necked Pheasant							Common Peafowl
	Kau	Hamakua	Puna	Kipukas	Kona	Maui	Lanai	Kona
R^2	0.39*	0.34*	0.26*	0.64*	0.25*	0.41*	0.12	0.19*
Moisture	−3.7*	−3.5*	−9.7*	···	···	−14.3*	···	−5.0*
Elevation	···	−5.9*	5.9*	−18.2*	9.9*	2.5	···	−13.2*
(Elevation)^2	···	6.8*	···	···	−8.4*	−2.2	···	···
Tree biomass	−10.2*	···	···	···	7.1*	···	···	6.4*
(Tree biomass)^2	8.4*	···	···	7.4*	···	···	···	−3.2
Crown cover	···	···	···	···	−7.7*	7.5*	···	−6.6*
Canopy height	···	3.9*	···	···	−3.0	···	···	−2.3
Koa	···	···	X	···	−7.2*	···	X	···
Ohia	···	···	···	···	···	−2.1	···	−5.4*
Naio	X	X	X	···	···	X	X	−3.0
Mamane	X	···	···	···	10.2*	···	X	···
Intro. trees	X	···	···	X	···	−6.0*	···	···
Shrub cover	−2.8	···	···	···	−8.3*	···	···	−6.7*
Ground cover	10.9*	−4.6*	···	···	4.2*	···	···	5.5*
Native shrubs	···	−10.8*	···	···	···	···	···	···
Intro. shrubs	X	···	···	···	5.2*	3.7*	···	···
Ground ferns	X	X	···	···	−7.8*	−4.6*	X	···
Matted ferns	···	···	···	···	−2.9	−2.9	−3.0	···
Tree ferns	···	X	···	X	···	···	X	···
Ieie	X	X	···	X	···	···	X	−2.3
Passiflora	X	−7.3*	X	X	···	···	X	8.5*
Native herbs	X	X	−4.1*	···	−2.8	···	X	···
Intro. herbs	X	X	···	5.7*	4.0*	3.1	X	···
Native grasses	···	4.0*	−3.9*	8.3*	−5.0*	4.5*	X	···
Intro. grasses	−10.7*	···	···	···	−3.4*	···	···	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

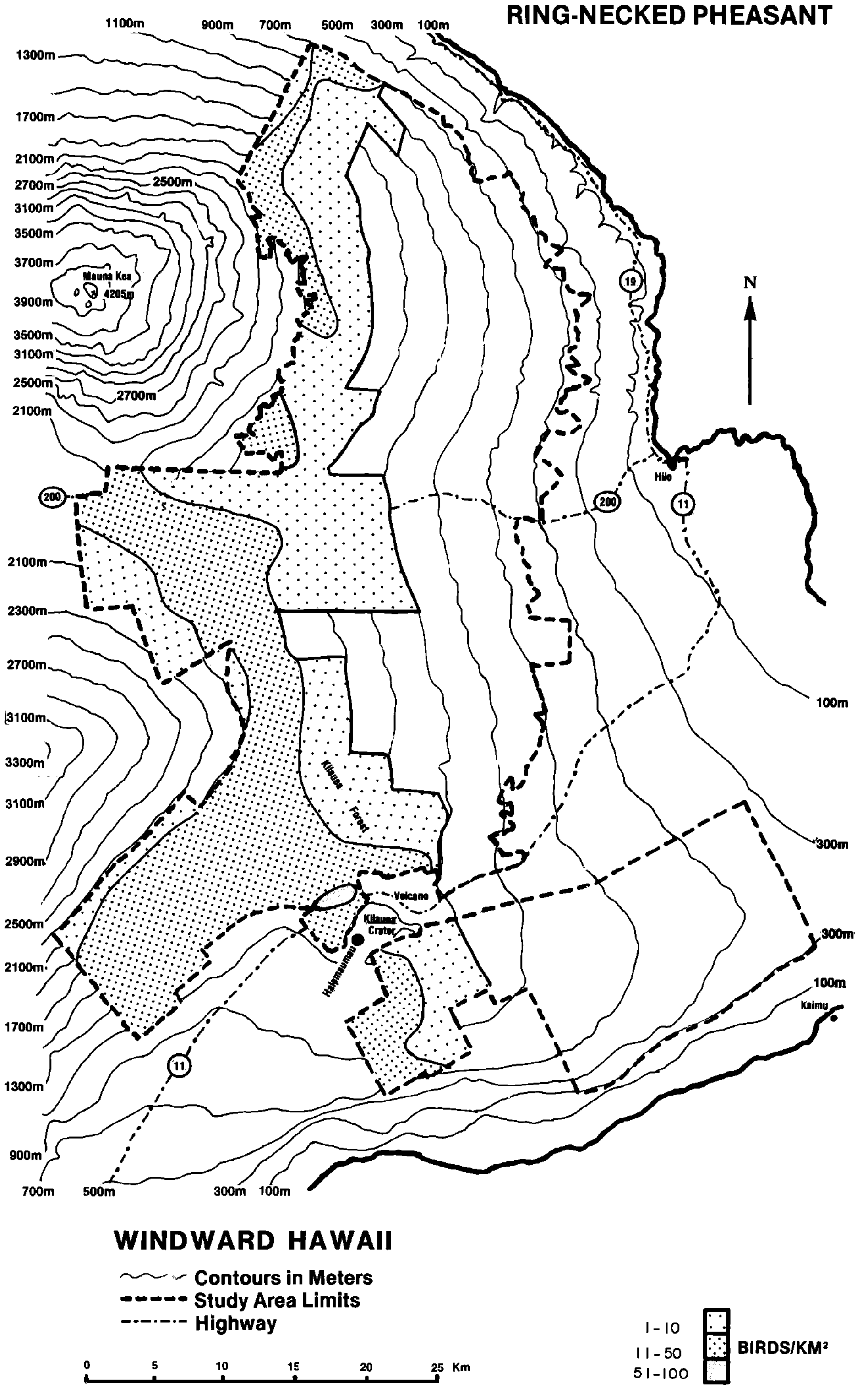


FIGURE 186. Distribution and abundance of the Ring-necked Pheasant in the windward Hawaii study areas.

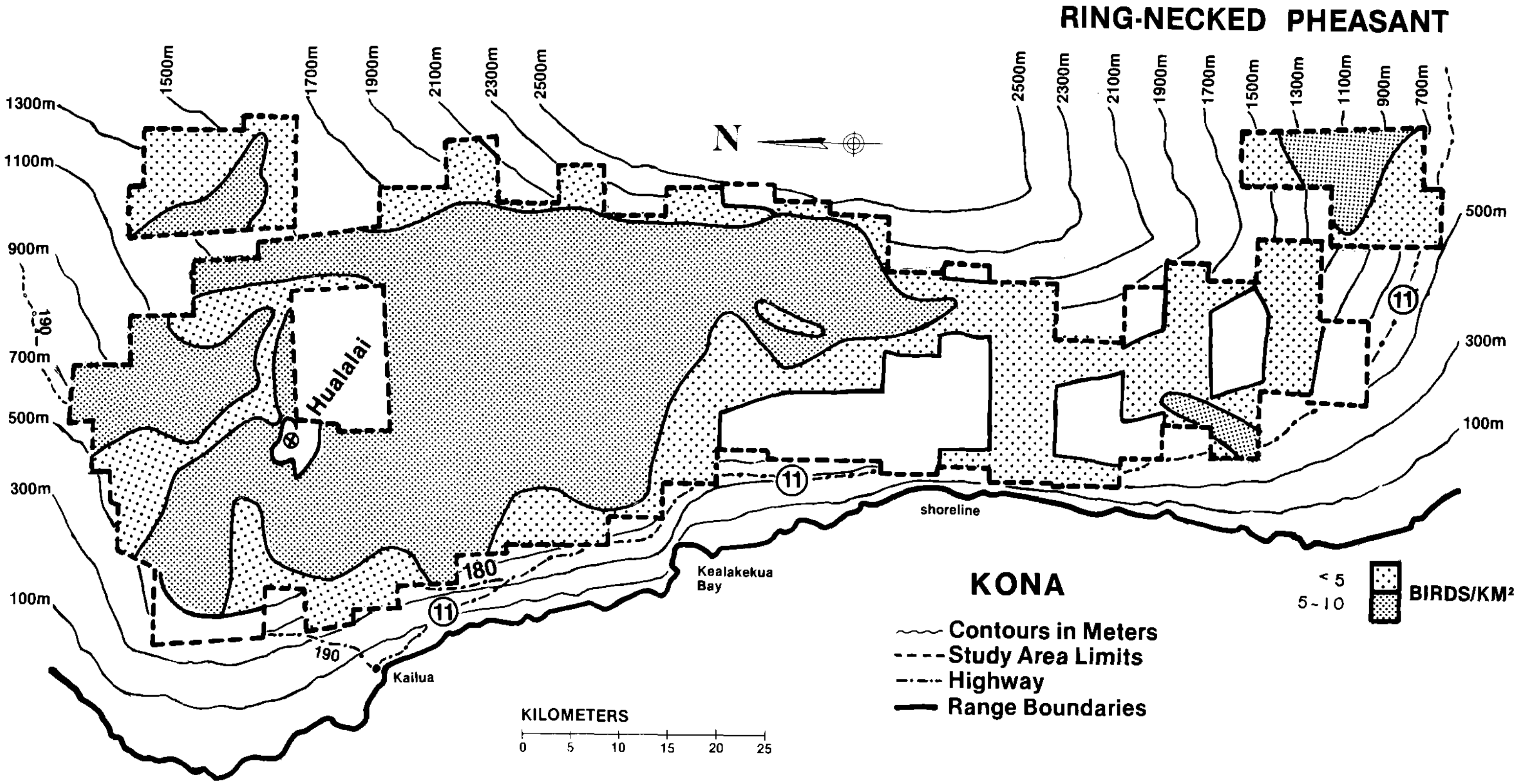


FIGURE 187. Distribution and abundance of the Ring-necked Pheasant in the Kona study area.

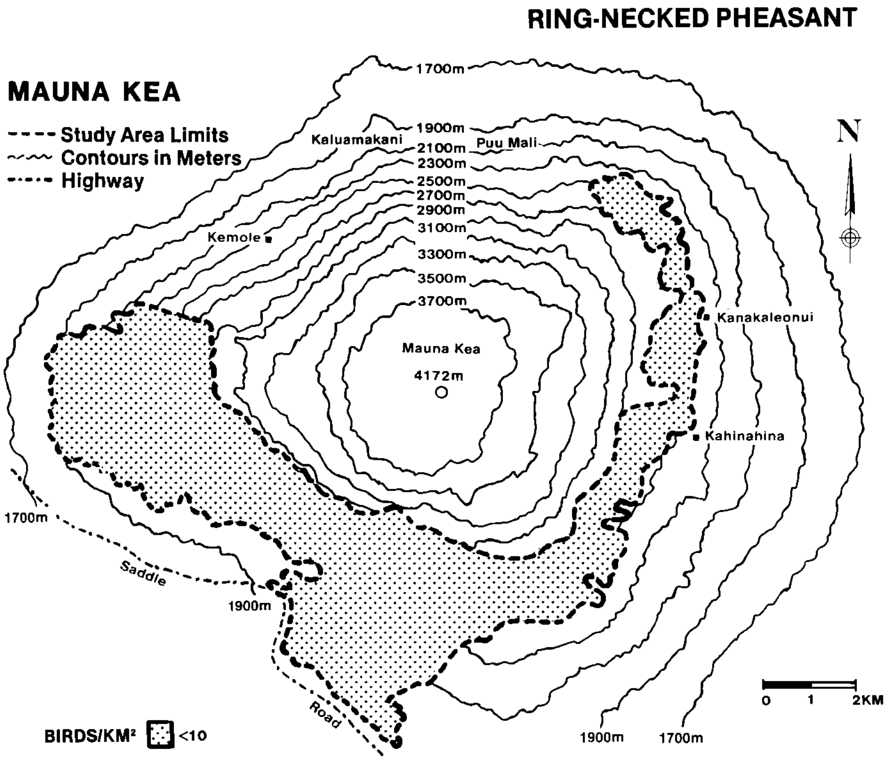


FIGURE 188. Distribution and abundance of the Ring-necked Pheasant in the Mauna Kea study area.

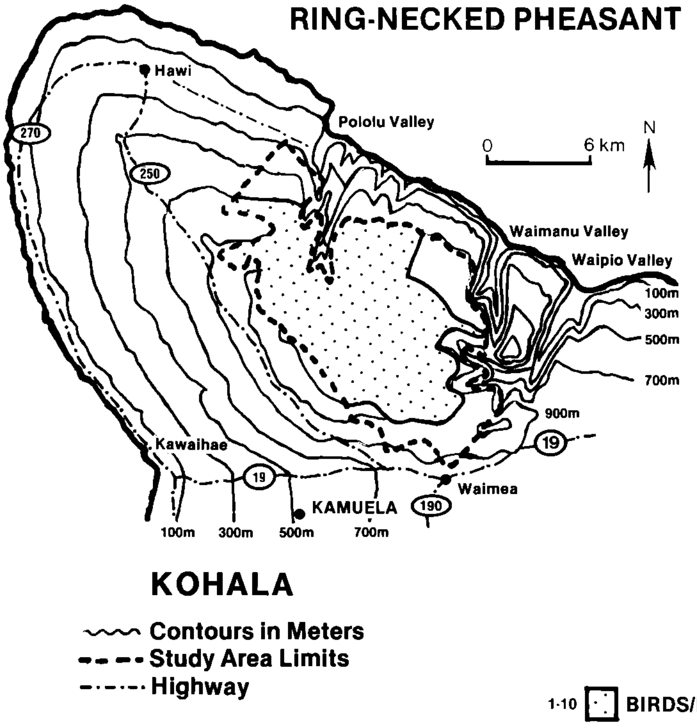


FIGURE 189. Distribution and abundance of the Ring-necked Pheasant in the Kohala study area.

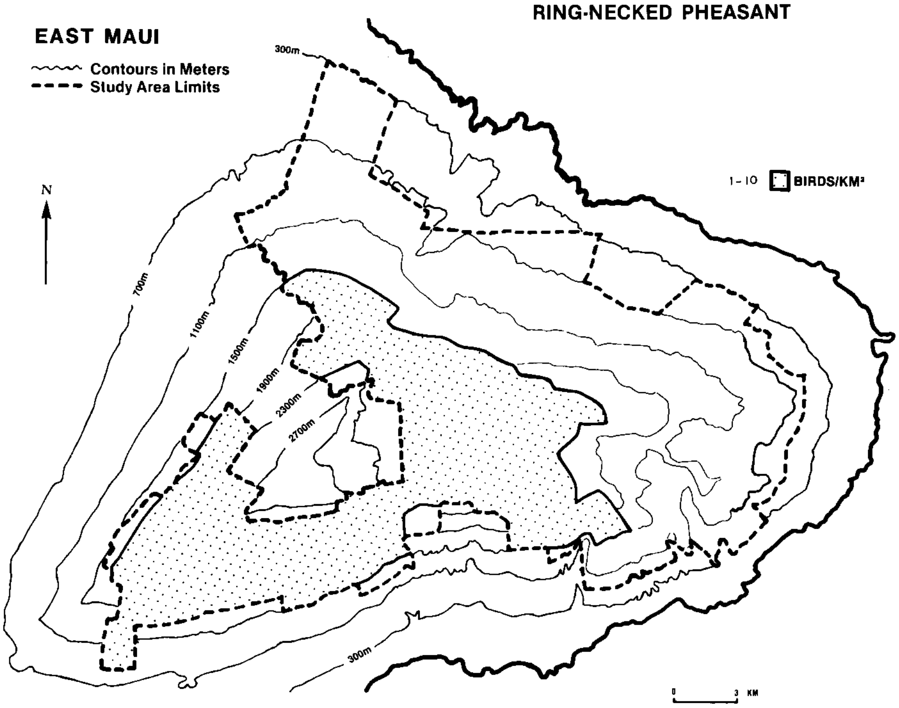


FIGURE 190. Distribution and abundance of the Ring-necked Pheasant in the East Maui study area.

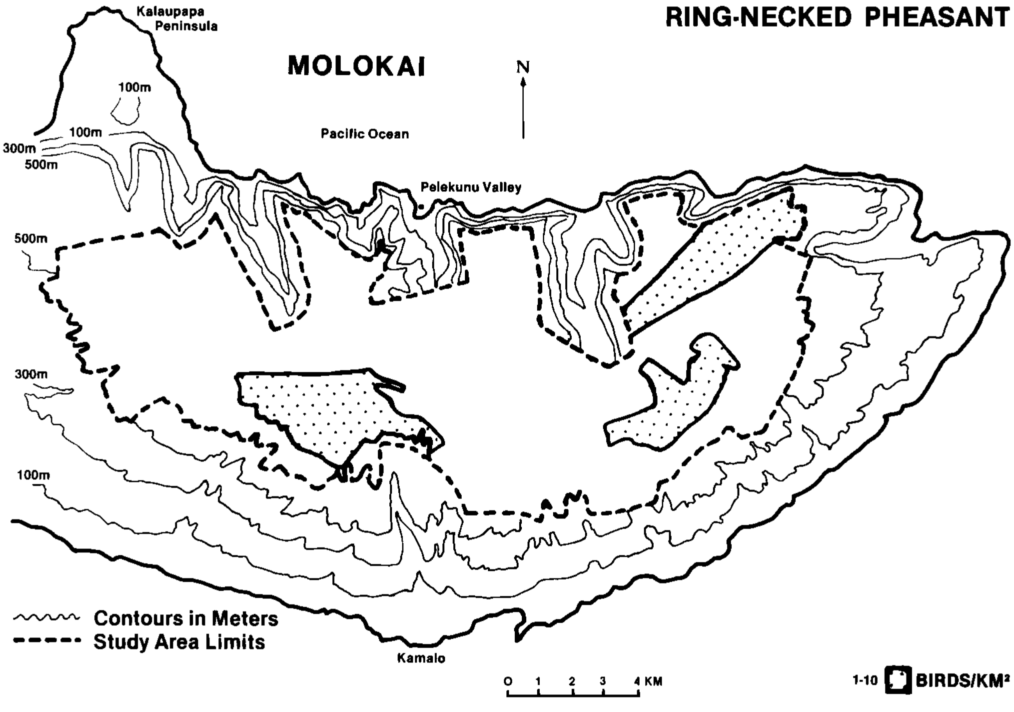


FIGURE 191. Distribution and abundance of the Ring-necked Pheasant in the Molokai study area.

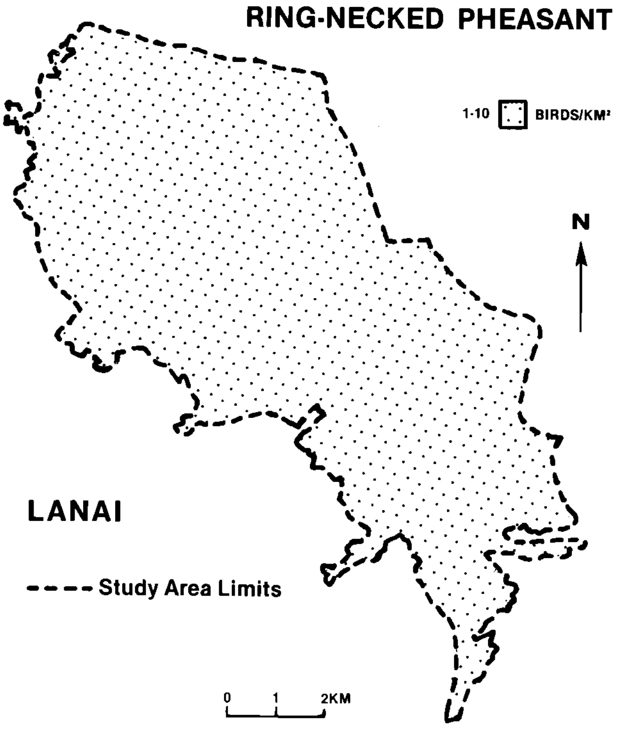


FIGURE 192. Distribution and abundance of the Ring-necked Pheasant in the Lanai study area.

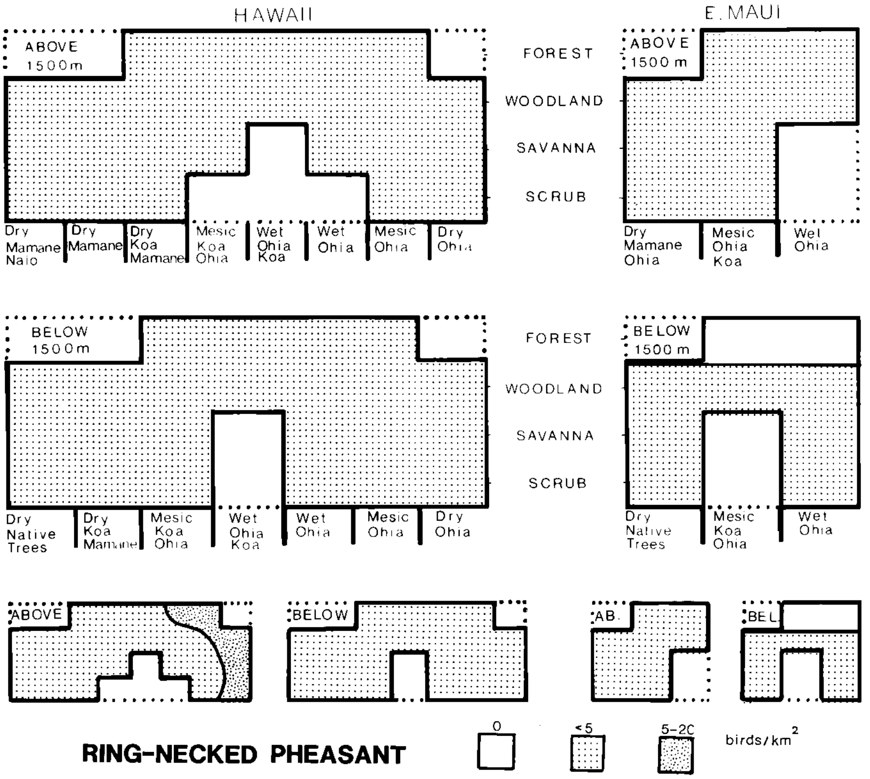


FIGURE 193. Habitat response graphs of the Ring-necked Pheasant. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

only slightly from those documented by Schwartz and Schwartz (1949, 1951b). The Mauna Kea and Mauna Loa populations are now linked at high elevations in windward Hawaii and the hiatus between upper and lower elevation populations in Kona is filled. On East Maui, pheasant filled in the Kahikinui area since 1949. On Lanai, distribution is now continuous over the entire study area.

The habitat response graphs merely indicate that Ring-necked Pheasant occur in almost every habitat type on Hawaii and Maui (Fig. 193). Crowing cocks are heard long distances, and some recorded birds were undoubtedly in a different habitat than the observer. The regression models (Table 42) show that Ring-necked Pheasant are more common in dry areas of scattered trees with little shrub cover, few matted ferns, and many introduced herbs. Wet habitats have negative responses in four of the seven models. A moisture term does not appear in the poorly-fit Lanai model, nor for the Kipukas or Kona areas where conditions are generally dry. Individual tree species have only modest effects on habitat response. The exception is mamane, strongly positive in two models and characteristic of dry open woodland.

Ring-necked Pheasant respond strongly to several understory components. Unbroken shrub cover and ground ferns are typical of many undisturbed wet native communities where birds are absent, but high densities occur where introduced shrubs reach high cover values because of disturbance by grazing or feral animals. The relation to shrub components in the regression models thus depicts positive response to disturbance, as also seen in the positive terms for introduced herbs and negative ones for native herbs. The negative terms for matted ferns in three models reflect the low forage value of dense fern understories (Schwartz and Schwartz 1949, 1951b).

In open areas, densities are generally correlated with ground cover. In the Kona regression model, the negative term for introduced grasses marks low densities in areas choked by kikuyu grass or fountain grass. Such areas may lack the diversity of fruit, browse, seeds, and insects that compose the typical diet (Schwartz and Schwartz 1949, 1951b). Moisture may ultimately limit pheasant in such areas, for fruit is a common source of water in dry areas (Schwartz and Schwartz 1949).

The picture of habitat response that developed from our analysis generally matches the range and mode of pheasant habitat response found by Schwartz and Schwartz (1949, 1951b). The typical habitat in the Hawaiian Islands is similar to the open brush and grain field habitat of South Dakota where extremely high populations occur (Kimball et al. 1956).

COMMON PEAFOWL (*Pavo cristatus*)

Common Peafowl were introduced in 1860 (Caum 1933); they are native to the Indian subcontinent. In the Hawaiian Islands they range from sea level to 1500 m elevation (Schwartz and Schwartz 1949), occasionally higher. The diet is omnivorous and resembles that of the Ring-necked Pheasant (Schwartz and Schwartz 1949). Peafowl were established on Hawaii, Maui, Molokai, Oahu, Kauai, and Niihau in the 1940s (Schwartz and Schwartz 1949).

Common Peafowl are fairly uncommon in Kona and East Maui (Tables 33, 34, 43, Figs. 194, 195), where we estimated total populations of 80 ± 10 (95% CI) and 8 ± 2 birds, respectively. The range appears to have expanded in Kona since 1949, but elsewhere on Hawaii and Maui it has changed little. The Molokai, Lanai, and Kauai study areas lie outside the range (Schwartz and Schwartz 1949). In the Hawaiian Islands, peafowl are usually associated with ranches and stockponds.

Common Peafowl occupy a wide range of more open habitats, and are most common in dry lower elevation areas (Table 42, Fig. 196). Because of the long distances that vocalizations carry, some birds were in a different vegetation type than the observer. In India, peafowl prefer dry woodlands with open growth (Ali and Ripley 1969). Association with open woodland is indicated in the regression model by an inverted parabola for tree biomass centered far above the range of values (i.e., nearly linear positive response) and by negative terms for crown cover and canopy height. Areas with high densities have little shrub cover but much ground cover.

Common Peafowl are commonly associated with passiflora, especially banana poka. The attraction of Common Peafowl to passiflora is reflected by the strongest term in the model, and the birds are possible dispersal agents for banana poka (Warshauer et al. 1983). Schwartz and Schwartz (1949) list passiflora as a common feature of typical habitat. In North Kona, Lewin (1971) found Common Peafowl most abundant in forests festooned with banana poka. In the East Maui study area, the main population coincides with an area of high passiflora cover.

WILD TURKEY (*Meleagris gallopavo*)

Turkeys were first introduced about 1815 from domestic stock (Caum 1933); later introductions were mostly wild stock from the subspecies *intermedia* and *merriami* of the southwest United

TABLE 43

DENSITY [MEAN (SE)] OF THE COMMON PEAFOWL AND WILD TURKEY BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Common Peafowl		Wild Turkey				
	Kona	E. Maui	Kau	Hamakua	Kona	Mauna Kea	E. Maui
Elevation							
100–300 m	···	···	···	···	···	···	···
300–500 m	0	0	···	0	0	···	0
500–700 m	+ (+)	0	0	0	1 (+)	···	0
700–900 m	1 (+)	1 (1)	0	1 (1)	2 (+)	···	0
900–1100 m	1 (+)	1 (+)	0	+ (+)	2 (+)	···	0
1100–1300 m	+ (+)	1 (+)	0	+ (+)	2 (+)	···	1 (1)
1300–1500 m	+ (+)	+ (+)	0	+ (+)	2 (+)	···	0
1500–1700 m	+ (+)	+ (+)	3 (3)	2 (+)	2 (+)	···	0
1700–1900 m	+ (+)	+ (+)	+ (+)	2 (1)	2 (+)	···	0
1900–2100 m	+ (+)	+ (+)	0	2 (1)	3 (+)	+ (+)	+ (+)
2100–2300 m	0	+ (+)	0	+ (+)	1 (+)	1 (1)	+ (+)
2300–2500 m	0	+ (+)	···	···	0	+ (+)	+ (+)
2500–2700 m	···	0	···	···	···	+ (+)	0
2700–2900 m	···	0	···	···	···	+ (+)	0
2900–3100 m	···	···	···	···	···	+ (+)	···
Habitat							
Ohia	+ (+)	0	1 (1)	0	2 (+)	···	0
Koa-ohia	+ (+)	+ (+)	0	1 (+)	2 (+)	···	0
Koa-mamane	+ (+)	···	···	1 (+)	4 (+)	···	···
Mamane-naio	+ (+)	···	···	···	3 (1)	+ (+)	···
Mamane	+ (+)	0	···	···	3 (+)	+ (+)	0
Other natives	+ (+)	+ (+)	···	6 (2)	1 (+)	···	+ (+)
Intro. trees	+ (+)	0	···	1 (1)	4 (1)	···	0
Treeless	+ (+)	0	···	0	+ (+)	···	0

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

States (Hewitt 1967). Turkeys increased in numbers on all islands (Munro 1944) and were plentiful until 1938. Between 1938 and 1941, a drastic reduction in numbers restricted Wild Turkey to a small population on leeward Hawaii (Schwartz and Schwartz 1949). By the 1970s, new releases of *intermedia* resulted in numbers sufficient to sustain public hunting (R. Bachman, R. L. Walker, pers. comm.).

Wild Turkeys are well established throughout Kona and on the upper slopes of Mauna Kea (Tables 33, 34, 43, Figs. 197–200). We estimated a total population of 2000 ± 150 (95% CI) birds in the study areas on Hawaii. On Maui, turkeys are rare on the lower slopes of Haleakala on the Auwahi Tract and in west Kahikinui (Fig. 201). Because turkeys flock, our density and population estimates are biased on the low side.

Wild Turkeys occupy a wider variety of habitats on Hawaii than on Maui (Fig. 202). This may simply reflect a population that is better established on Hawaii. The regression models (Table 44) indicate that turkeys are most common at higher elevations in open woodland with ground cover. This generally matches the open woodland habitat of populations in Texas and the American Southwest (Bent 1932, Hewitt 1967).

In both regression models some variables act as correction terms and require careful interpretation. In Kona, crown cover and canopy height balance tree biomass. The net effect shows that turkeys are associated with open woodlands. In Hamakua three tree species balance tree biomass, but mamane actually has a positive correlation (r = 0.11) with turkey density. The net effect reflects the absence of turkey from treeless areas and heavy forest, and lower densities in pure mamane than in mixed mamane-naio. The discrepancy between the Hamakua and Kona mamane terms is thus a result of model mechanics.

In both regression models, turkeys are positively associated with ground cover and passiflora but negatively associated with native grasses. Shrub cover has a negative term in the Hamakua model, and shrub cover could enter the final model for Kona as a negative term sig-

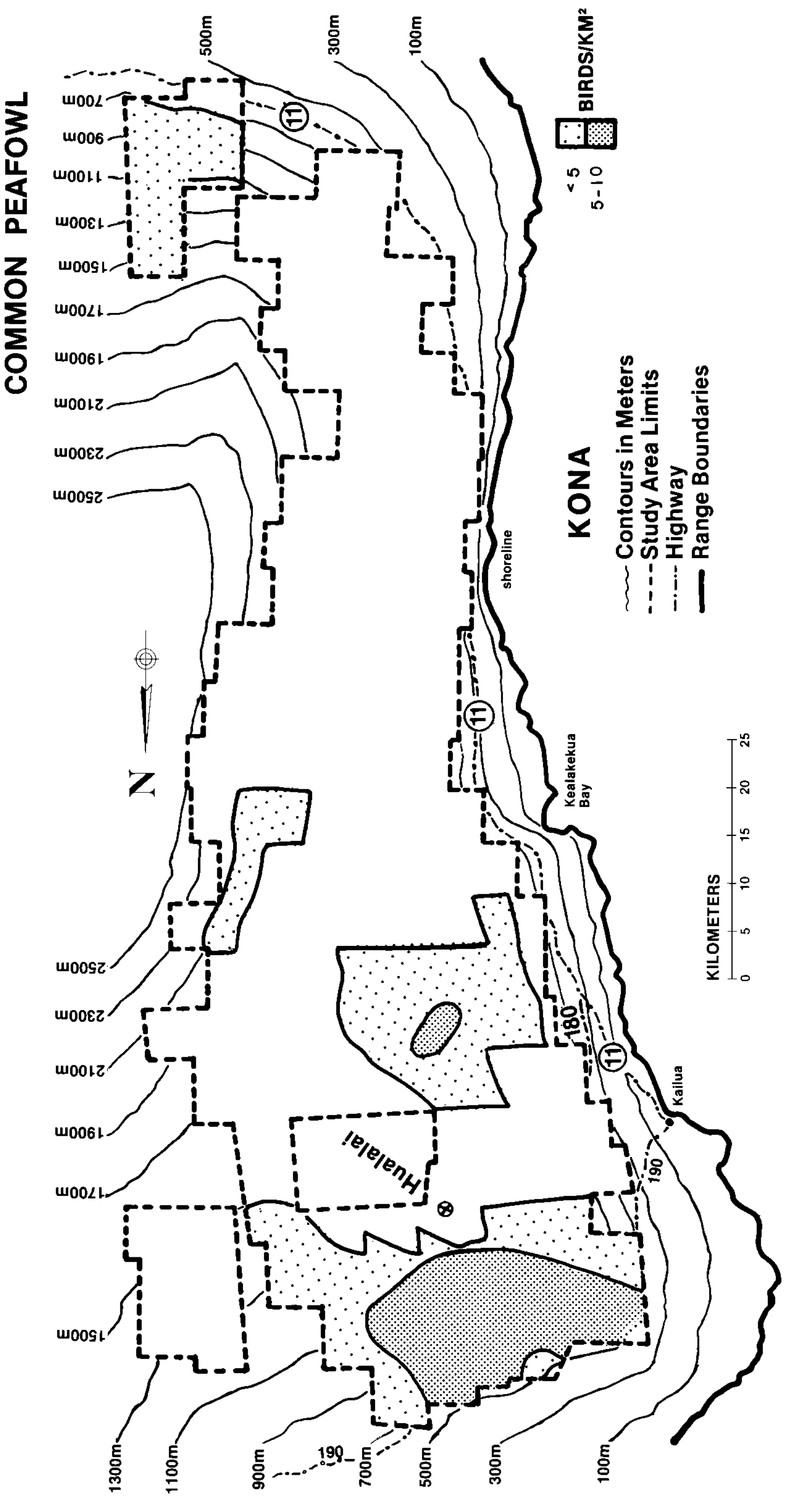


FIGURE 194. Distribution and abundance of the Common Peafowl in the Kona study area.

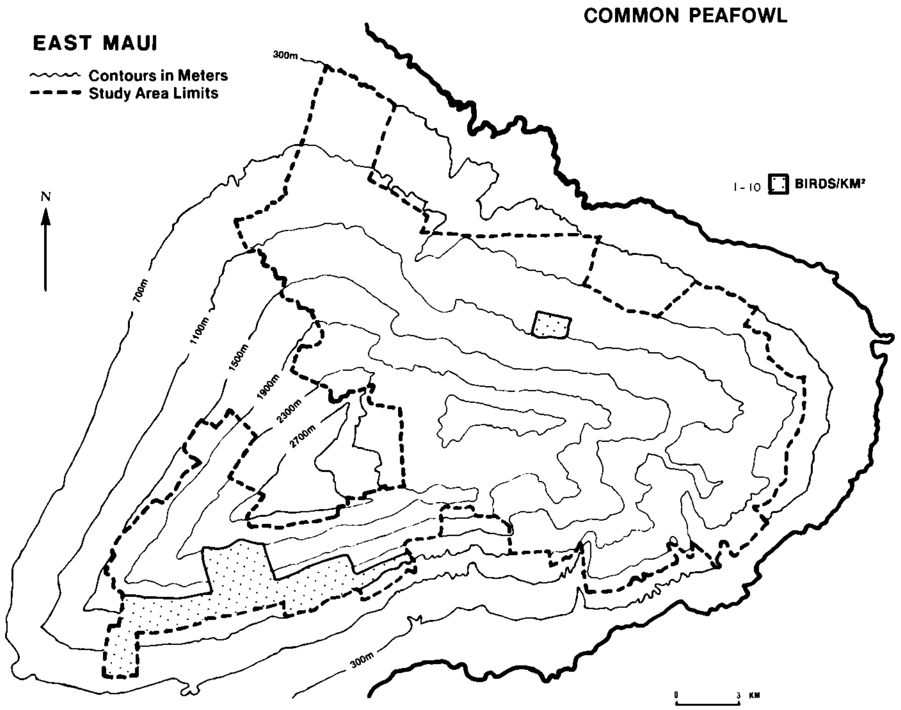


FIGURE 195. Distribution and abundance of the Common Peafowl in the East Maui study area.

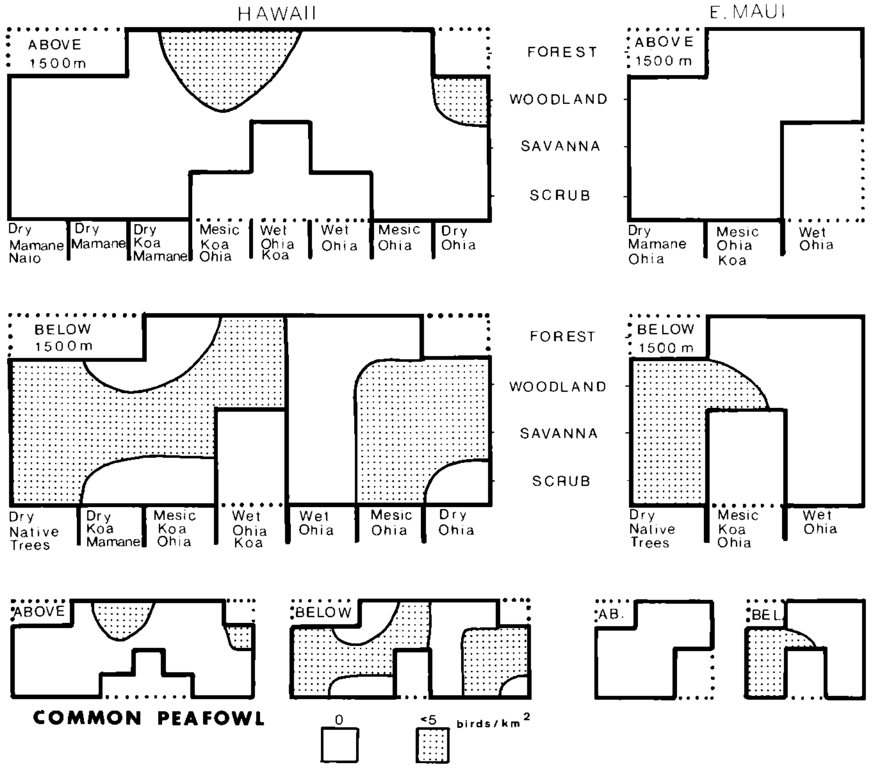


FIGURE 196. Habitat response graphs of the Common Peafowl. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

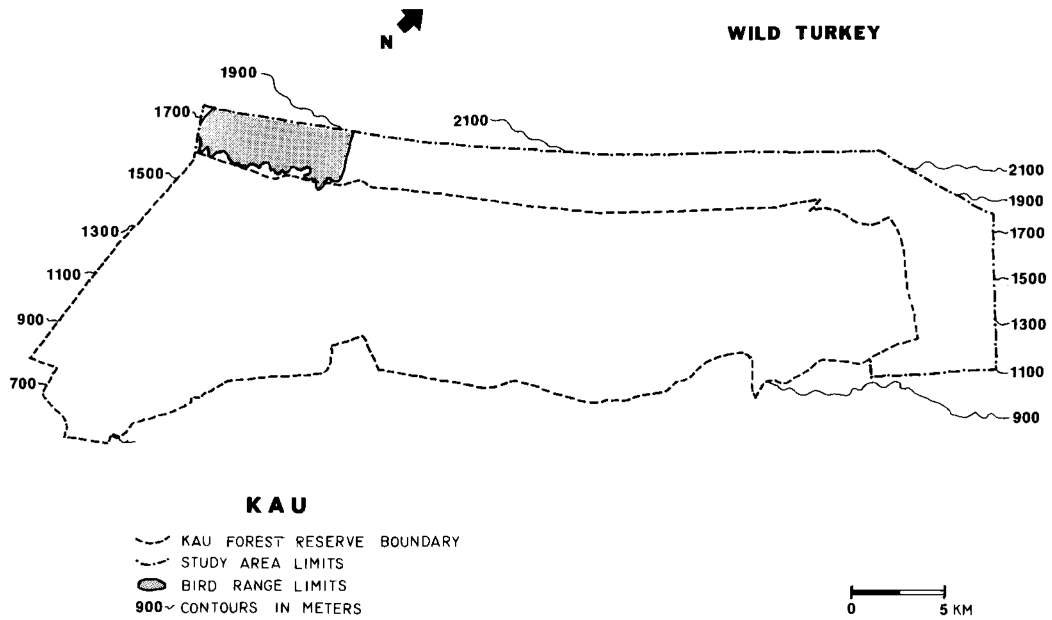


FIGURE 197. Distribution and abundance of the Wild Turkey in the Kau study area. (Density within range is less than 5 birds/km^2.)

TABLE 44
REGRESSION MODELS FOR HABITAT RESPONSE OF THE WILD TURKEY AND CALIFORNIA QUAIL[a]

	Wild Turkey		California Quail				
	Hamakua	Kona	Hamakua	Puna	Kipukas	Kona	Mauna Kea
R^2	0.24*	0.19*	0.17*	0.10*	0.45*	0.22*	0.16*
Moisture	···	···	···	−5.5*	−4.0*	−3.2	X
Elevation	4.1*	7.0*	···	···	−7.1*	···	−3.4*
(Elevation)^2	···	−5.9*	···	···	···	8.1*	···
Tree biomass	4.8*	5.4*	6.4*	3.7*	···	2.0	···
(Tree biomass)^2	···	···	···	···	···	···	···
Crown cover	···	−5.5*	···	−2.8	···	···	···
Canopy height	···	−3.0	···	···	6.4*	···	···
Koa	···	···	···	X	2.4	−5.4*	X
Ohia	−6.9*	···	−9.3*	···	−6.5*	−3.8*	X
Naio	X	2.3	X	X	−2.6	3.2	−2.0
Mamane	−6.9*	9.4*	9.1*	···	···	7.2*	···
Intro. trees	−4.0*	···	−4.6*	···	X	···	X
Shrub cover	−8.8*	···	···	···	···	···	−4.5*
Ground cover	3.5*	7.4*	−6.0*	−2.6	···	···	···
Native shrubs	···	···	8.8*	2.6	···	···	X
Intro. shrubs	···	···	···	···	···	···	X
Ground ferns	X	−4.4*	X	···	···	2.4	X
Matted ferns	···	···	···	···	···	···	X
Tree ferns	X	−5.2*	X	···	X	···	X
Ieie	X	···	X	···	X	···	X
Passiflora	8.8*	4.6*	···	X	X	−3.3	X
Native herbs	X	···	X	−2.8	···	−2.6	X
Intro. herbs	X	···	X	···	4.9*	2.7	···
Native grasses	−7.4*	−4.3*	6.2*	···	2.7	−6.6*	···
Intro. grasses	···	···	6.0*	···	···	···	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

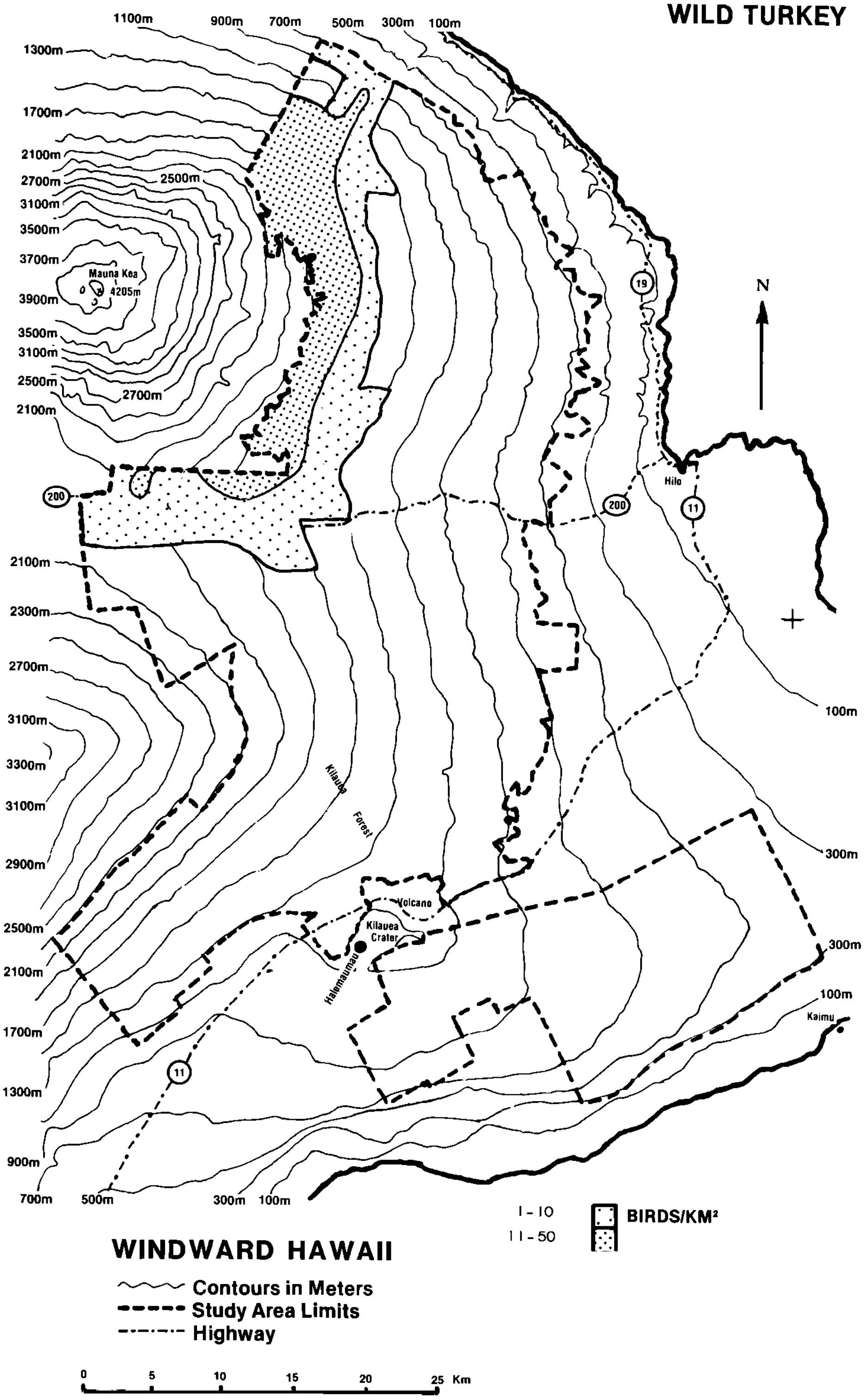


FIGURE 198. Distribution and abundance of the Wild Turkey in the windward Hawaii study areas.

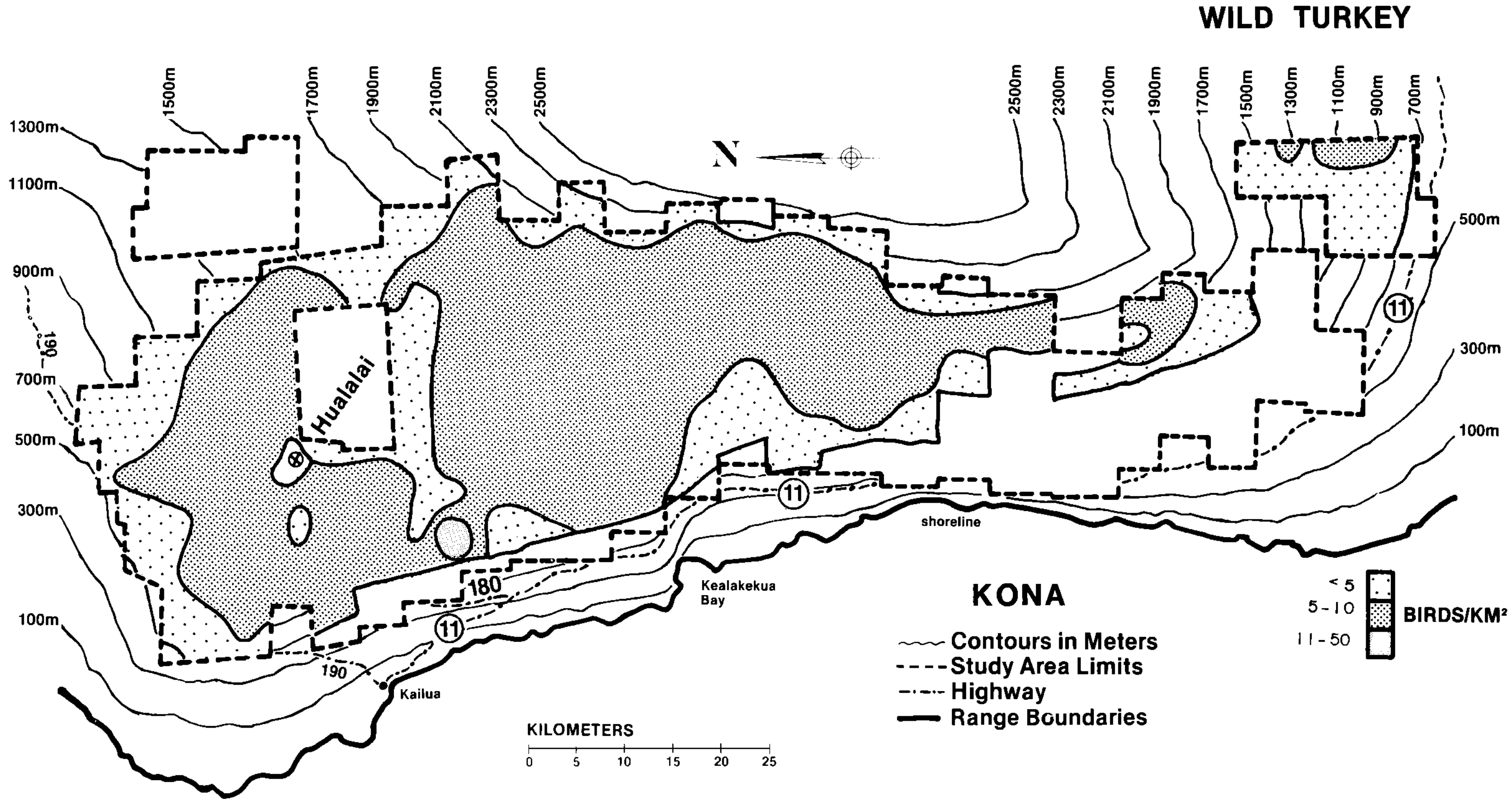


FIGURE 199. Distribution and abundance of the Wild Turkey in the Kona study area.

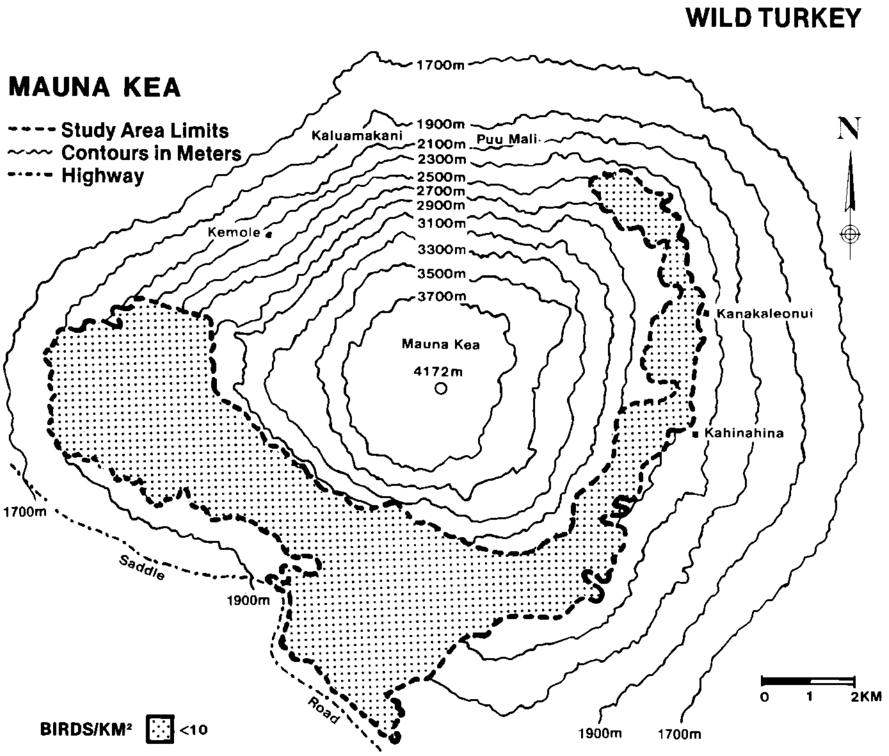


FIGURE 200. Distribution and abundance of the Wild Turkey in the Mauna Kea study area.

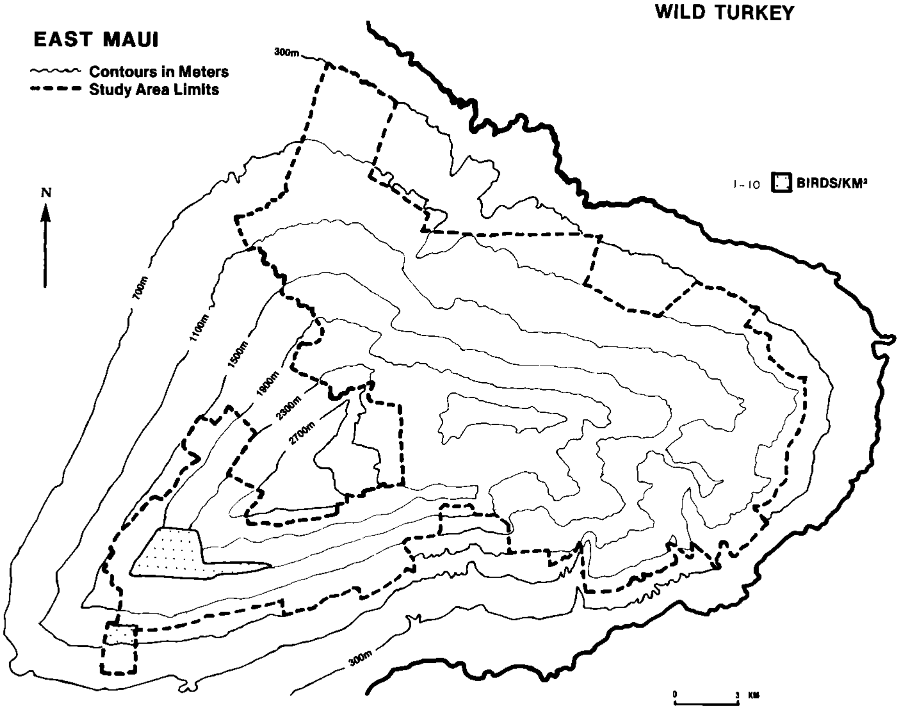


FIGURE 201. Distribution and abundance of the Wild Turkey in the East Maui study area.

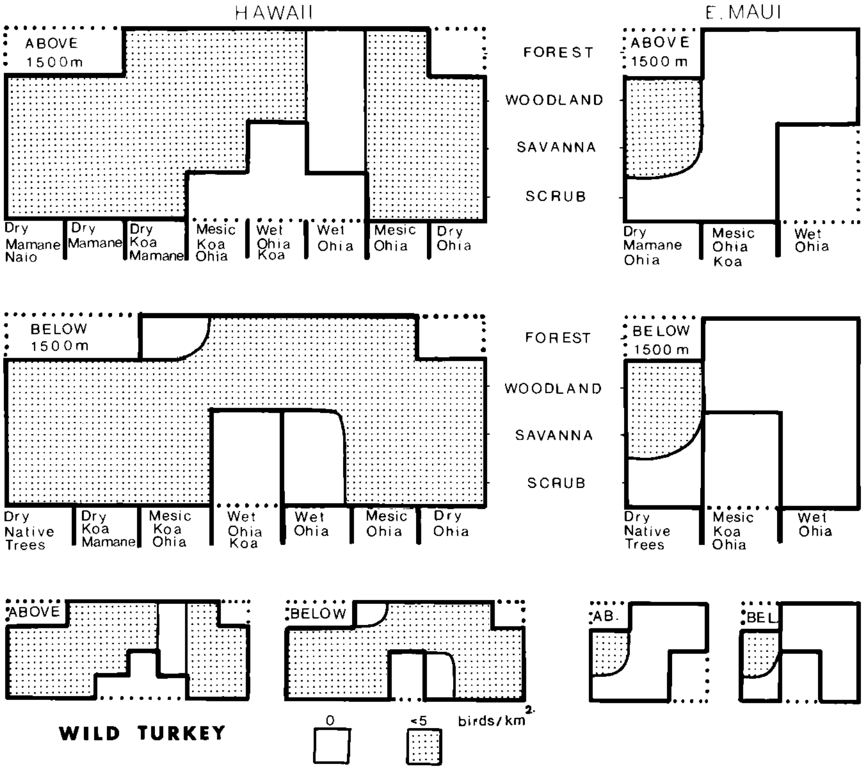


FIGURE 202. Habitat response graphs of the Wild Turkey (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

nificant at the 0.07 level. The association with passiflora supports the indictment of Wild Turkeys as dispersal agents of banana poka (Warshauer et al. 1983).

CALIFORNIA QUAIL
(*Callipepla californica*)

California Quail were introduced to the Hawaiian Islands from California before 1855 (Caum 1933). Munro (1944) considered them well established and common on Molokai and Hawaii in the 1890s and reported birds on Kauai and Niihau. He stated that the Lanai population was extirpated. They are now present on all main islands except Oahu (R. L. Walker, pers. comm.). California Quail are native to western North America where they occur in habitats from desert scrub to open woodlands (Grinnell and Miller 1944).

Because quail flock, our density estimates are biased on the low side. We found California Quail in a variety of habitat types and over a wide elevational range in seven study areas (Tables 33, 34, 45, Figs. 203–206). On Hawaii 2800 ± 700 (95% CI) birds inhabit our study areas. Contrary to Schwartz and Schwartz (1949, 1950), we did not find birds above 1500 m elevation in ohia scrub in Kau, nor at all in south Kona. Populations are well established in the drier upper portions of Hawaii Volcanoes National Park, in north Kona, and in the mamane-naio woodland on Mauna Kea. Densities appear to have increased in the national park over the 1940–1975 interval (Conant 1975, Banko and Banko 1980). On East Maui an estimated 50 ± 20 birds occur in west Kahikinui. Only scattered birds were observed on Lanai.

Highest quail densities are in dry mamane-naio scrublands and savannas above 1500 m (Fig. 207). The regression models (Table 44) show that quail are most commonly associated with dry areas over a range of elevation and habitat types. The models suggest that California Quail have little response to tree biomass, crown cover, or canopy height. Densities tend to be higher in mamane and lower in ohia and introduced tree habitats.

The negative response to native grasses in the Kona regression model corresponds to low densities in alpine scrub, where lack of water and cold temperatures may limit numbers. Passiflora infestations do not attract high densities, but in-

TABLE 45

DENSITY [MEAN (SE)] OF THE CALIFORNIA QUAIL BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	E. Maui	Lanai
Elevation							
100–300 m	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·
300–500 m	0	0	· · ·	+ (+)	· · ·	0	· · ·
500–700 m	0	0	· · ·	1 (1)	· · ·	0	+ (+)
700–900 m	0	4 (2)	· · ·	2 (1)	· · ·	0	+ (+)
900–1100 m	0	1 (1)	· · ·	+ (+)	· · ·	0	+ (+)
1100–1300 m	1 (1)	1 (+)	5 (1)	1 (+)	· · ·	1 (1)	· · ·
1300–1500 m	1 (+)	· · ·	5 (1)	1 (+)	· · ·	+ (+)	· · ·
1500–1700 m	+ (+)	· · ·	5 (1)	2 (+)	· · ·	+ (1)	· · ·
1700–1900 m	2 (1)	· · ·	5 (1)	2 (+)	· · ·	2 (1)	· · ·
1900–2100 m	0	· · ·	1 (+)	3 (+)	19 (10)	1 (+)	· · ·
2100–2300 m	2 (2)	· · ·	2 (1)	4 (1)	30 (11)	1 (1)	· · ·
2300–2500 m	· · ·	· · ·	· · ·	1 (1)	12 (6)	3 (1)	· · ·
2500–2700 m	· · ·	· · ·	· · ·	· · ·	3 (1)	8 (5)	· · ·
2700–2900 m	· · ·	· · ·	· · ·	· · ·	2 (+)	0	· · ·
2900–3100 m	· · ·	· · ·	· · ·	· · ·	1 (1)	· · ·	· · ·
Habitat							
Ohia	1 (+)	2 (1)	2 (+)	1 (+)	· · ·	0	· · ·
Koa-ohia	+ (+)	· · ·	3 (1)	+ (+)	· · ·	0	· · ·
Koa-mamane	2 (2)	· · ·	6 (1)	3 (+)	· · ·	· · ·	· · ·
Mamane-naio	· · ·	· · ·	· · ·	2 (1)	11 (4)	· · ·	· · ·
Mamane	· · ·	· · ·	· · ·	5 (+)	10 (4)	0	· · ·
Other natives	3 (1)	· · ·	8 (+)	2 (+)	· · ·	2 (+)	1 (1)
Intro. trees	0	· · ·	· · ·	1 (+)	· · ·	0	+ (+)
Treeless	0	0	+ (+)	+ (+)	· · ·	+ (+)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; · · · indicates stratum was not sampled in study area.

troduced herbs, a common food source, do. This relation is also seen in the diet; where browse and seeds are major items and fruit is unimportant (Schwartz and Schwartz 1950).

Suitable habitat for California Quail is a mosaic of cover types, food sources, and watering points (Leopold 1977). Their absence in rainforests and cultivated areas in Hawaii was noted by Schwartz and Schwartz (1949), although birds occur occasionally in ohia dieback areas with 400-cm annual precipitation (S. Mountainspring, pers. observ.). The requirement for water, often met by stock watering troughs or game watering tanks, is essential for good population densities (Schwartz and Schwartz 1949), and appears to restrict the range at high elevations in the Kona and Kipukas study areas.

ROCK DOVE (*Columba livia*)

Rock Doves were introduced to the Hawaiian Islands as early as 1796 (Schwartz and Schwartz 1949). They occur on all main islands and are well established in many urban areas. They feed chiefly on seeds, with larval insects next in dietary importance (Schwartz and Schwartz 1949). Rock Doves were sighted flying near forest edges and occasionally in the dry mamane-naio woodland near Mauna Kea State Park (J. M. Scott, pers. observ.). These are assumed to be recent escapes or domestic birds, although they may be vagrants from feral populations.

SPOTTED DOVE (*Streptopelia chinensis*)

Spotted Doves, known locally as Lace-necked or Chinese Doves, were introduced before 1880 (Caum 1933) and are native to most of the Oriental zoogeographical region. Spotted Doves are most abundant from sea level to 1200 m elevation and are widely distributed on all the islands (Schwartz and Schwartz 1949, 1951a; Lewin 1971); our survey primarily sampled peripheral range. The call notes carry quite far, and some of the birds recorded may have occupied a different habitat than that of the observer. The habitat responses noted may also fail to take into account the 6–8 km distances between some roosting and feeding areas (Schwartz and Schwartz 1949). Spotted Doves feed chiefly on seeds and insects on the ground (Schwartz and Schwartz 1949, Goodwin 1970).

We found Spotted Doves on all the islands surveyed (Tables 33, 34, 46). A total of 1100 ± 150 (95% CI) birds was estimated for our study

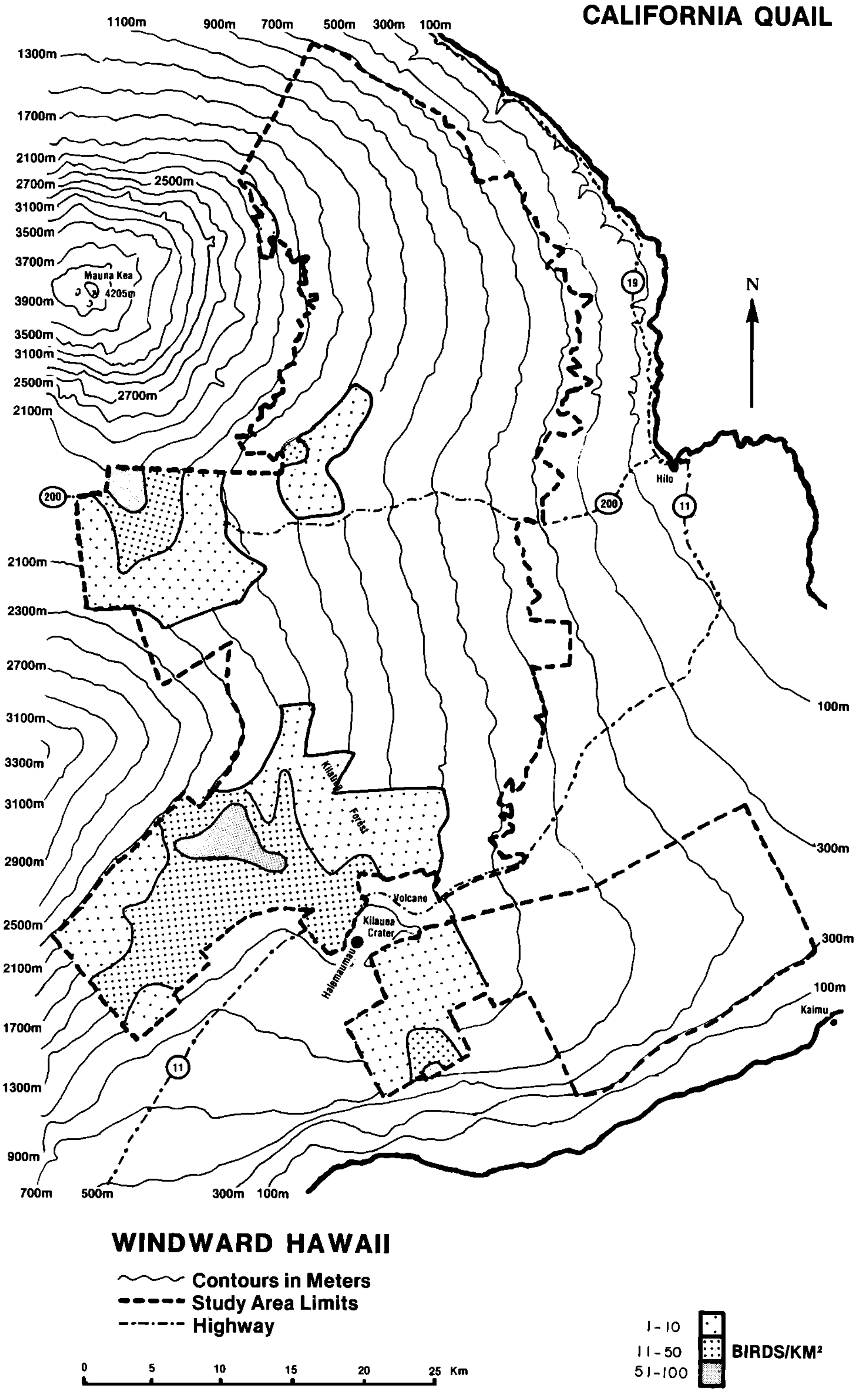


FIGURE 203. Distribution and abundance of the California Quail in the windward Hawaii study areas.

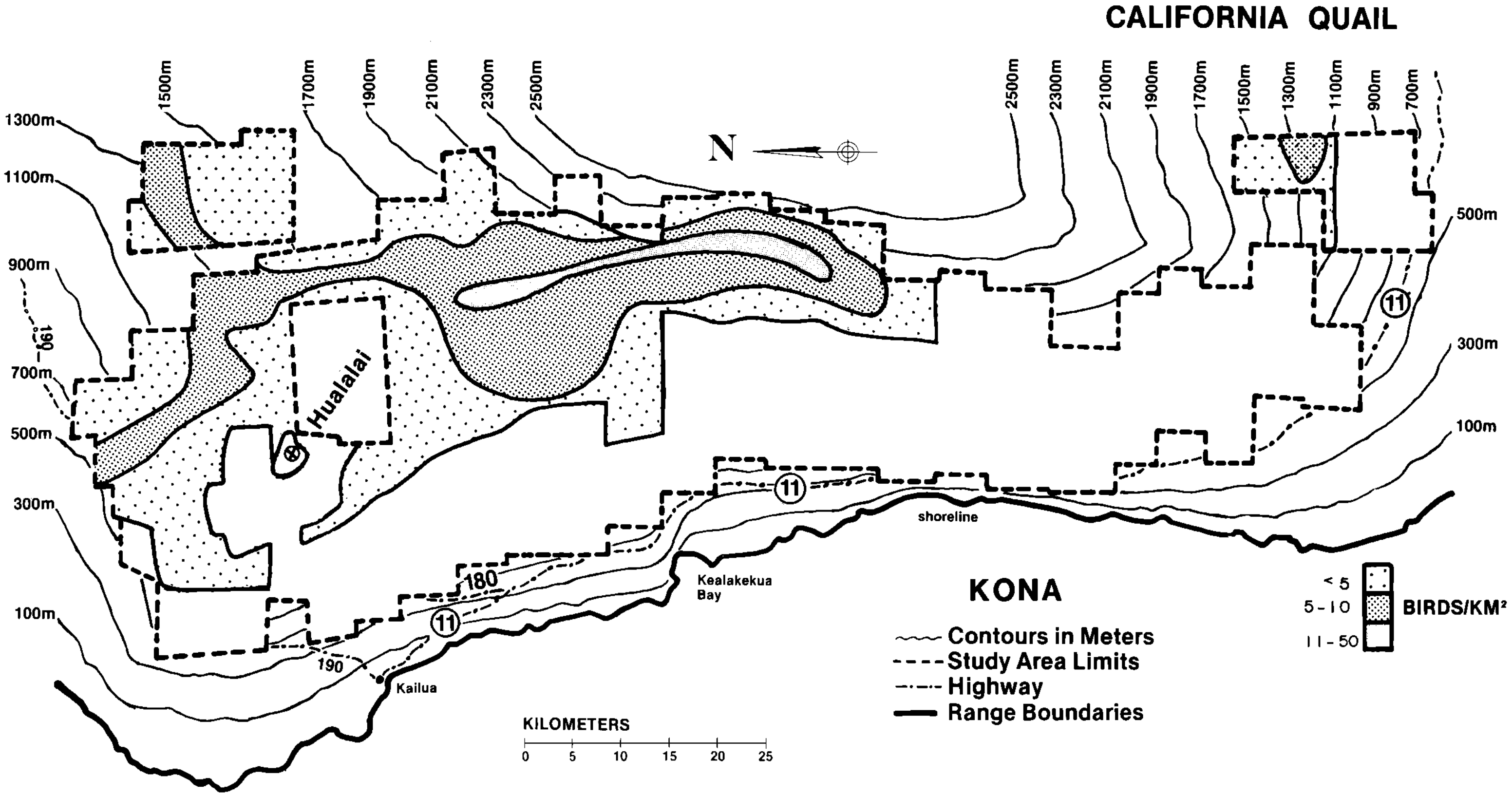


FIGURE 204. Distribution and abundance of the California Quail in the Kona study area.

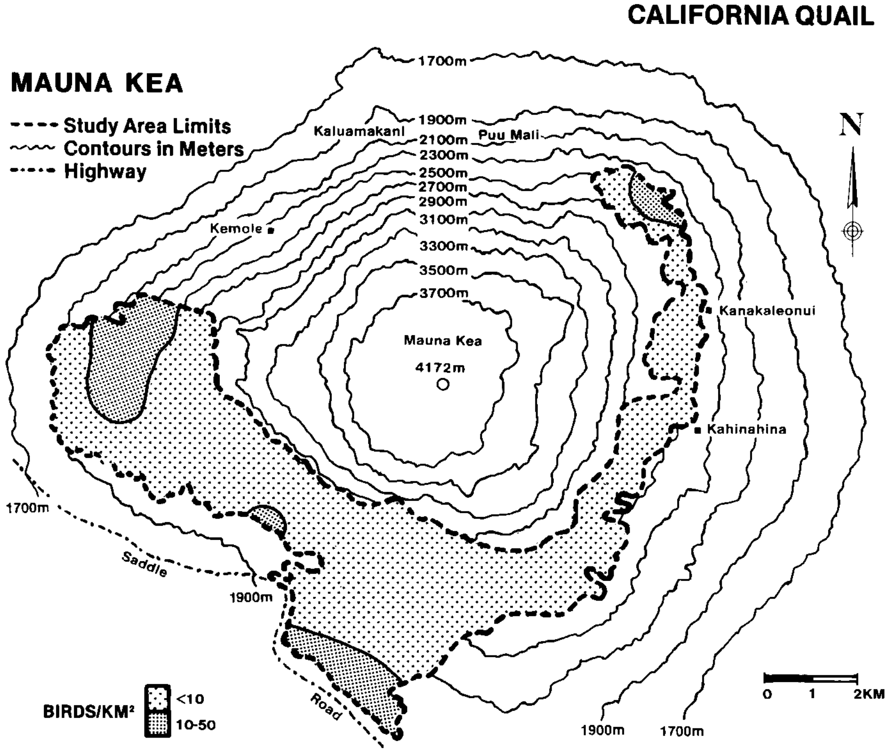


FIGURE 205. Distribution and abundance of the California Quail in the Mauna Kea study area.

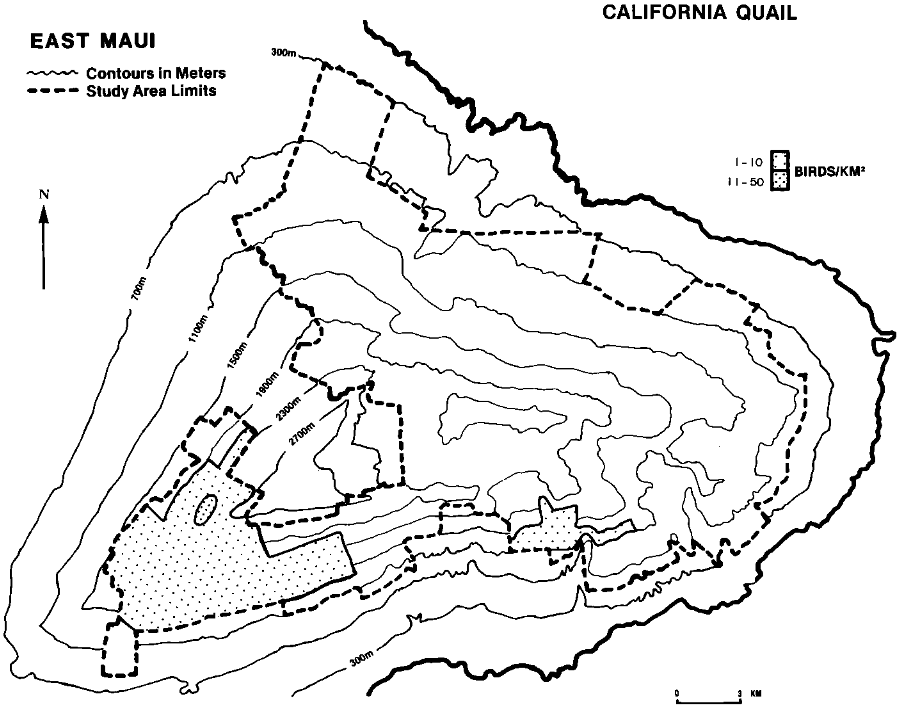


FIGURE 206. Distribution and abundance of the California Quail in the East Maui study area.

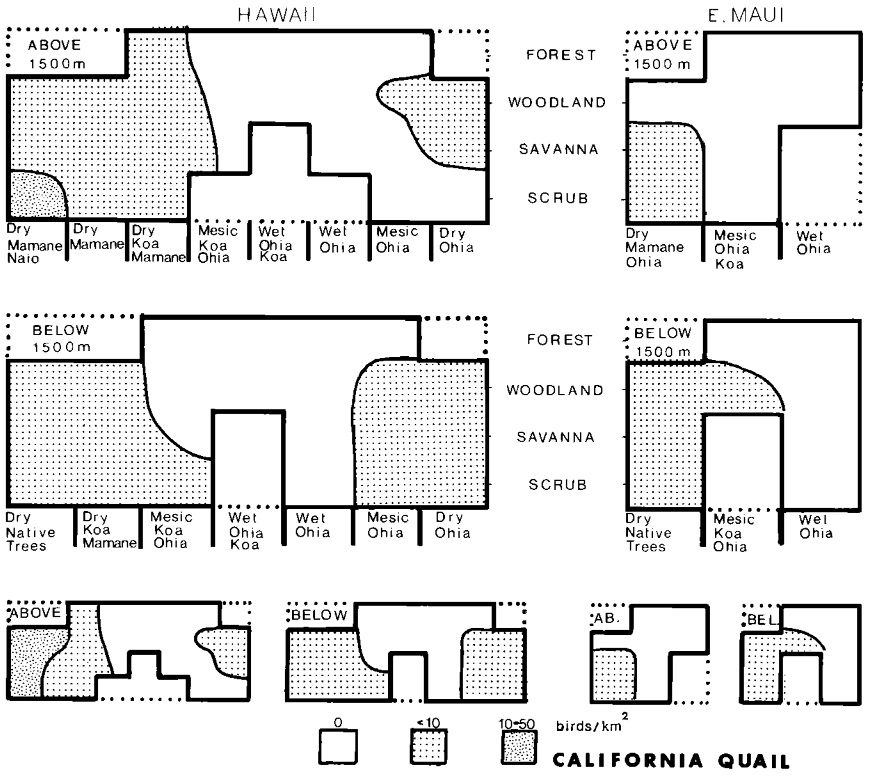


FIGURE 207. Habitat response graphs of the California Quail. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

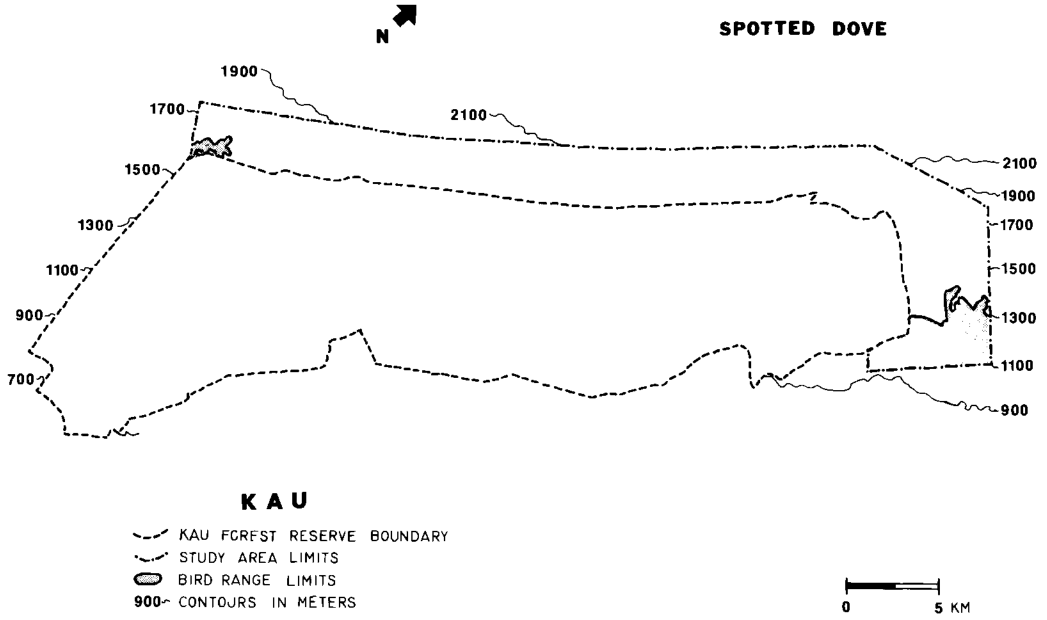


FIGURE 208. Distribution and abundance of the Spotted Dove in the Kau study area. (Density within range is less than 10 birds/km².)

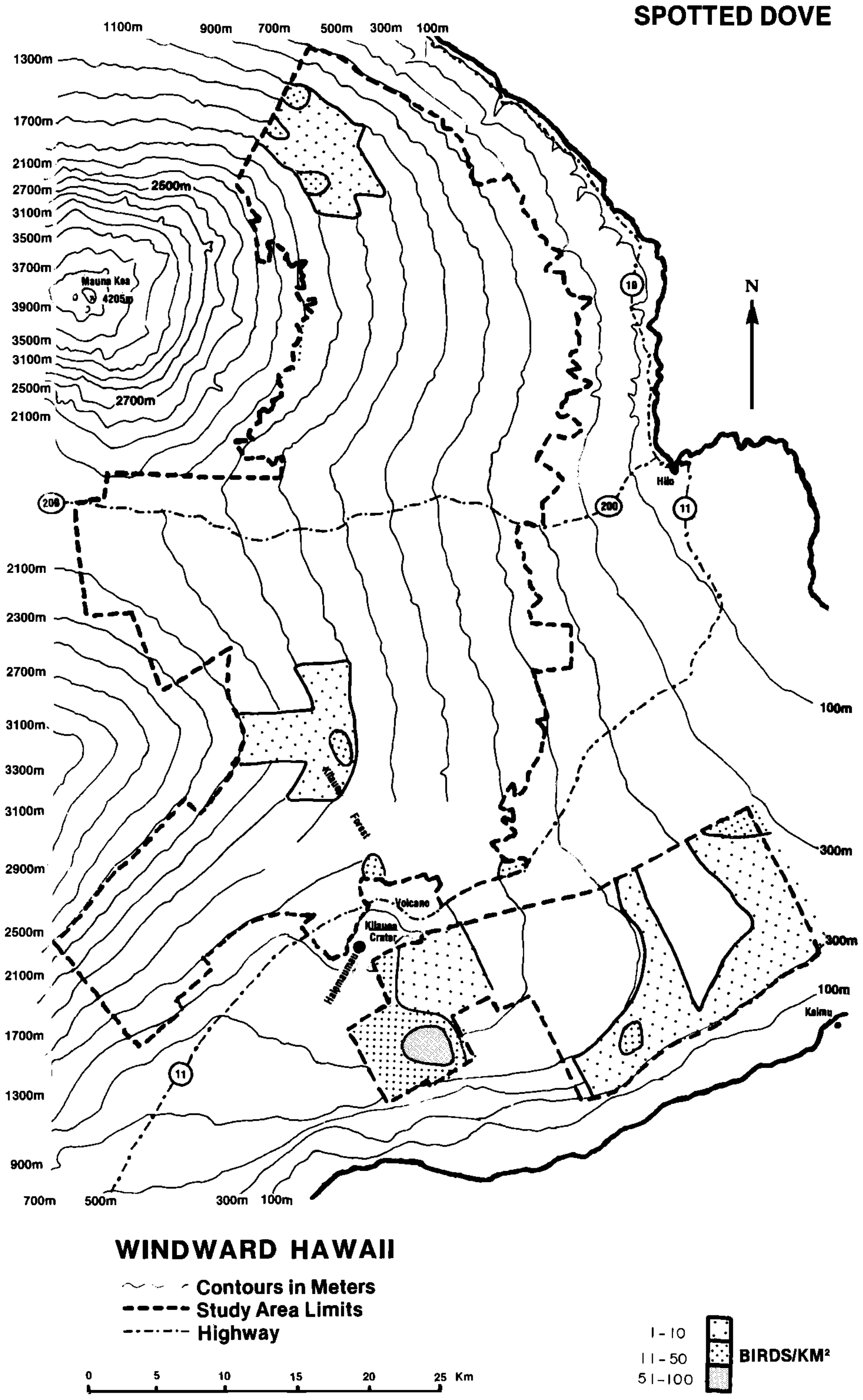


FIGURE 209. Distribution and abundance of the Spotted Dove in the windward Hawaii study areas.

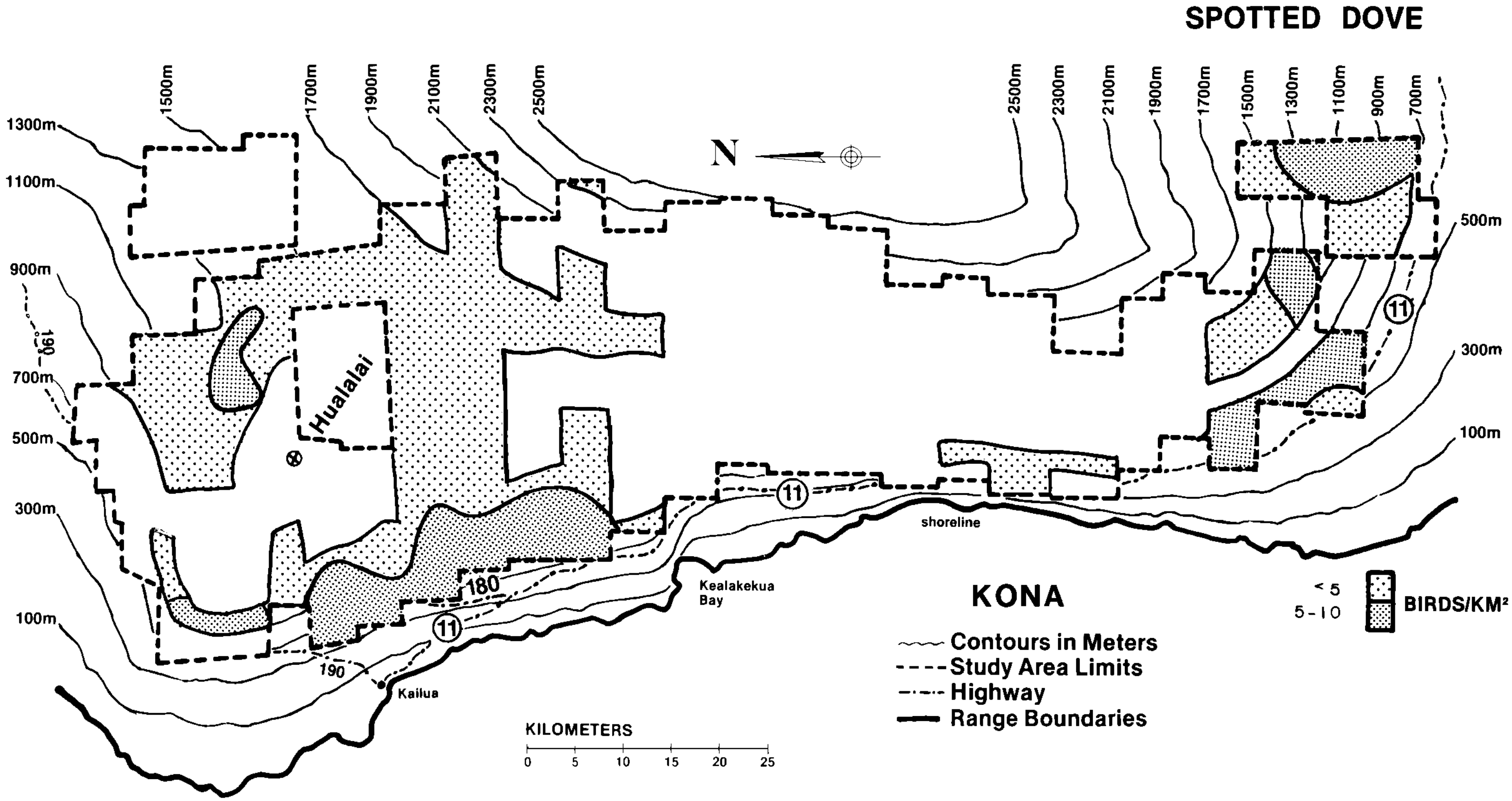


FIGURE 210. Distribution and abundance of the Spotted Dove in the Kona study area.

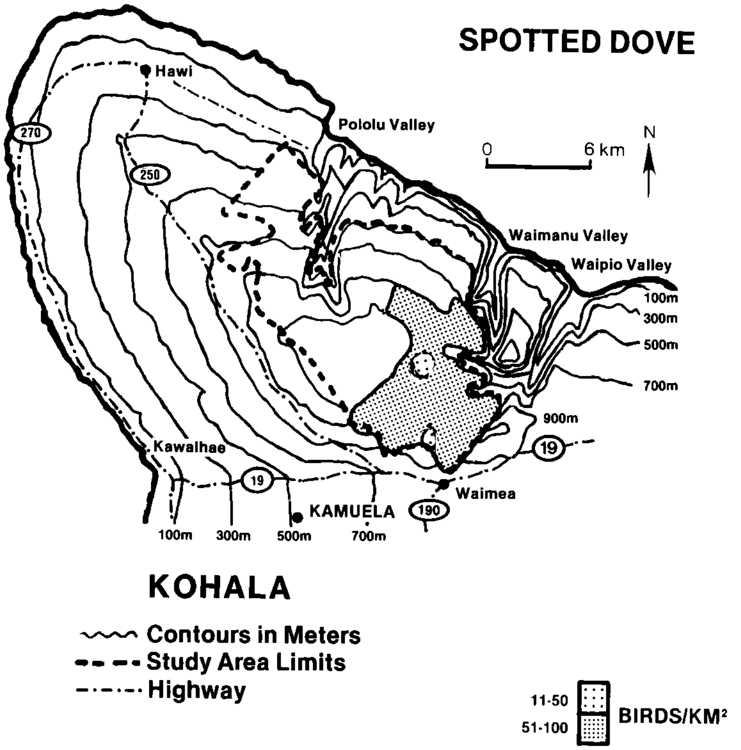


FIGURE 211. Distribution and abundance of the Spotted Dove in the Kohala study area.

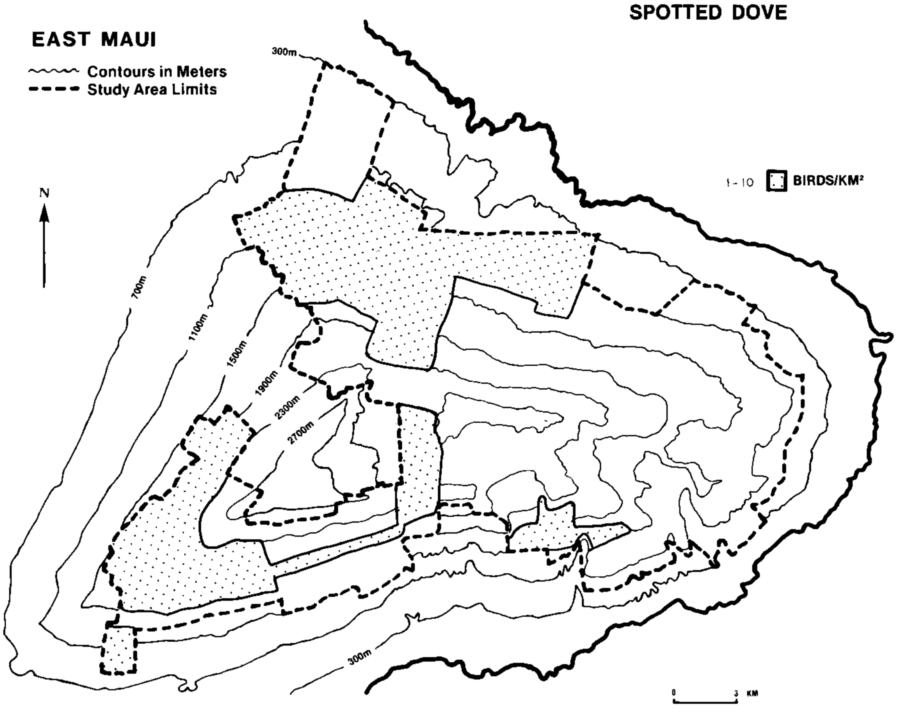


FIGURE 212. Distribution and abundance of the Spotted Dove in the East Maui study area.

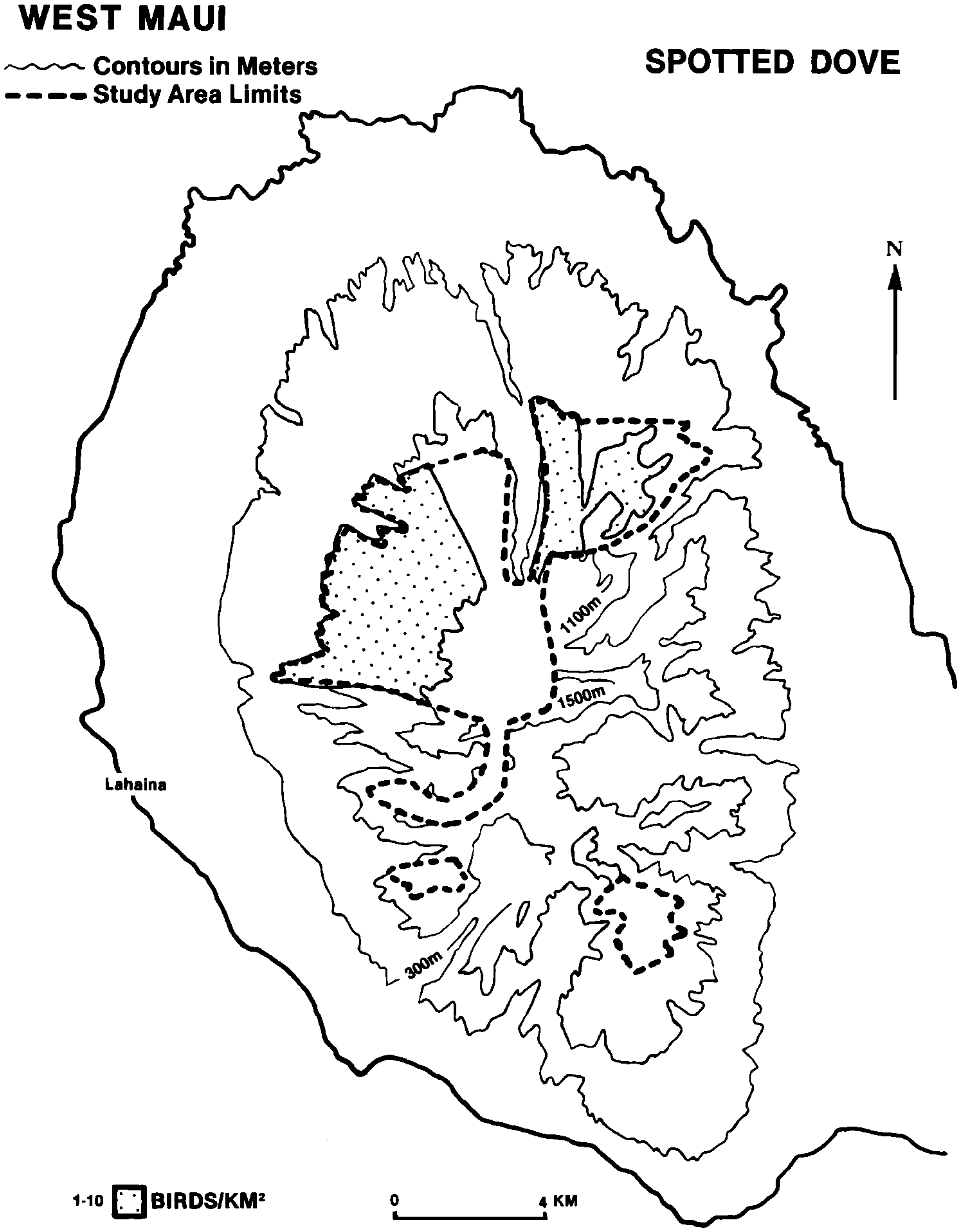


FIGURE 213. Distribution and abundance of the Spotted Dove in the West Maui study area.

areas. They are well established within the Puna, Kona, and Molokai study areas, but occur at low densities and as scattered populations in other study areas (Figs. 208–216). The range of Spotted Doves has expanded greatly on Hawaii, Maui, and Molokai since the survey by Schwartz and Schwartz (1949). In Kona, good numbers of Spotted Doves occur at Puu Waawaa, on the Kahuku tract, and in agricultural areas in south Kona (Honomalino Tract to Manuka Tract) and south and east of Kailua. On East Maui, birds occur on the northwest slopes of Haleakala, at low elevations in Keanae Valley, and at low densities across Kahikinui. On Molokai, birds show a massive intrusion into the western half of the study area and the northern valleys; one bird was

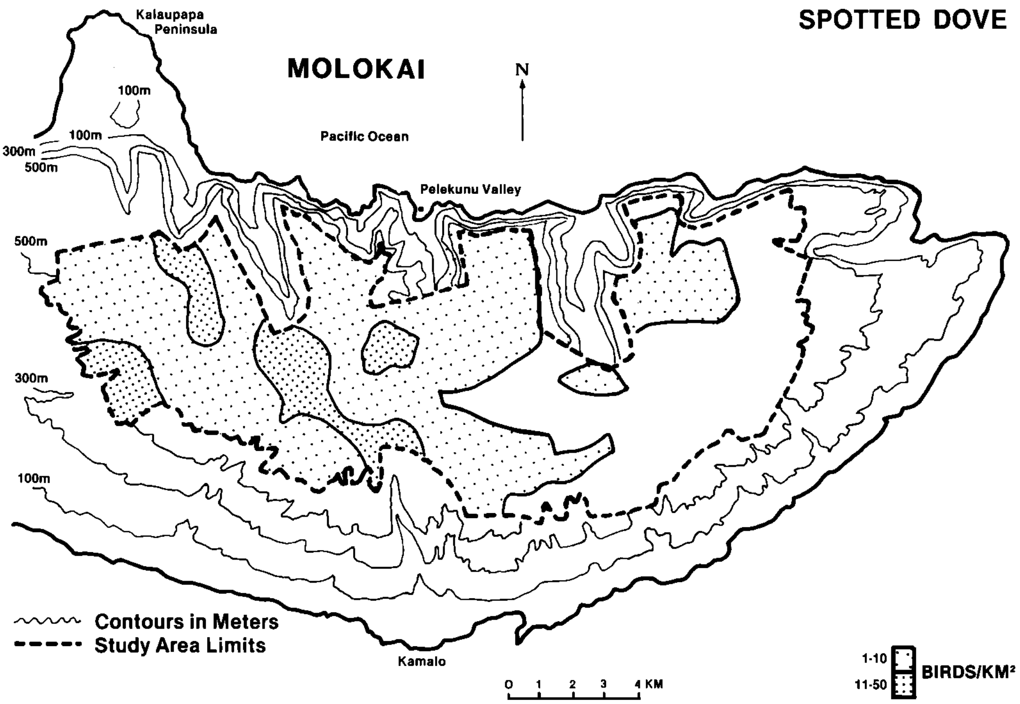


FIGURE 214. Distribution and abundance of the Spotted Dove in the Molokai study area.

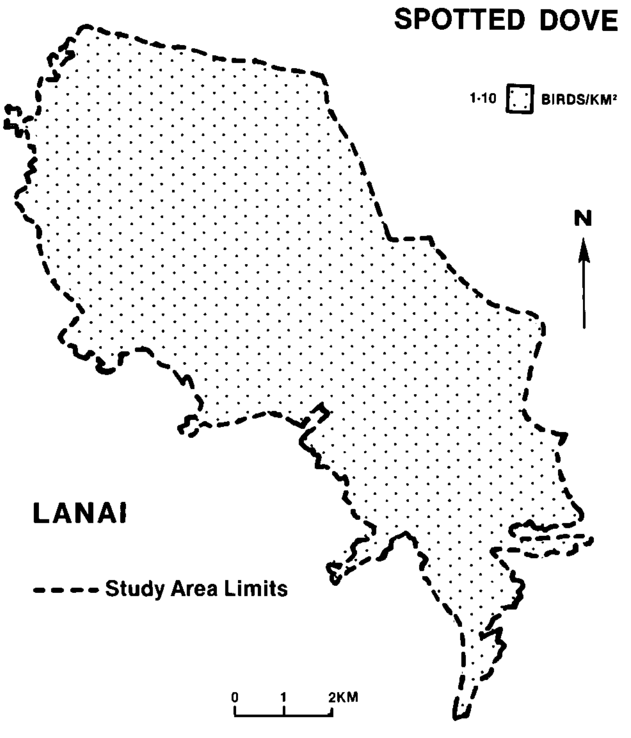


FIGURE 215. Distribution and abundance of the Spotted Dove in the Lanai study area.

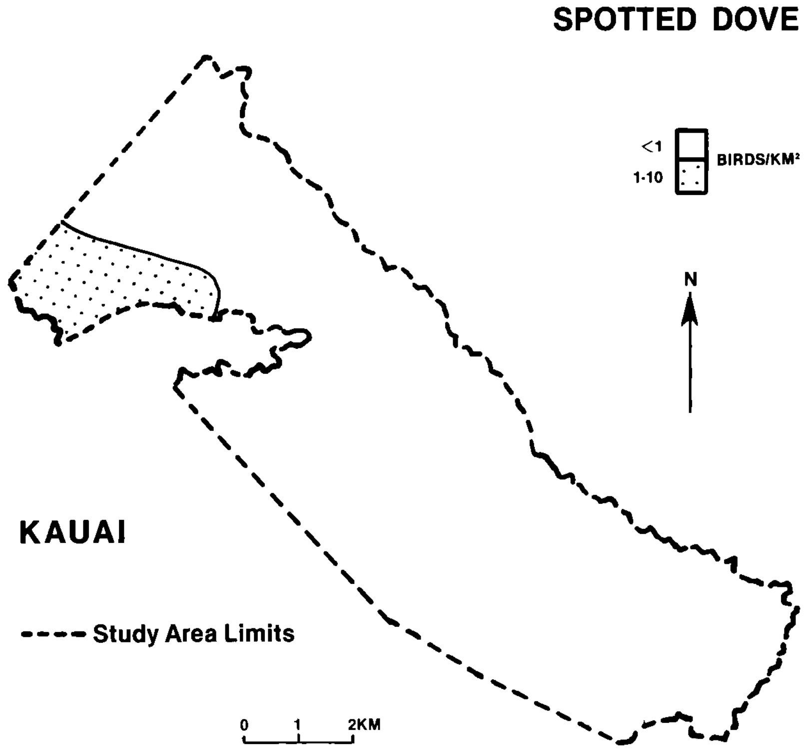


FIGURE 216. Distribution and abundance of the Spotted Dove in the Kauai study area.

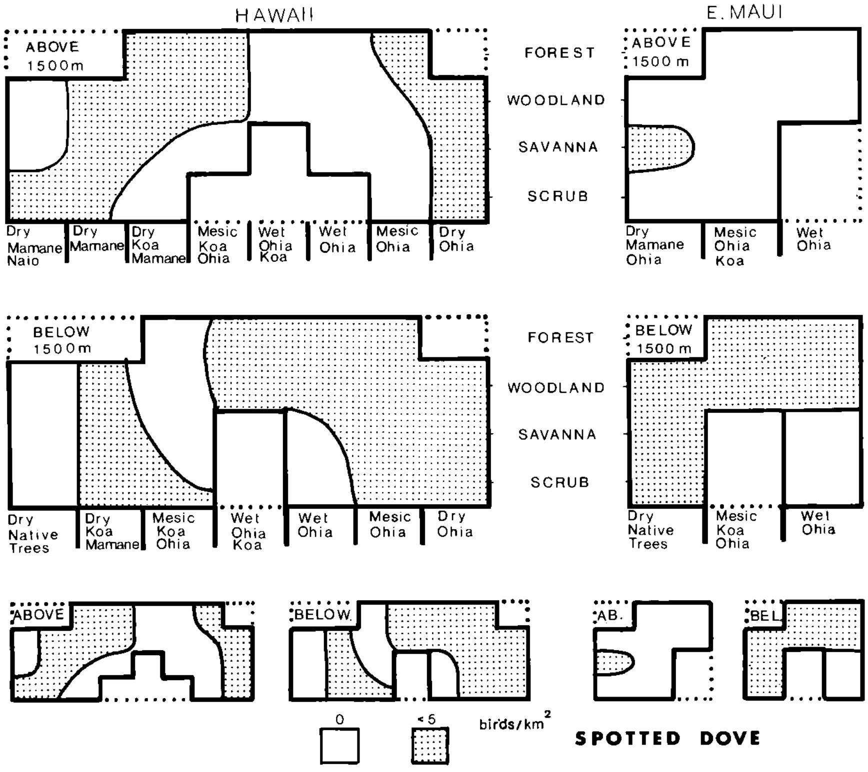


FIGURE 217. Habitat response graphs of the Spotted Dove. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 46
DENSITY [MEAN (SE)] OF THE SPOTTED DOVE BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Kohala	E. Maui	W. Maui	Molokai	Lanai	Kauai
Elevation											
100–300 m	···	···	···	···	···	···	···	···	+ (+)	···	···
300–500 m	···	+ (+)	0	···	6 (2)	0	0	···	10 (4)	···	···
500–700 m	0	+ (+)	0	···	2 (+)	0	1 (+)	0	9 (3)	2 (1)	···
700–900 m	+ (+)	2 (1)	12 (2)	···	1 (+)	0	1 (+)	1 (+)	2 (+)	+ (+)	···
900–1100 m	27 (10)	+ (+)	9 (2)	···	1 (+)	3 (3)	2 (1)	+ (+)	5 (1)	1 (1)	···
1100–1300 m	+ (+)	1 (1)	2 (1)	1 (1)	1 (+)	+ (+)	1 (1)	+ (+)	4 (1)	···	1 (+)
1300–1500 m	0	1 (+)	···	0	1 (+)	3 (3)	+ (+)	+ (+)	+ (+)	···	+ (+)
1500–1700 m	37 (12)	+ (+)	···	0	1 (+)	0	1 (+)	+ (+)	···	···	···
1700–1900 m	0	+ (+)	···	0	+ (+)	···	1 (+)	+ (+)	···	···	···
1900–2100 m	0	+ (+)	···	+ (+)	+ (+)	···	+ (+)	···	···	···	···
2100–2300 m	0	0	···	0	0	···	+ (+)	···	···	···	···
2300–2500 m	···	···	···	···	0	···	+ (+)	···	···	···	···
2500–2700 m	···	···	···	···	···	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	···	···	···	···	···	···
Habitat											
Ohia	31 (10)	+ (+)	3 (1)	1 (+)	1 (+)	+ (+)	+ (+)	+ (+)	4 (1)	···	+ (+)
Koa-ohia	5 (5)	+ (+)	···	+ (+)	2 (+)	···	+ (+)	···	···	···	···
Koa-mamane	···	+ (+)	···	0	+ (+)	···	···	···	···	···	···
Mamane-naio	···	···	···	···	+ (+)	···	···	···	···	···	···
Mamane	···	···	···	···	+ (+)	···	0	···	···	···	···
Other natives	···	3 (1)	···	0	1 (+)	···	2 (+)	···	5 (1)	+ (+)	···
Intro. trees	···	1 (1)	···	···	3 (1)	2 (2)	2 (1)	0	5 (1)	1 (+)	···
Treeless	0	+ (+)	1 (+)	0	1 (+)	···	+ (+)	0	+ (+)	+ (+)	0

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

TABLE 47
REGRESSION MODELS FOR HABITAT RESPONSE OF THE SPOTTED DOVE AND ZEBRA DOVE[a]

	Spotted Dove					Zebra Dove	
	Hamakua	Puna	Kona	Maui	Molokai	Kona	Molokai
R^2	0.10*	0.50*	0.10*	0.15*	0.26*	0.17*	0.17*
Moisture	−5.0*	−8.1*	···	−7.6*	−10.1*	−5.1*	−4.4*
Elevation	2.9	···	−7.2*	···	5.9*	−11.3*	···
(Elevation)^2	−3.3*	···	···	−6.6*	···	···	···
Tree biomass	···	···	···	···	4.5*	···	5.4*
(Tree biomass)^2	3.5*	6.9*	···	7.2*	···	···	···
Crown cover	−3.0	−2.7	···	···	···	···	···
Canopy height	3.8*	−2.7	···	···	···	···	···
Koa	−2.5	X	···	−4.0*	X	···	X
Ohia	−7.0*	···	···	−4.5*	3.5*	···	−5.9*
Naio	X	X	···	X	X	−2.7	X
Mamane	−5.6*	6.0*	···	···	X	7.4*	X
Intro. trees	2.5	···	7.9*	···	···	7.3*	···
Shrub cover	−2.7	3.2	···	···	···	−5.6*	···
Ground cover	···	···	−4.6*	···	···	···	···
Native shrubs	···	4.3*	···	···	···	···	···
Intro. shrubs	−3.3	···	4.7*	···	···	···	···
Ground ferns	X	−3.4*	···	···	−3.5*	−4.1*	···
Matted ferns	···	···	−3.8*	···	···	−3.7*	···
Tree ferns	X	−3.9*	−5.6*	···	···	···	···
Ieie	X	···	···	···	X	−3.2	X
Passiflora	···	X	···	7.9*	X	···	X
Native herbs	X	−2.6	···	···	···	···	···
Intro. herbs	X	···	···	−3.5*	2.9	3.6*	···
Native grasses	−3.0	−3.7*	···	···	···	···	···
Intro. grasses	···	···	···	···	3.6*	···	···

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

sighted from the Olokui Plateau along the seacliff. On West Maui, Lanai, and Kauai, the distribution of Spotted Doves has changed little from 1949. We found birds as high as 2000 m elevation on Hawaii and 2300 m on Maui.

Spotted Doves are widely distributed at all elevations in low numbers, although they are usually absent from high elevation forests and grasslands (Fig. 217). The regression models (Table 47) show that the species is most common in dry, low elevation woodlands with introduced trees and grasses. Spotted Doves occupy similar habitats in India (Ali and Ripley 1970) and southeast Asia (Smythies 1953), especially agricultural lands. No variable met the entry criteria in the Lanai model. Moisture has a negative term in four of five models, and elevation has a negative term in study areas with a mean elevation above 1000 m. Positive terms for tree biomass, balanced in most models by negative terms for crown cover, ohia, or koa, indicate association with savanna, pasture, woodland, and open forest. Spotted Doves have negative responses to all three fern variables; not only are ferns more common in wet areas and forest interiors, but they also close the ground story where birds primarily feed. Higher densities are associated with passiflora, and birds may act as dispersal agents for banana poka (Warshauer et al. 1983). Introduced grasses tend to have positive terms and are an important element of the diet (Schwartz and Schwartz 1949, 1951a). Available water may limit distribution in some areas (Caum 1933).

ZEBRA DOVE (*Geopelia striata*)

Zebra Doves, also known as Barred Doves, were introduced to the Hawaiian Islands in 1922 (Caum 1933) and are native to the Indo-Malay and Australasian regions. The characteristic habitat is cleared, open, or lightly forested areas below 1000 m elevation (Schwartz and Schwartz 1949, Goodwin 1970, Lewin 1971); our study areas were therefore mainly on the range periphery. Berger (1981) considered this species common to abundant on all the main islands. The diet consists almost entirely of seeds from the ground (Schwartz and Schwartz 1951c).

Zebra Doves occur in six study areas (Tables 33, 34, 48, Figs. 218–221). On Hawaii an esti-

TABLE 48

DENSITY [MEAN (SE)] OF THE ZEBRA DOVE AND MOURNING DOVE BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Zebra Dove						Mourning Dove
	Hamakua	Kipukas	Kona	E. Maui	Molokai	Lanai	Kona
Elevation							
100–300 m	···	···	···	···	0	···	···
300–500 m	0	···	3 (1)	0	3 (3)	···	0
500–700 m	0	···	6 (1)	0	9 (4)	+ (+)	+ (+)
700–900 m	0	···	4 (1)	3 (2)	8 (4)	+ (+)	+ (+)
900–1100 m	0	···	1 (+)	8 (1)	1 (+)	1 (+)	+ (+)
1100–1300 m	+ (+)	3 (2)	2 (+)	12 (3)	+ (+)	···	+ (+)
1300–1500 m	2 (1)	1 (+)	3 (+)	0		···	+ (+)
1500–1700 m	0	+ (+)	2 (+)	0	···	···	+ (+)
1700–1900 m	+ (+)	0	+ (+)	0	···	···	+ (+)
1900–2100 m	+ (+)	+ (+)	+ (+)	0	···	···	+ (+)
2100–2300 m	0	0	1 (+)	+ (+)	···	···	0
2300–2500 m	···	···	+ (+)	0	···	···	0
2500–2700 m	···	···	···	0	···	···	···
2700–2900 m	···	···	···	0	···	···	···
2900–3100 m	···	···	···	···	···	···	···
Habitat							
Ohia	1 (1)	+ (+)	3 (+)	0	1 (1)	···	+ (+)
Koa-ohia	1 (1)	10 (3)	2 (+)	0	···	···	+ (+)
Koa-mamane	0	+ (+)	2 (+)	···	···	···	+ (+)
Mamane-naio	···	···	+ (+)	···	···	···	+
Mamane	···	···	2 (+)	0	···	···	0
Other natives	+ (+)	+ (+)	3 (1)	7 (1)	2 (2)	1 (+)	+ (+)
Intro. trees	0	···	3 (1)	0	5 (2)	1 (+)	+ (+)
Treeless	+ (+)	+ (+)	1 (1)	0	0	+ (+)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

mated 1200 ± 150 (95% CI) birds occur in the Kona, Hamakua, and Kipukas study areas. The range on Hawaii has expanded considerably since the surveys of Schwartz and Schwartz (1949). Although the Schwartzes failed to find them on windward Hawaii, they are now well established in urban and agricultural areas (J. M. Scott, pers. observ.). We found birds on East Maui, Molokai, and Lanai, but only on Molokai was their occurrence more than occasional.

Zebra Doves occur in very low densities in a variety of vegetation types and over a wide range of elevations, from sea level to 2300 m on Hawaii and Maui. They were absent only from wet ohia forests. They occupy fewer habitat types above 1500 m than below (Fig. 222), probably because the range limit is near 1000 m.

The regression models (Table 47) show that within our study areas Zebra Doves are most common in dry areas at lower elevations with mamane or introduced trees, but have low densities in areas with high amounts of shrub cover, ohia, ground ferns, or matted ferns. In Asia they seldom occur in wet forests or dense brush except at forest margins and clearings, but are particularly common on agricultural lands (Schwartz and Schwartz 1949, Goodwin 1970).

In the Molokai regression model, tree biomass is a balance term for ohia and serves as a "proxy" for positive responses to introduced trees; this is seen in the correlations between bird density and tree biomass ($r = 0.04$), ohia (-0.30), and introduced trees (0.29). The latter two values are the second and third highest bird-habitat correlations for this species. The mechanics of model construction entered tree biomass first, then at a lower level chose ohia over introduced trees. A more representative model might use introduced trees instead of tree biomass, but would not differ statistically from the one given.

MOURNING DOVE (*Zenaida macroura*)

Mourning Doves are native to most of North America (A.O.U. 1983). They were first introduced to Hawaii in 1929, but failed to establish a population. Birds from California game farms were released during 1962-1965 on Puu Waawaa Ranch in Kona (Lewin 1971). A hunting season was established in October 1969 pursuant to incidental takes by gamebird hunters in 1968, and

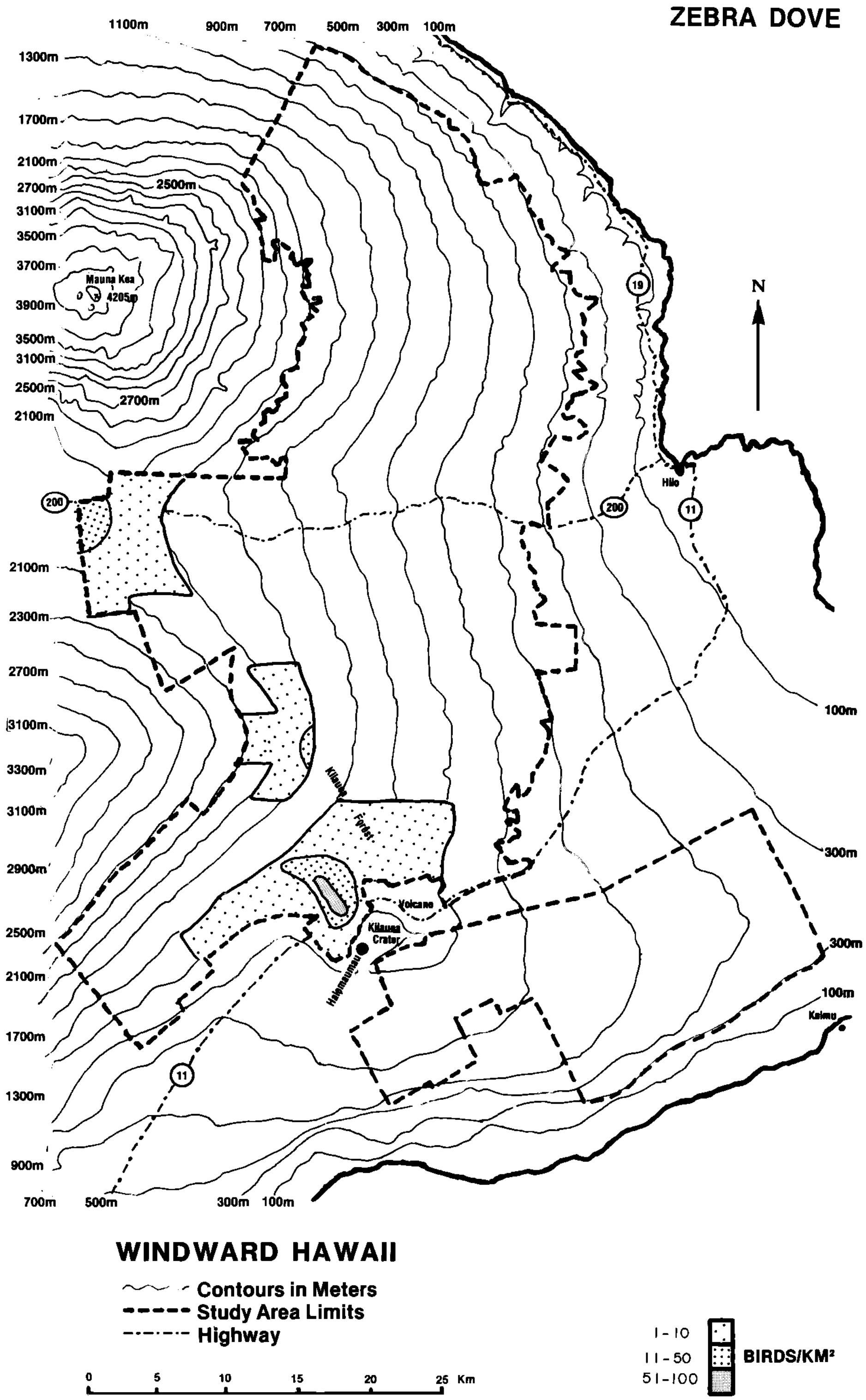


FIGURE 218. Distribution and abundance of the Zebra Dove in the windward Hawaii study areas.

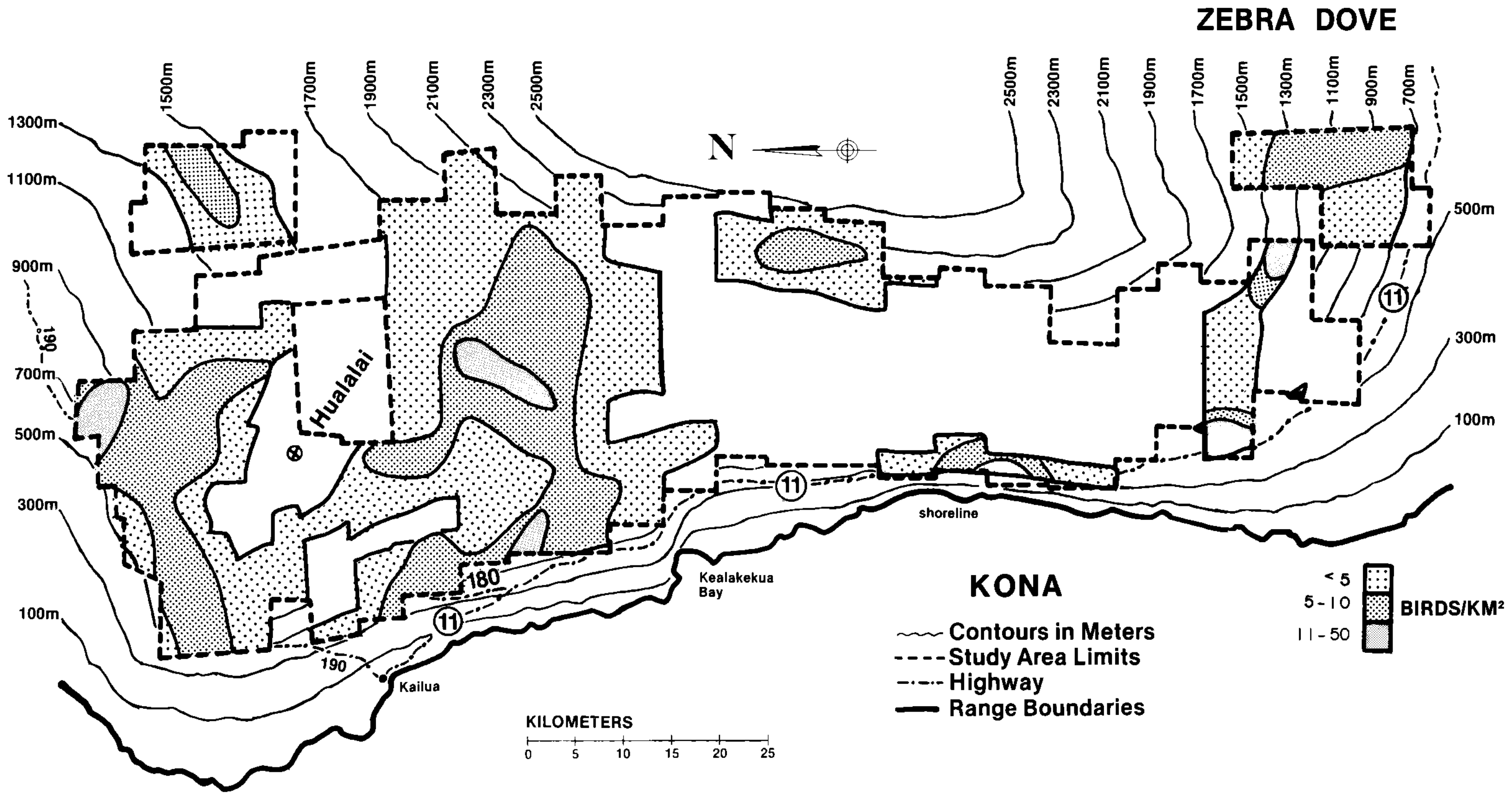


FIGURE 219. Distribution and abundance of the Zebra Dove in the Kona study area.

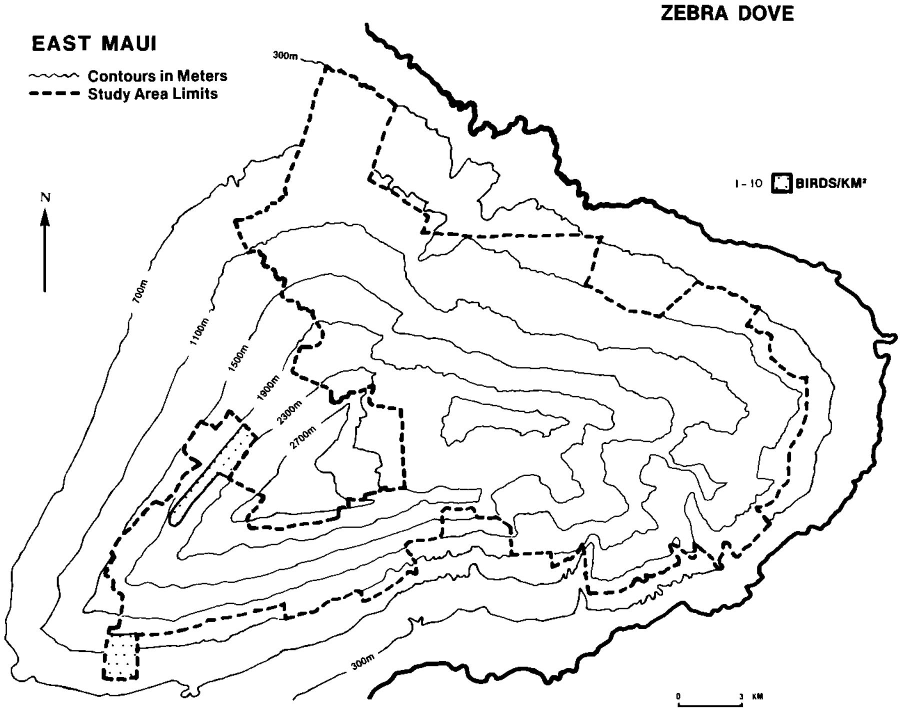


FIGURE 220. Distribution and abundance of the Zebra Dove in the East Maui study area.

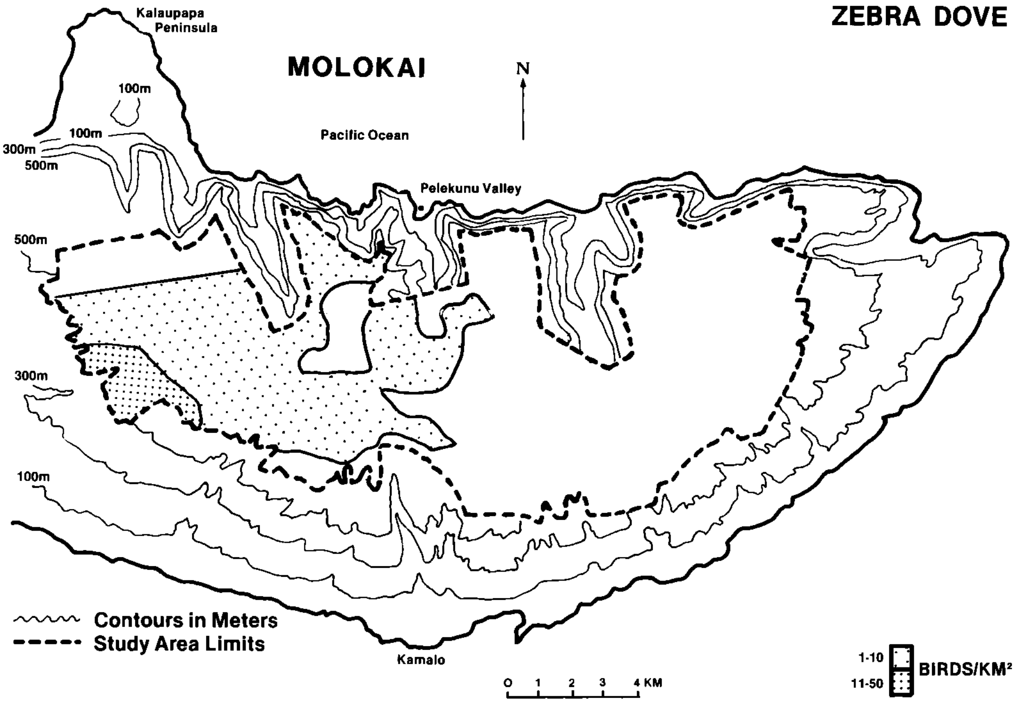


FIGURE 221. Distribution and abundance of the Zebra Dove in the Molokai study area.

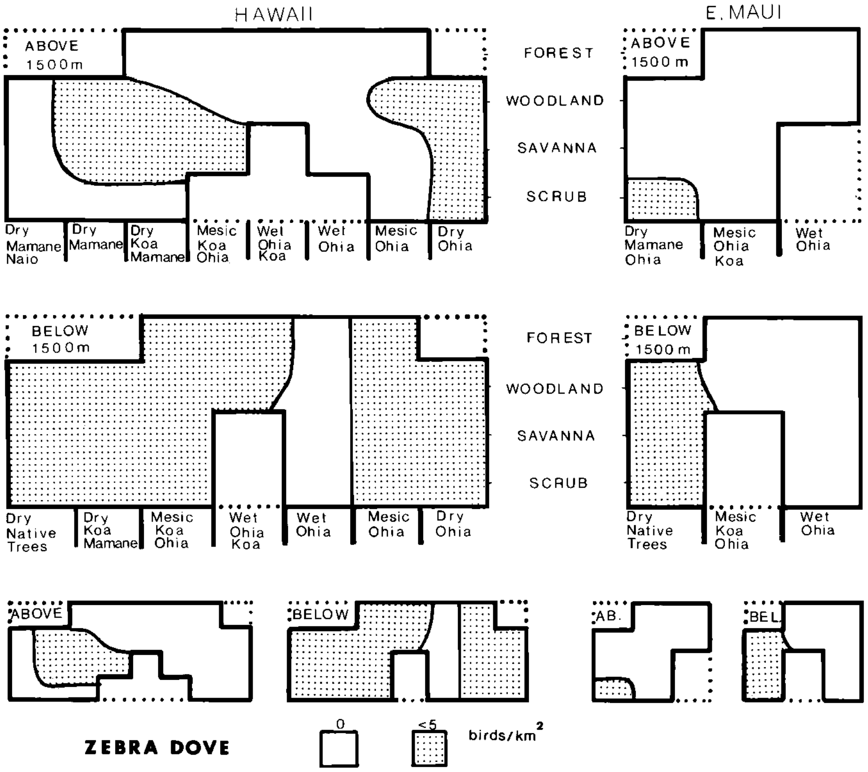


FIGURE 222. Habitat response graphs of the Zebra Dove. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

in 1974 the population was estimated at 500–1500 birds (R. L. Walker, pers. comm.).

We found Mourning Doves only in the Kona study area, restricted to the north slopes of Hualalai and the high-elevation open woodland on Mauna Loa (Table 48, Fig. 223). We estimated the population to be 8 ± 6 (95% CI) birds (Table 33). Although we did not sample much of the lowland areas on Hawaii, we failed to find them outside Puu Waawaa Ranch, as have others (J. Giffin, pers. comm.). The core population is centered at low-elevation feedlots near Puu Waawaa (R. L. Walker, pers. comm.), an area we did not sample. The habitat response graphs indicate occurrence in dry open habitats below 1500 m (Fig. 224). The patchy pattern reflects the recent introduction.

COMMON BARN-OWL (*Tyto alba*)

This species was introduced on Hawaii in 1958 from California in hopes of controlling rats in sugar cane fields (Tomich 1962). We had only 10 incidental observations and station records for this species. Five of these were in Kona. The others were on windward Hawaii, Kohala, Molokai, and East Maui. Although its nocturnal habits may account in part for these low numbers, we suspect that this species has not yet established sizeable populations in the native forests and may be limited by suitable nesting and roosting sites in many areas. It is common in sugar cane fields and other lowland agricultural areas on Hawaii, Maui (J. M. Scott, C. B. Kepler, pers. observ.), Oahu (M. Morin, pers. comm.), and Kauai (Au and Swedberg 1966).

EURASIAN SKYLARK (*Alauda arvensis*)

Eurasian Skylarks were introduced from England in 1865 (Caum 1933). Munro (1944) considered them well established on all the islands as did Berger (1972). However, in recent years they have declined in abundance on Oahu and are apparently no longer found on Kauai (Berger 1981).

We found Eurasian Skylarks only on Hawaii and Maui (Tables 33, 34, 49, Figs. 225–229), where an estimated 10,000 ± 1500 (95% CI) and 400 ± 100 birds occur in the study areas on those respective islands. Birds occur at low densities throughout the open upper-elevation forests of

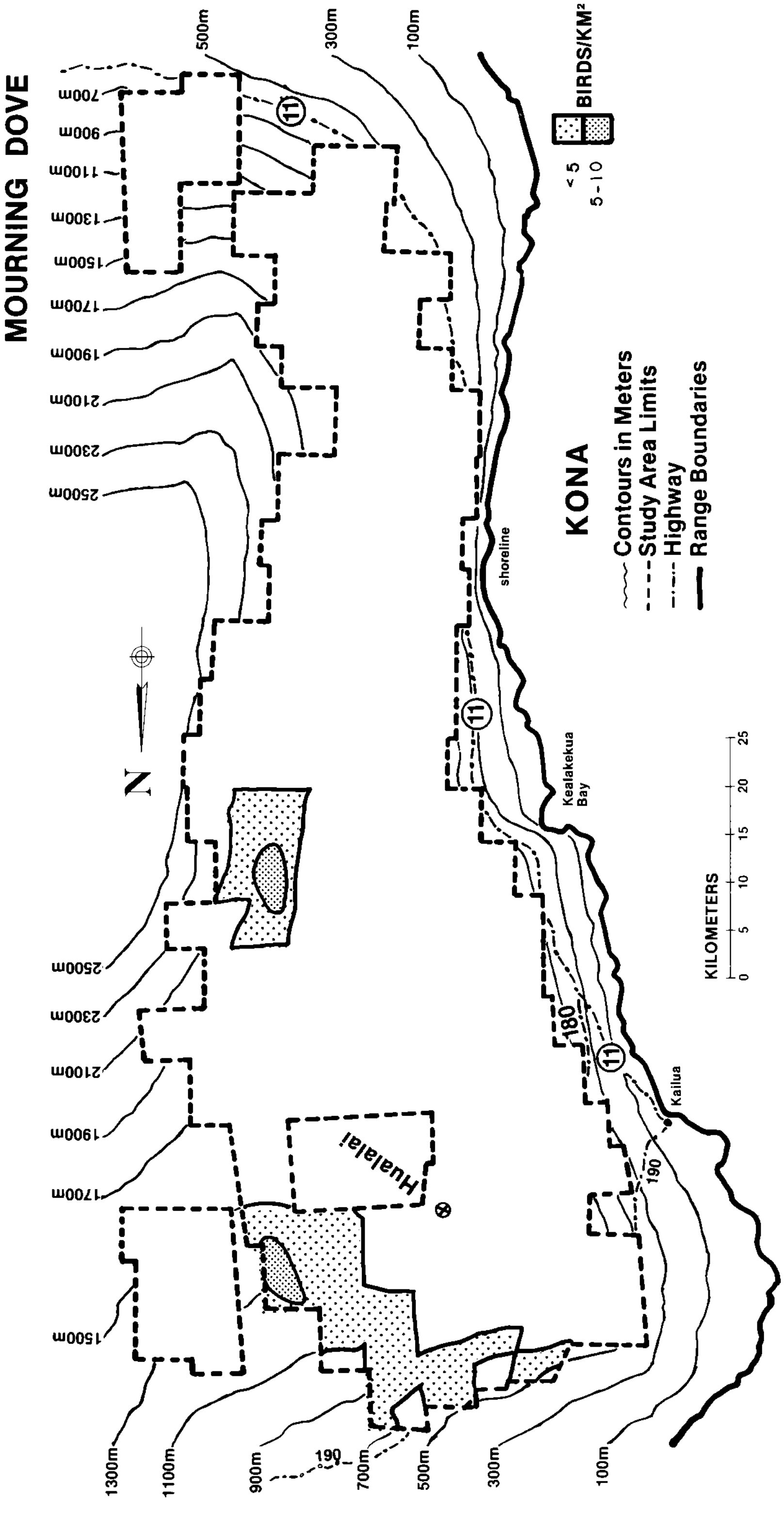


FIGURE 223. Distribution and abundance of the Mourning Dove in the Kona study area.

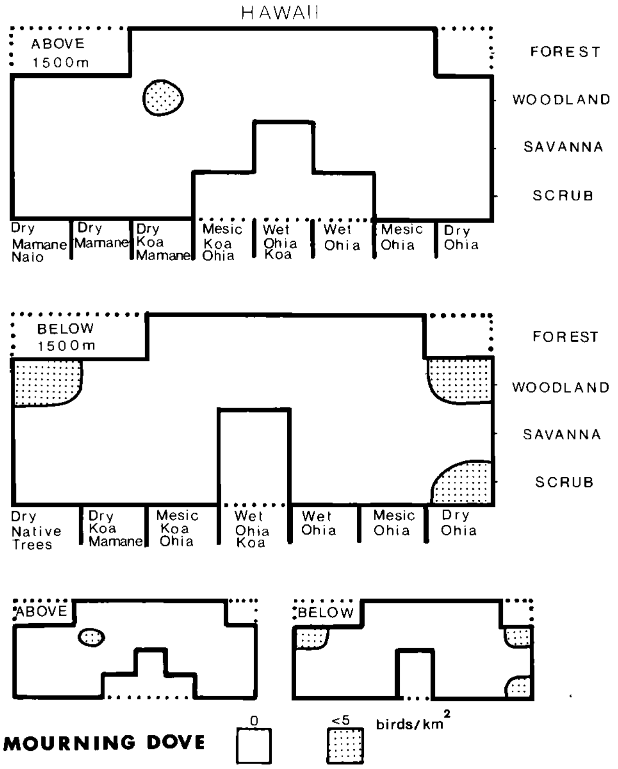


FIGURE 224. Habitat response graphs of the Mourning Dove. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

windward Hawaii and are scattered throughout Kona and Mauna Kea at higher densities. The one bird recorded in Kohala was singing from open pastures outside the study area. Skylarks are widely distributed in the crater district and drier slopes of Haleakala. They occur from sea level to 3000 m on Hawaii and to 2700 m on Maui.

Eurasian Skylarks are most common in dry scrub, savanna, and woodland, with lower densities in mesic habitats (Table 50, Fig. 230). Wet habitats are unoccupied on Maui, but small numbers occur along woodland edges on Hawaii. In general, skylarks frequent degraded, fragmented, and deforested habitat. Many observations were aural detections of birds at considerable distances from the actual station. The positive terms in the regression models for canopy height represent birds heard by observers situated in tall koa and eucalyptus groves on the edges of pastures. The negative response to ohia reflects absence in forest interiors. High densities in mamane woodlands are reflected in the positive terms in two models. Densities tend to be lower in areas with introduced trees such as guava, or with closed shrub and ground cover. Scattered ground cover is required for nest concealment (Berger 1981).

Japanese Bush-Warbler (*Cettia diphone*)

Japanese Bush-Warblers, also called Uguisu, were introduced to Oahu in 1929 (Caum 1933). Native to Japan and other parts of Asia, they are largely insectivorous but also take fruit and nectar (Berger 1981). Japanese Bush-Warblers were first noted on Molokai and Lanai in 1979 (Pyle 1979, P. Conant 1980) and on Maui in 1980 (Carothers and Hansen 1982). Since our study they have dramatically increased on Molokai (C. B. Kepler, pers. observ.).

We found Japanese Bush-Warblers only on East Maui and Molokai. They were uncommon on Molokai with a fragmented distributional pattern in those areas sampled in 1979. They were well established on the Olokui Plateau during the 1980 survey (Tables 34, 51, Fig. 231). We estimated 200 ± 80 (95% CI) birds in the Molokai study area. Our record for East Maui is the first for the island.

The regression model for Molokai (Table 50) shows that birds are more common at higher elevations in areas with a high cover of native

TABLE 49

Density [mean (se)] of the Eurasian Skylark by Elevation, Habitat, and Study Area[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui
Elevation								
100–300 m	···	···	···	···	···	···	···	···
300–500 m	···	0	0	···	0	···	0	0
500–700 m	0	0	0	···	6 (2)	···	0	0
700–900 m	0	0	0	···	5 (1)	···	0	3 (3)
900–1100 m	0	0	+ (+)	···	7 (1)	···	0	11 (3)
1100–1300 m	0	6 (4)	0	7 (2)	4 (1)	···	+ (+)	25 (6)
1300–1500 m	0	5 (1)	···	7 (1)	6 (1)	···	0	8 (3)
1500–1700 m	0	2 (1)	···	3 (1)	12 (1)	···	0	5 (3)
1700–1900 m	0	8 (2)	···	1 (+)	8 (1)	···	···	2 (1)
1900–2100 m	6 (6)	4 (1)	···	2 (1)	8 (1)	28 (7)	···	2 (1)
2100–2300 m	0	17 (3)	···	+ (+)	7 (1)	40 (9)	···	5 (2)
2300–2500 m	···	···	···	···	4 (1)	36 (6)	···	3 (1)
2500–2700 m	···	···	···	···	···	27 (4)	···	6 (3)
2700–2900 m	···	···	···	···	···	29 (4)	···	0
2900–3100 m	···	···	···	···	···	22 (13)	···	···
Habitat								
Ohia	6 (6)	2 (1)	+ (+)	2 (+)	4 (+)	···	+ (+)	0
Koa-ohia	0	4 (1)	···	3 (1)	4 (1)	···	···	5 (3)
Koa-mamane	···	10 (2)	···	3 (1)	14 (1)	···	···	···
Mamane-naio	···	···	···	···	3 (2)	11 (2)	···	···
Mamane	···	···	···	···	20 (2)	53 (4)	···	22 (12)
Other natives	···	7 (2)	···	13 (2)	16 (6)	···	···	7 (1)
Intro. trees	···	2 (1)	···	···	6 (2)	···	0	7 (4)
Treeless	0	+ (+)	+ (+)	+ (+)	8 (2)	···	···	2 (1)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

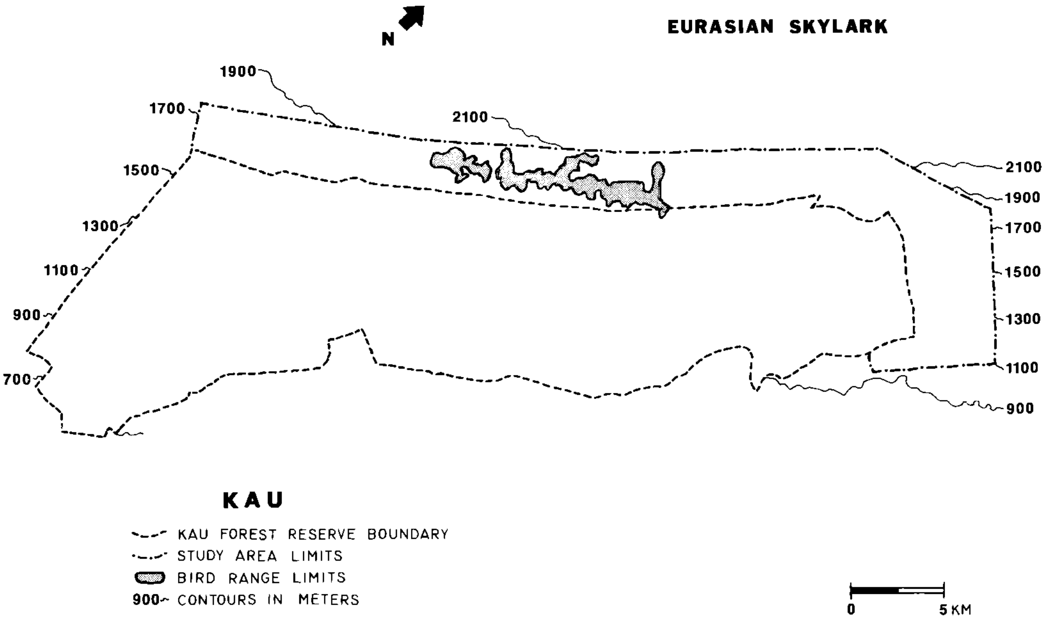


FIGURE 225. Distribution and abundance of the Eurasian Skylark in the Kau study area. (Density within range is less than 10 birds/km^2.)

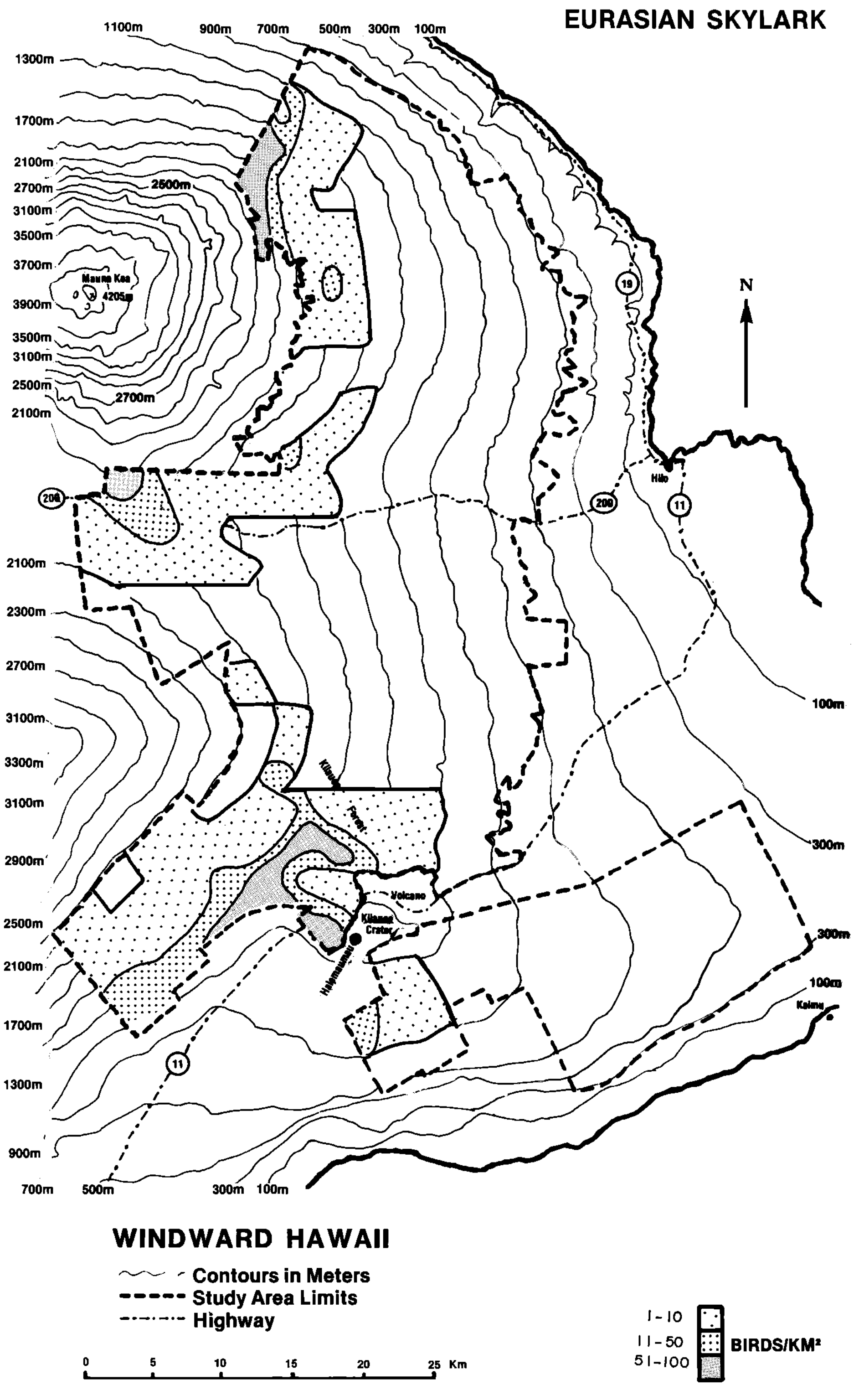


FIGURE 226. Distribution and abundance of the Eurasian Skylark in the windward Hawaii study areas.

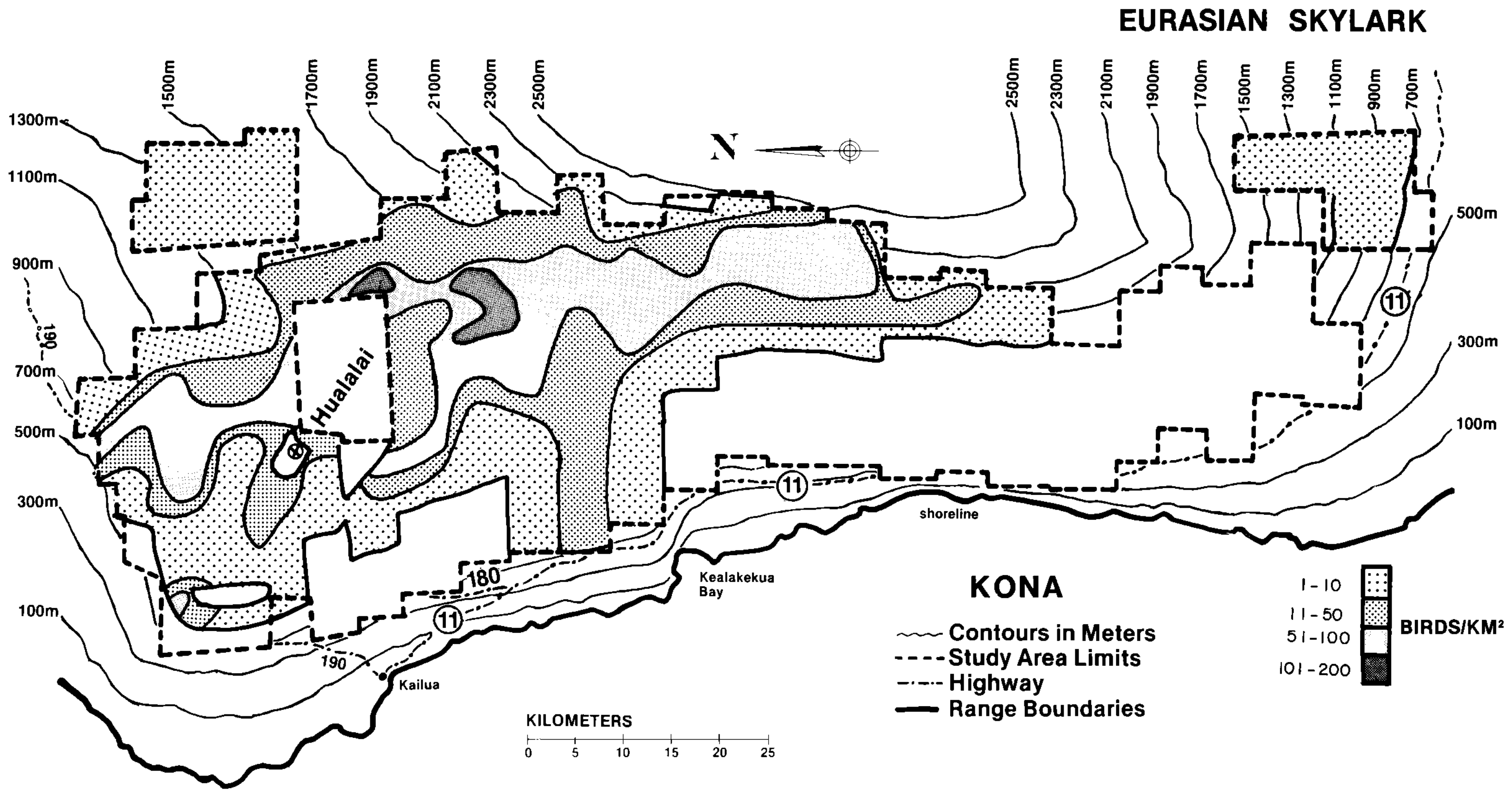


FIGURE 227. Distribution and abundance of the Eurasian Skylark in the Kona study area.

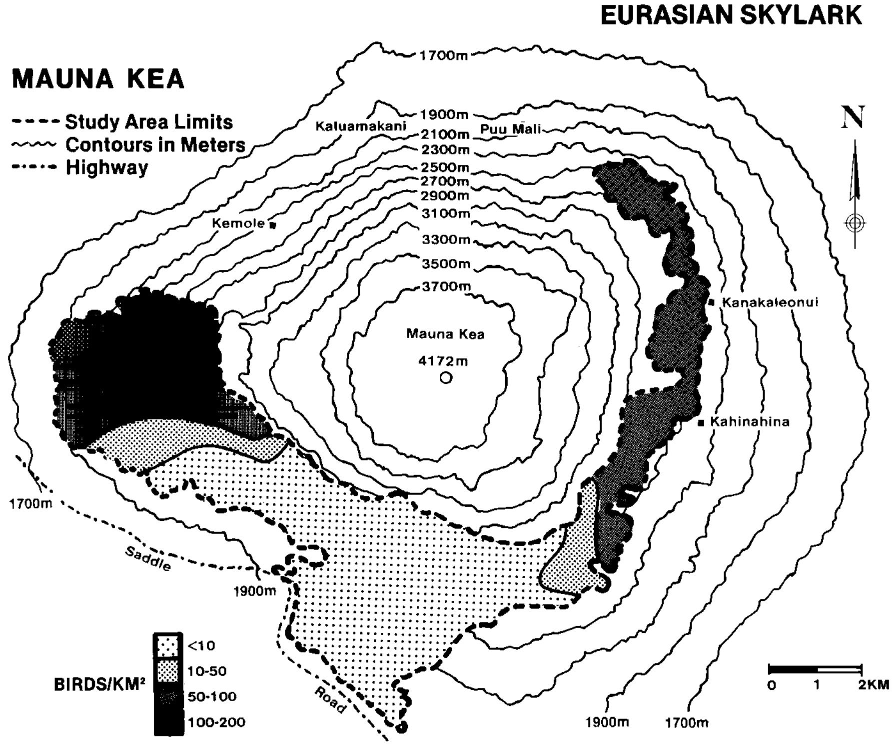


FIGURE 228. Distribution and abundance of the Eurasian Skylark in the Mauna Kea study area.

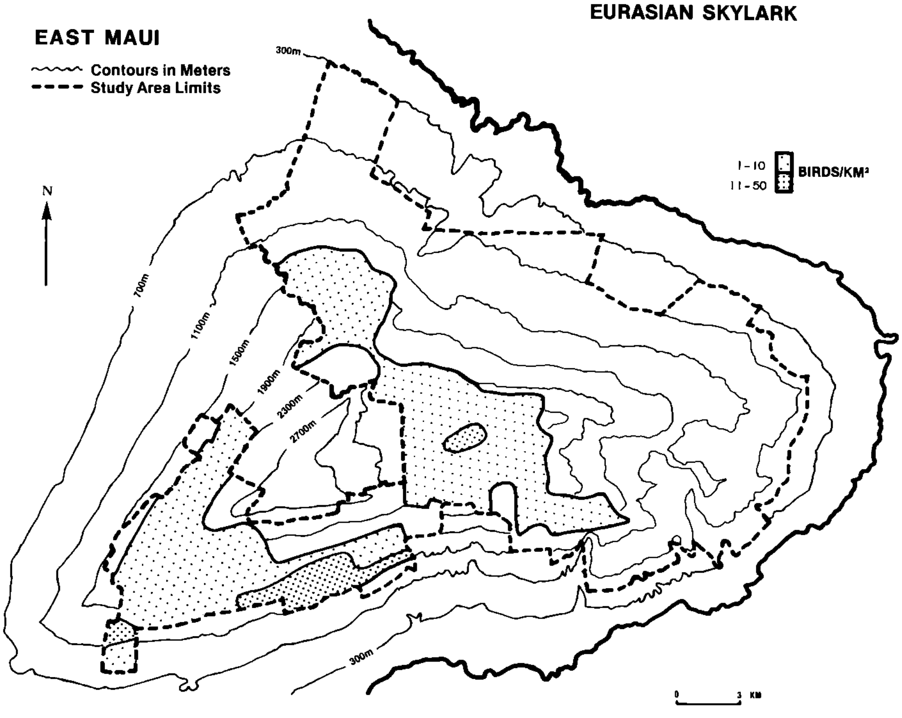


FIGURE 229. Distribution and abundance of the Eurasian Skylark in the East Maui study area.

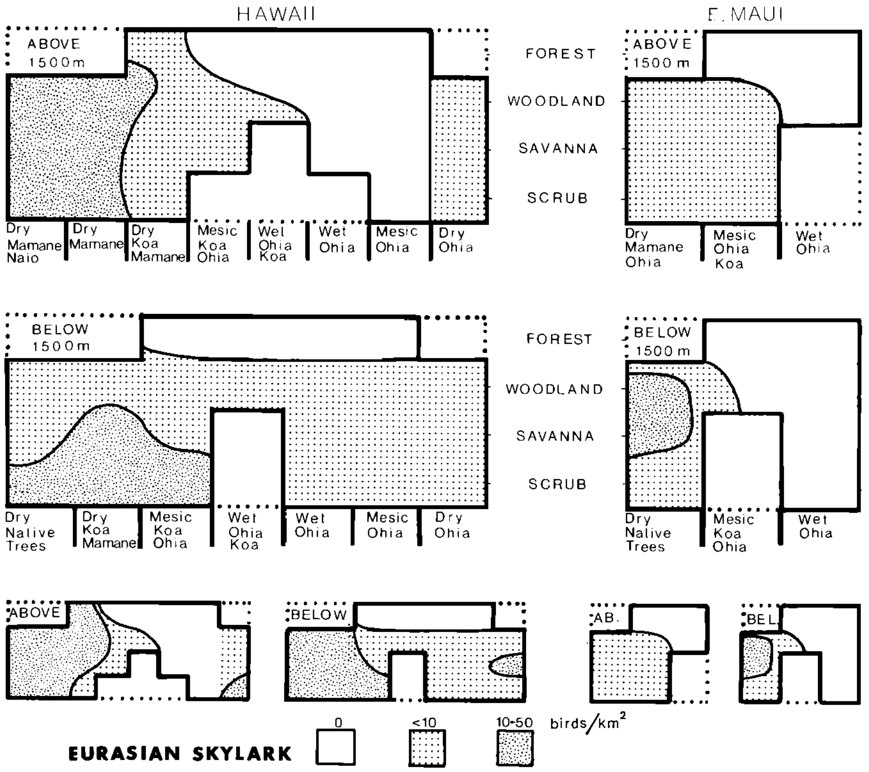


FIGURE 230. Habitat response graphs of the Eurasian Skylark. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

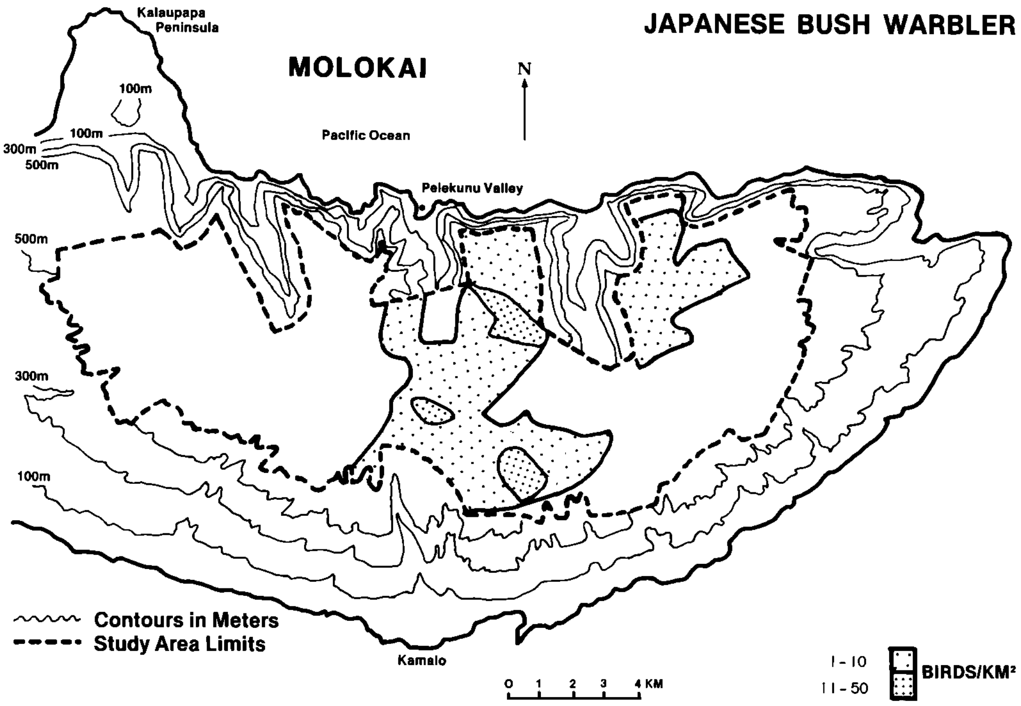


FIGURE 231. Distribution and abundance of the Japanese Bush-Warbler in the Molokai study area.

TABLE 50

REGRESSION MODELS FOR HABITAT RESPONSE OF THE EURASIAN SKYLARK, JAPANESE BUSH-WARBLER, AND NORTHERN MOCKINGBIRD[a]

	Eurasian Skylark					Japanese Bush-Warbler	Northern Mockingbird	
	Hamakua	Kipukas	Kona	Mauna Kea	Maui	Molokai	Mauna Kea	Maui
R^2	0.43*	0.29*	0.39*	0.47*	0.20*	0.21*	0.08*	0.48*
Moisture	−6.0*	−4.6*	···	X	−9.6*	···	X	−7.6*
Elevation	···	−4.3*	4.8*	···	···	−2.3	3.8*	3.9*
(Elevation)^2	···	3.5*	−3.1	−5.1*	···	2.7	···	···
Tree biomass	2.4	···	5.0*	···	···	···	···	−3.0
(Tree biomass)^2	···	···	−3.0	···	···	···	···	−4.7*
Crown cover	···	···	−7.2*	···	···	···	···	4.0*
Canopy height	4.9*	4.4*	···	2.2	4.5*	···	2.4	···
Koa	···	···	−3.6*	X	···	X	X	−4.8*
Ohia	−9.8*	−5.4*	−6.0*	X	···	···	X	−6.3*
Naio	X	···	···	−11.8*	X	X	3.1	X
Mamane	15.6*	···	15.6*	···	···	X	···	11.4*
Intro. trees	−5.8*	X	···	X	−3.8*	···	X	−6.6*
Shrub cover	−7.3*	···	−3.8*	−4.6*	−3.9*	···	···	···
Ground cover	−3.1	···	···	−4.6*	5.6*	···	···	···
Native shrubs	···	···	···	X	−3.9*	···	X	···
Intro. shrubs	···	···	···	X	···	···	X	4.4*
Ground ferns	···	···	···	X	−3.6*	···	X	−3.2
Matted ferns	···	···	···	X	···	···	X	···
Tree ferns	X	X	···	X	···	···	X	···
Ieie	X	X	3.9*	X	···	X	X	···
Passiflora	−3.0	X	−2.6	X	···	X	X	4.3*
Native herbs	X	···	···	X	···	4.1*	X	−3.9*
Intro. herbs	X	···	···	···	···	···	···	···
Native grasses	3.3	−3.2	−5.2*	4.2*	···	7.5*	···	···
Intro. grasses	3.0	···	···	···	···	···	···	−5.8*
Ohia flowers	X	X	X	X	X	···	X	···
Olapa fruit	X	X	X	X	X	···	X	···
Mamane flowers	X	X	X	X	X	X	···	−3.5*
Mamane fruit	X	X	X	X	X	X	···	X
Naio fruit	X	X	X	X	X	X	···	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

herbs and grasses. The elevational response in the model is partly a sampling artifact because birds were usually recorded along cliff faces, and these sites were sampled at the top due to logistics. Cliffs may be a component of preferred habitat and appeared to be the first sites colonized on Maui and Molokai. Berger (1981) characterized this species as occurring primarily in habitats with luxuriant undergrowth, reflected in our model by the terms for native herbs and grasses. In Japan the species has a similar preference for areas with a brushy understory (Kiyosu 1965).

WHITE-RUMPED SHAMA
(*Copsychus malabaricus*)

Native to southeast Asia, White-rumped Shamas were first released in the Hawaiian Islands on Oahu in 1940 (Harpham 1953). In 1960 on Kauai, they were a "moderately common resident locally, usually in inhabited lowland areas" (Richardson and Bowles 1964). They are now common on leeward and windward Oahu (Berger 1981), but we know of no records for islands other than Kauai and Oahu. This species is largely insectivorous (Berger 1981).

We found White-rumped Shamas only on Kauai (Fig. 232) where they occur in low densities on the edge of the Alakai Swamp (Tables 34, 51). There were too few observations to interpret habitat response. We estimated a population of 45 ± 35 (95% CI) birds in the study area. Sincock et al. (1984) had two incidental sightings during 1968–1973 in this area, and estimated a total of 19,000 ± 23,000 birds in the native forests on Kauai.

TABLE 51
DENSITY [MEAN (SE)] OF THE JAPANESE BUSH-WARBLER, WHITE-RUMPED SHAMA, AND NORTHERN MOCKINGBIRD BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Japanese Bush-Warbler		White-rumped Shama	Northern Mockingbird				
	East Maui	Molokai	Kauai	Kona	Mauna Kea	East Maui	West Maui	Molokai
Elevation								
100–300 m	···	0	···	···	···	···	···	0
300–500 m	0	0	···	0	···	0	···	0
500–700 m	0	56 (32)	···	0	···	0	4 (4)	9 (6)
700–900 m	0	2 (2)	···	0	···	25 (13)	1 (1)	4 (1)
900–1100 m	0	6 (3)	···	0	···	29 (3)	+ (+)	1 (+)
1100–1300 m	1 (1)	17 (4)	2 (1)	0	···	31 (3)	+ (+)	0
1300–1500 m	+ (+)	18 (8)	+ (+)	3 (1)	···	14 (4)	0	0
1500–1700 m	+ (+)	···	···	3 (1)	···	14 (4)	0	···
1700–1900 m	+ (+)	···	···	0	···	11 (2)	0	···
1900–2100 m	0	···	···	0	2 (2)	11 (2)	···	···
2100–2300 m	0	···	···	0	5 (3)	8 (2)	···	···
2300–2500 m	0	···	···	0	3 (1)	13 (4)	···	···
2500–2700 m	0	···	···	···	5 (2)	21 (7)	···	···
2700–2900 m	0	···	···	···	8 (2)	+ (+)	···	···
2900–3100 m	···	···	···	···	3 (3)	···	···	···
Habitat								
Ohia	+ (+)	10 (2)	1 (1)	3 (1)	···	0	+ (+)	+ (+)
Koa-ohia	0	···	···	0	···	1 (1)	···	···
Koa-mamane	···	···	···	0	···	···	···	···
Mamane-naio	···	···	···	0	2 (1)	···	···	···
Mamane	0	···	···	0	5 (1)	10 (5)	···	···
Other natives	0	+ (+)	···	0	···	26 (6)	···	5 (5)
Intro. trees	0	+ (+)	···	0	···	5 (5)	···	3 (2)
Treeless	+ (+)	0	+ (+)	0	···	4 (1)	···	+ (+)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

MELODIOUS LAUGHING-THRUSH
(*Garrulax canorus*)

Melodious Laughing-thrushes, also known as Hwa-mei or Chinese Thrushes, were liberated during the great 1900 fire in Honolulu (Caum 1933). These babblers (Timaliinae) are native to southeast Asia. Munro (1944) considered them well established even in the deepest forests but did not list the islands occupied. Berger (1981) summarized that they were apparently well established on Hawaii, Maui, Oahu, and Kauai.

Melodious Laughing-thrushes occur in nine study areas (Tables 33, 34, 52, Figs. 233–239). On Hawaii an estimated 10,000 ± 500 (95% CI) birds occupy our study areas. On Mauna Kea, Melodious Laughing-thrushes are mainly restricted to areas with naio. On windward Hawaii the species has a dynamic range. Birds were rarely reported in Hawaii Volcanoes National Park during the 1940–1975 interval (Baldwin 1953, Conant 1975, Banko and Banko 1980). The range limit running northwest of Kilauea Crater across the Hamakua study area (Fig. 233) represents the 1977 position. High densities in the southwest part of the Puna study area probably reflect changes that occurred as late as 1979. In the mesic and wet forests around Kilauea Crater and in Kipuka Puaulu, Melodious Laughing-thrushes increased from occasional vagrants to fairly common residents in the 1980–1984 period (J. M. Scott, S. Mountainspring, pers. observ.). Birds have apparently not yet colonized the Kau study area, although they occur below the area (J. D. Jacobi, pers. comm.). The pattern in Kona suggests that birds were beginning to invade in 1978, possibly from the Mauna Kea population. Although birds were fairly common in the Kohala study area in 1979 (53% of the stations occupied), they were very scarce (1 bird on 47 counts) in 1970–1972 (van Riper 1982).

On East Maui, Melodious Laughing-thrushes are fairly common in low- to mid-elevation mesic and wet forests, and in dry areas along gulches and near water. Although they are absent from high-elevation wet forests on Maui, the pattern in Hamakua suggests that they will eventually

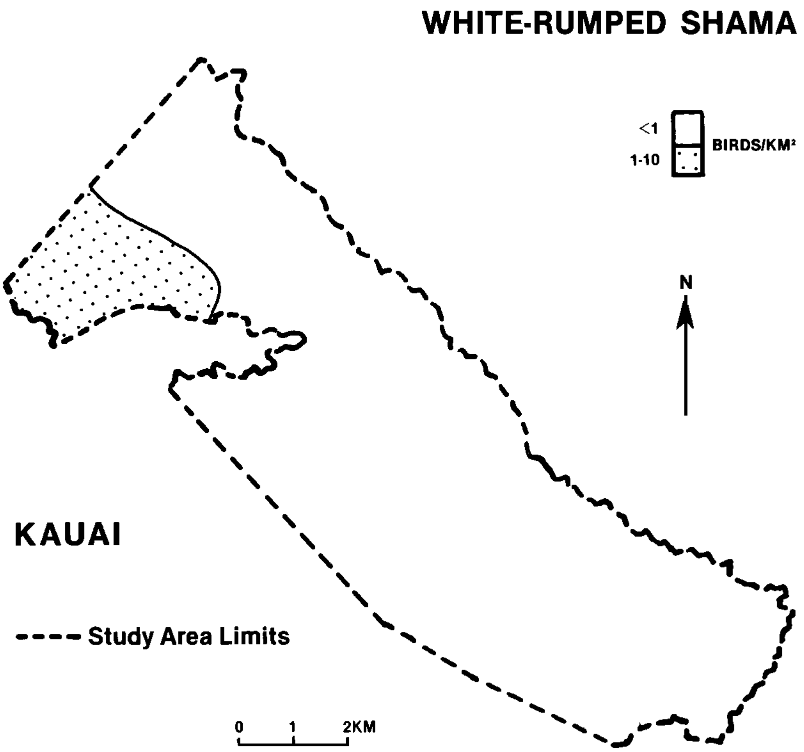


FIGURE 232. Distribution and abundance of the White-rumped Shama in the Kauai study area.

TABLE 52

DENSITY [MEAN (SE)] OF THE MELODIOUS LAUGHING-THRUSH BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Kauai
Elevation									
100–300 m	···	···	···	···	···	···	···	···	···
300–500 m	9 (3)	27 (1)	···	0	···	0	9 (3)	···	···
500–700 m	9 (1)	14 (1)	···	0	···	32 (8)	18 (2)	7 (3)	···
700–900 m	15 (1)	7 (1)	···	0	···	17 (5)	8 (1)	4 (1)	···
900–1100 m	6 (1)	6 (1)	···	0	···	14 (3)	9 (1)	1 (1)	···
1100–1300 m	7 (1)	1 (1)	0	+ (+)	···	18 (3)	10 (2)	2 (1)	22 (2)
1300–1500 m	2 (+)	···	0	2 (1)	···	12 (2)	9 (1)	1 (1)	7 (1)
1500–1700 m	1 (+)	···	0	+ (+)	···	4 (2)	4 (1)	+ (+)	···
1700–1900 m	1 (+)	···	+ (+)	+ (+)	···	···	2 (+)	+ (+)	···
1900–2100 m	+ (+)	···	+ (+)	0	1 (1)	···	2 (1)	···	···
2100–2300 m	0	···	0	0	1 (1)	···	1 (1)	···	···
2300–2500 m	···	···	···	0	5 (1)	···	+ (+)	···	···
2500–2700 m	···	···	···	···	5 (2)	···	+ (+)	···	···
2700–2900 m	···	···	···	···	3 (2)	···	0	···	···
2900–3100 m	···	···	···	···	+ (+)	···	···	···	···
Habitat									
Ohia	5 (+)	13 (1)	+ (+)	+ (+)	···	15 (1)	6 (1)	3 (1)	15 (1)
Koa-ohia	8 (1)	···	+ (+)	0	···	···	13 (2)	···	···
Koa-mamane	+ (+)	···	+ (+)	+ (+)	···	···	···	···	···
Mamane-naio	···	···	···	0	4 (1)	···	···	···	···
Mamane	···	···	···	0	+ (+)	···	12 (12)	···	···
Other natives	1 (1)	···	+ (+)	0	···	···	2 (1)	···	···
Intro. trees	13 (1)	···	···	0	···	24 (7)	10 (1)	14 (14)	···
Treeless	4 (1)	+ (+)	+ (+)	0	···	···	3 (1)	+ (+)	+ (+)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

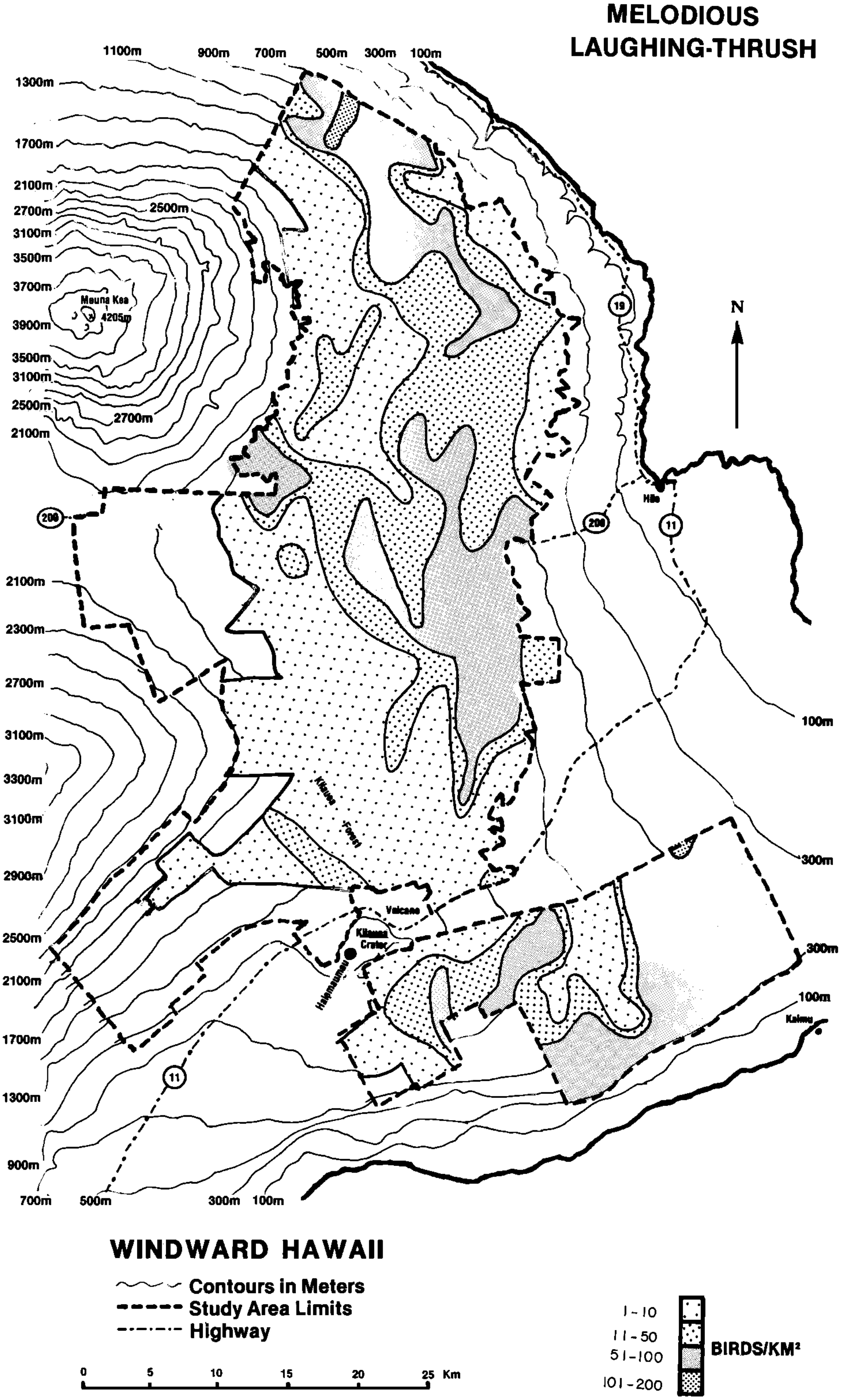


FIGURE 233. Distribution and abundance of the Melodious Laughing-thrush in the windward Hawaii study areas.

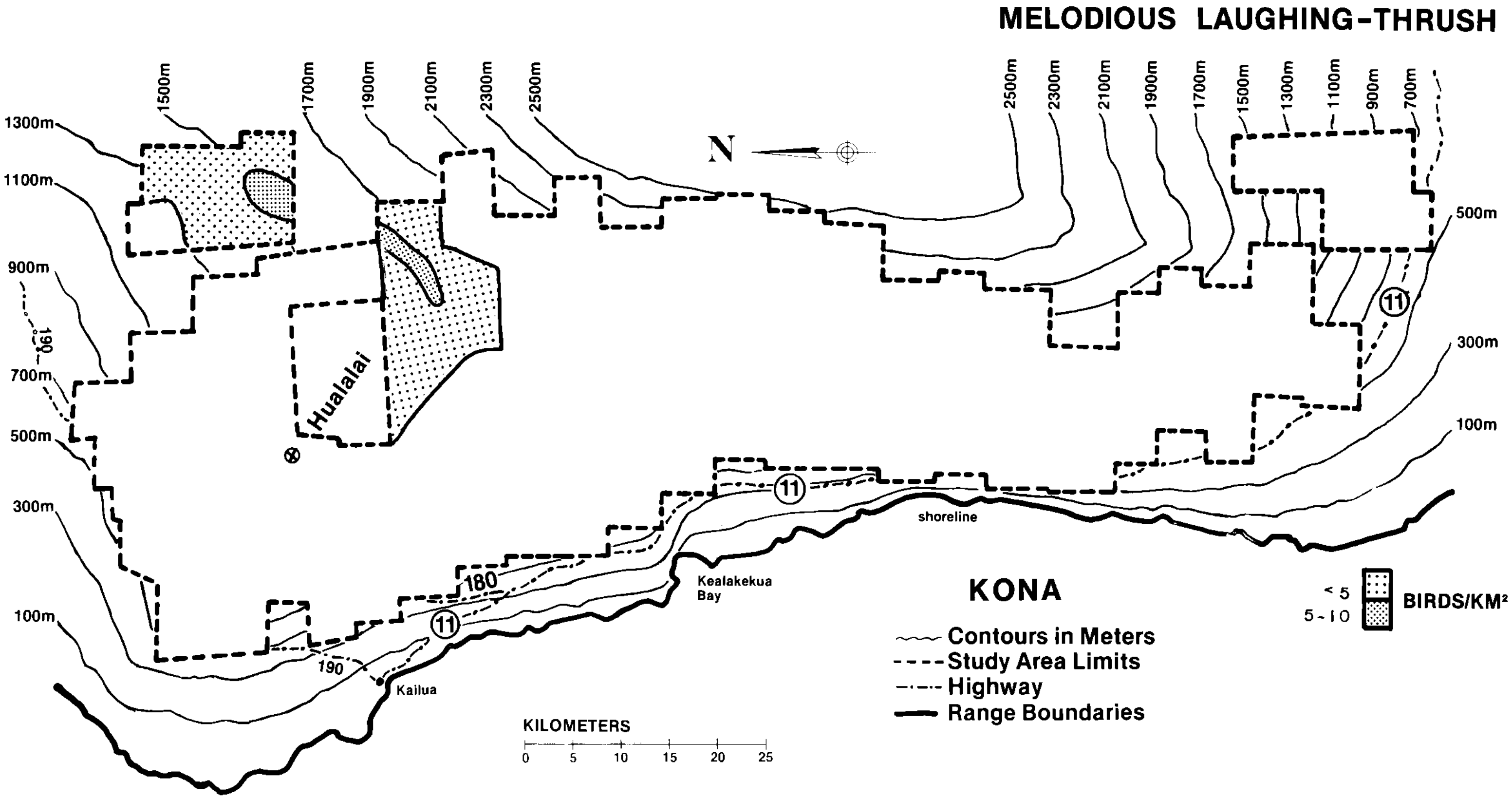


FIGURE 234. Distribution and abundance of the Melodious Laughing-thrush in the Kona study area.

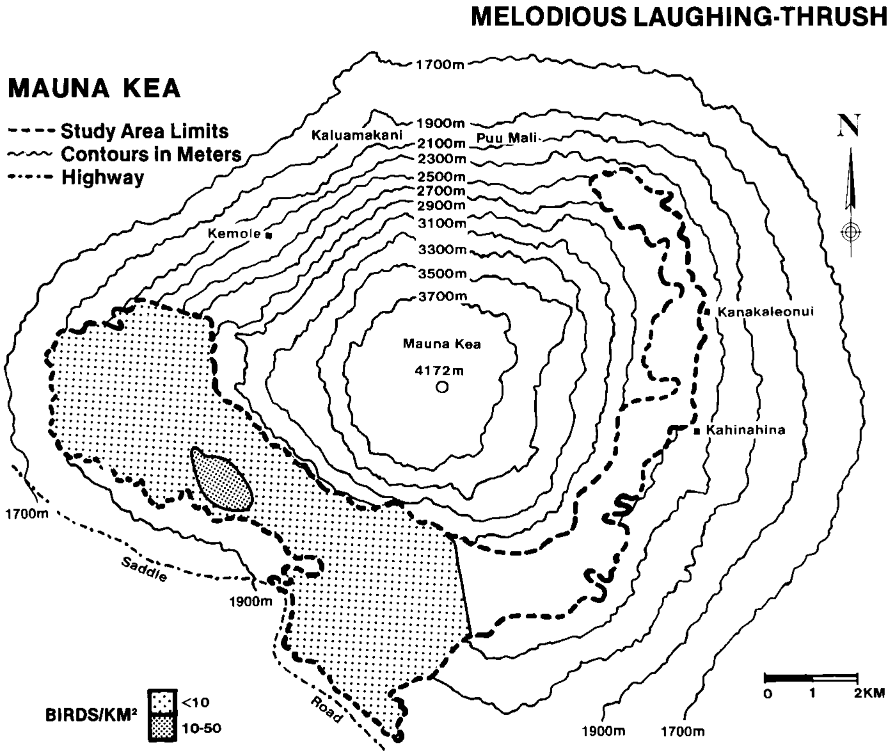


FIGURE 235. Distribution and abundance of the Melodious Laughing-thrush in the Mauna Kea study area.

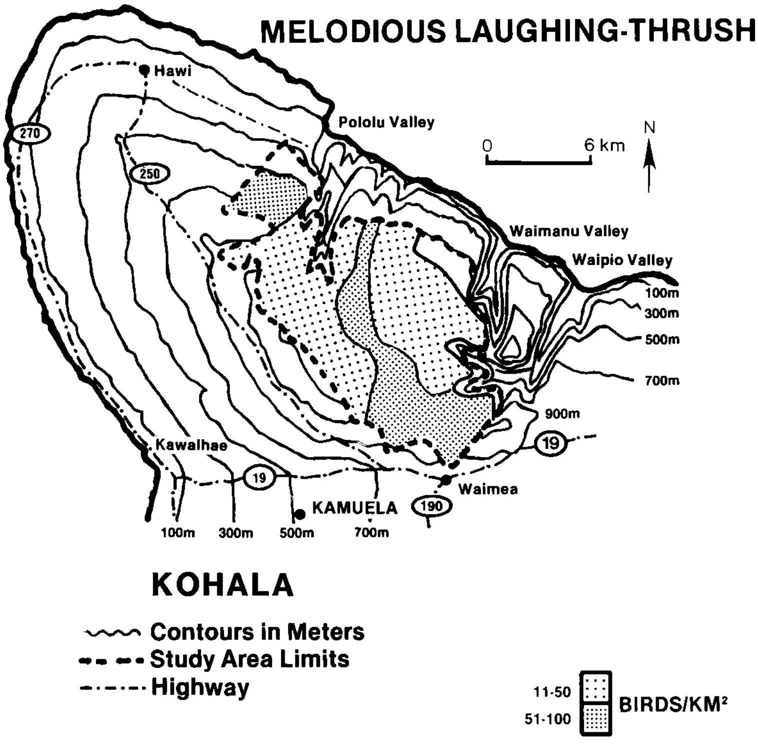


FIGURE 236. Distribution and abundance of the Melodious Laughing-thrush in the Kohala study area.

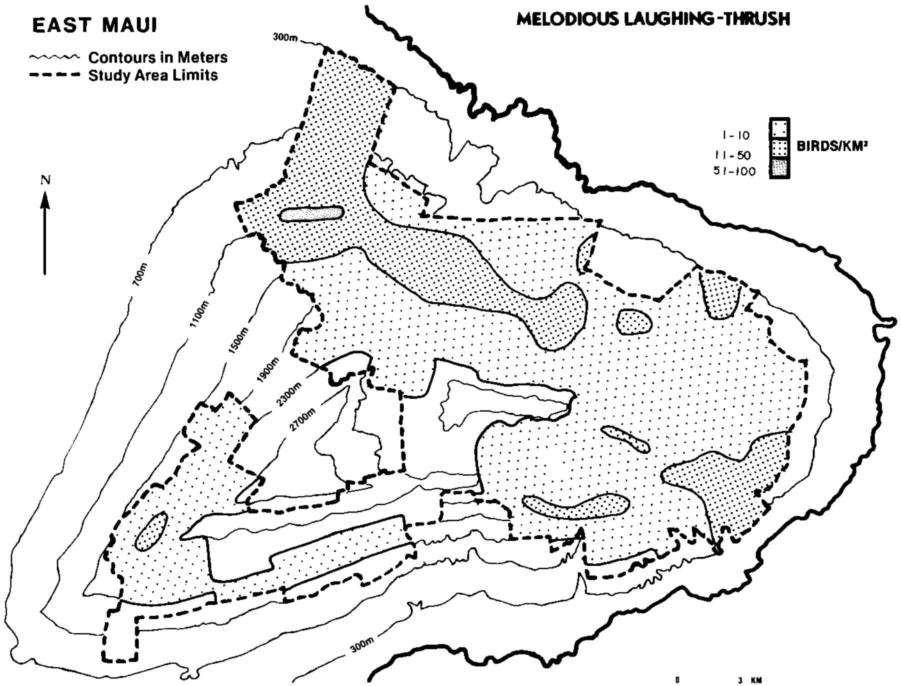


FIGURE 237. Distribution and abundance of the Melodious Laughing-thrush in the East Maui study area.

colonize this habitat on Maui. Warner (1967) reported no birds from Kipahulu Valley; 13 years later they were fairly common below 1500 m elevation. In many respects the dynamic range expansion of the Melodious Laughing-thrush paralleled the population explosion many observers reported for Japanese White-eyes 20 years earlier. We estimated a total of 2100 ± 300 (95% CI) birds in the East Maui study area. Densities were lower on West Maui, and we failed to find birds on Molokai and Lanai.

On Kauai, Melodious Laughing-thrushes have low densities that decrease in the higher, wetter areas of the south Alakai. Our estimate of 450 ± 75 (95% CI) birds compares well with an estimate of 240 ± 150 birds for the same area in 1968–1973 (Sincock et al. 1984). Sincock estimated a total of 13,000 ± 4000 birds in native forests on Kauai.

Melodious Laughing-thrushes occur from sea level to 2900 m on Hawaii and to 2500 m on Maui. They are most common below 1000 m in most areas, but reach fairly high densities up to 1500 m in the Kohala study area.

Melodious Laughing-thrushes tend to be habitat generalists that are most common at lower elevations, as seen in all regression models (Table 53). Birds occupy a wide breadth of habitat types, from very wet forests to dry scrub, with a slight inclination for lower stature forests (Fig. 240). The regression models show little response to individual trees, another indication of generalized habitat requirements.

Although Melodious Laughing-thrushes show little response to total shrub or ground cover in the regression models, they have substantial positive response to individual understory components, notably native shrubs, introduced shrubs, ground ferns, and matted ferns. This suggests that they prefer brushy understories with structural and floristic diversity. Association with matted ferns is unusual among Hawaiian birds, but matted ferns are good habitat because birds feed and skulk low in the understory and frequent the dense inpenetrable cover. In China, Melodious Laughing-thrushes likewise feed near the ground, are shy, and prefer dense understories (Étchécopar and Hüe 1983). The negative response to passiflora suggests that they are not particularly involved in the population expansion of banana poka. The positive term in the Mauna Kea model for naio fruit no doubt reflects its use for moisture and food.

RED-BILLED LEIOTHRIX (*Leiothrix lutea*)

The Red-billed Leiothrix, also known as the Hill Robin or Pekin Nightingale, is a babbler native to southern China and northern India; it

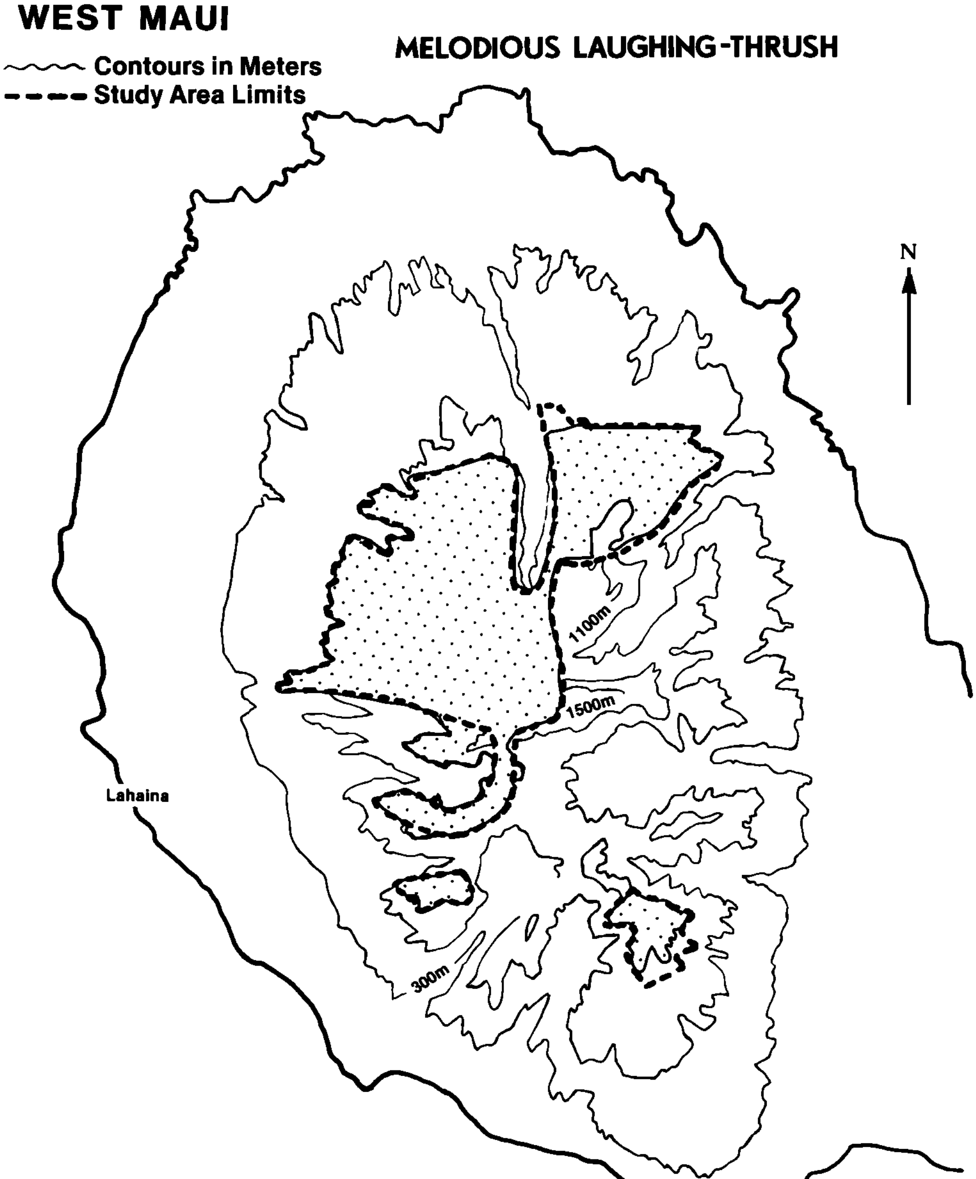


FIGURE 238. Distribution and abundance of the Melodious Laughing-thrush in the West Maui study area.

was introduced to the Hawaiian Islands as early as 1911 (Fisher and Baldwin 1947). They were first released on Hawaii in 1928 or 1929 (Caum 1933, Berger 1975b). By the 1970s they were well established on Hawaii, Maui, Molokai, Oahu, and Kauai (Berger 1972).

The Red-billed Leiothrix occurs in all study areas except Lanai and Kauai (Tables 33, 34, 54, Figs. 241–248). On Hawaii 98,000 ± 4000 (95% CI) birds occupy the study areas. On Mauna Kea, birds occur at very low densities throughout the study area, reaching high densities only in denser woodlands with naio or water sources. Birds are well distributed on windward Hawaii above 1000 m elevation, but low densities occur at lower elevations. At elevations below 1200 m in Ha-

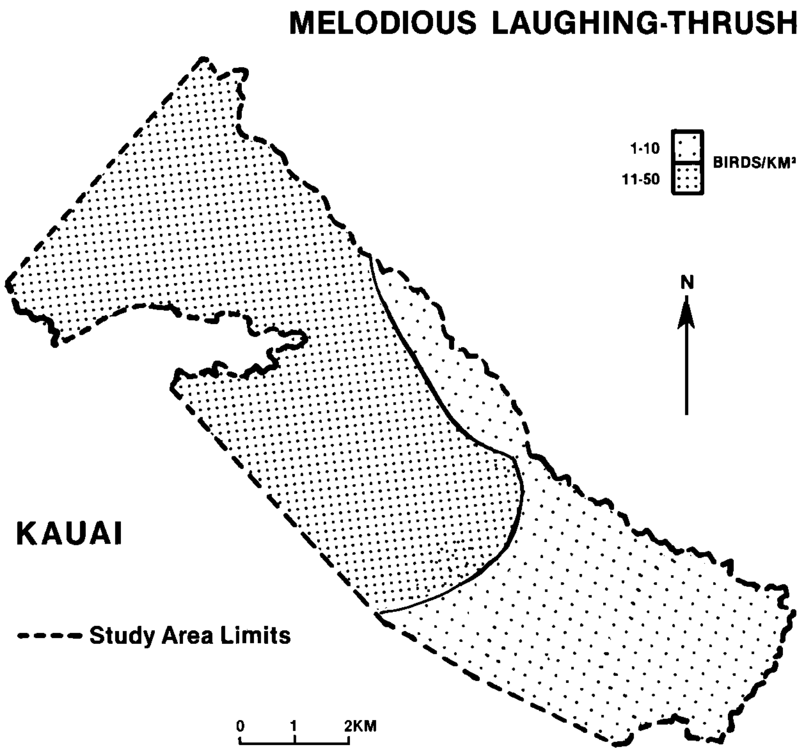


FIGURE 239. Distribution and abundance of the Melodious Laughing-thrush in the Kauai study area.

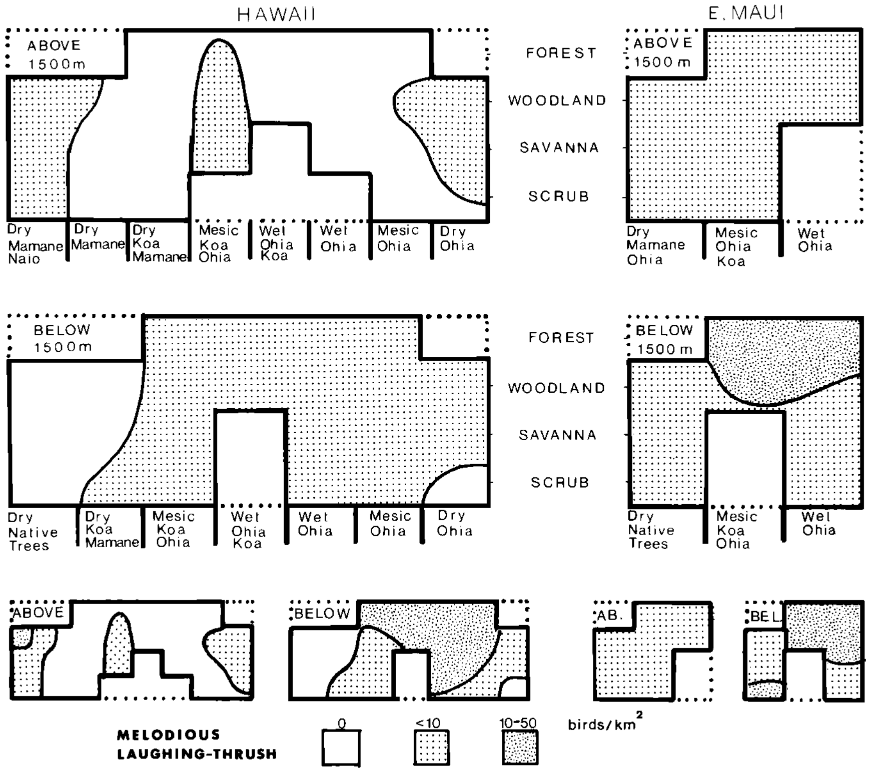


FIGURE 240. Habitat response graphs of the Melodious Laughing-thrush. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 53
REGRESSION MODELS FOR HABITAT RESPONSE OF THE MELODIOUS LAUGHING-THRUSH[a]

	Hamakua	Puna	Mauna Kea	Kohala	Maui	Kauai
R^2	0.23*	0.50*	0.19*	0.12*	0.22*	0.28*
Moisture	−6.9*	···	X	X	−4.9*	X
Elevation	4.9*	−10.6*	2.9	−3.3	−7.5*	−6.1*
(Elevation)^2	−7.9*	···	−2.7	···	···	···
Tree biomass	···	3.5*	···	···	···	···
(Tree biomass)^2	···	−3.3*	···	···	···	···
Crown cover	···	···	···	···	···	···
Canopy height	···	−5.7*	···	···	···	···
Koa	···	X	X	X	3.9*	X
Ohia	···	···	X	···	···	X
Naio	X	X	···	X	X	X
Mamane	3.5*	···	···	X	···	X
Intro. trees	−3.8*	2.7	X	···	7.9*	X
Shrub cover	···	···	···	···	···	···
Ground cover	−5.2*	···	···	···	−2.2	···
Native shrubs	6.9*	···	X	···	2.7	···
Intro. shrubs	6.1*	3.6*	X	···	···	···
Ground ferns	X	···	X	2.7	3.1	···
Matted ferns	4.8*	10.1*	X	3.7*	2.1	···
Tree ferns	X	···	X	···	4.9*	···
Ieie	X	3.9*	X	X	−4.7*	2.6
Passiflora	···	X	X	···	···	X
Native herbs	X	···	X	···	···	···
Intro. herbs	X	···	4.6*	···	···	−3.0
Native grasses	5.4*	···	···	···	···	···
Intro. grasses	···	···	···	···	···	···
Ohia flowers	···	···	X	···	···	···
Olapa fruit	···	−3.9*	X	···	2.3	···
Mamane flowers	X	X	···	X	···	X
Mamane fruit	X	X	···	X	X	X
Naio fruit	X	X	6.3*	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

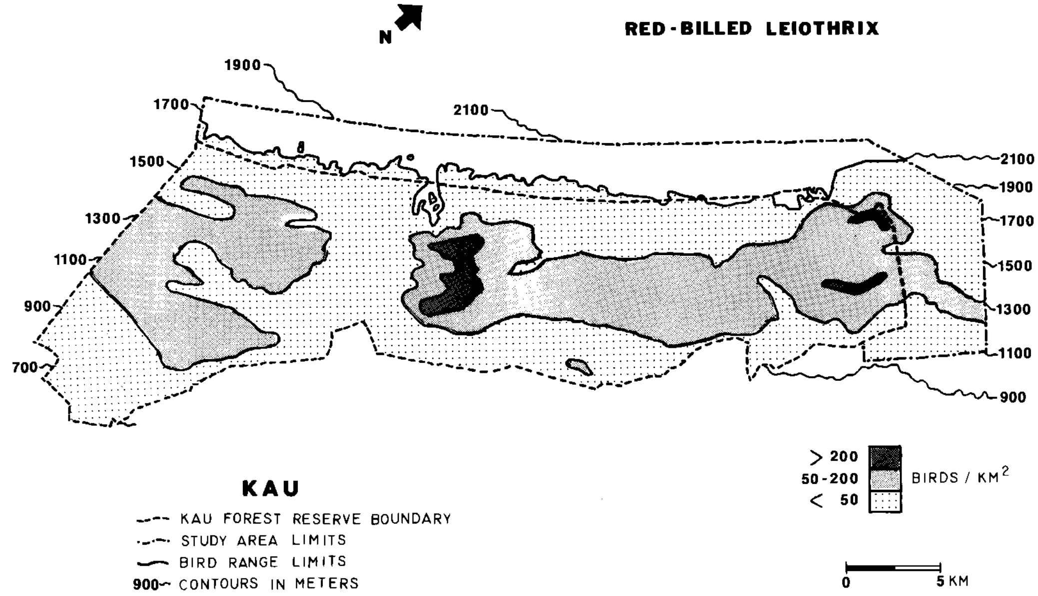


FIGURE 241. Distribution and abundance of the Red-billed Leiothrix in the Kau study area.

TABLE 54

DENSITY [MEAN (SE)] OF THE RED-BILLED LEIOTHRIX BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai
Elevation										
100–300 m	···	···	···	···	···	···	···	···	···	0
300–500 m	···	+ (+)	0	···	9 (4)	···	+ (+)	0	···	1 (1)
500–700 m	+ (+)	4 (1)	0	···	8 (2)	···	11 (11)	13 (4)	0	2 (2)
700–900 m	11 (3)	11 (2)	0	···	6 (1)	···	34 (23)	42 (7)	13 (6)	6 (2)
900–1100 m	63 (8)	36 (3)	0	···	21 (2)	···	82 (13)	57 (6)	21 (8)	20 (4)
1100–1300 m	82 (6)	82 (3)	4 (3)	0	32 (3)	···	74 (12)	69 (6)	49 (10)	89 (6)
1300–1500 m	91 (6)	93 (5)	···	0	26 (3)	···	126 (17)	102 (7)	38 (10)	77 (12)
1500–1700 m	56 (7)	118 (6)	···	30 (8)	10 (2)	···	199 (20)	106 (8)	21 (8)	···
1700–1900 m	24 (5)	99 (9)	···	13 (6)	14 (2)	···	···	101 (9)	46 (12)	···
1900–2100 m	2 (2)	16 (8)	···	+ (+)	16 (3)	48 (11)	···	81 (10)	···	···
2100–2300 m	0	4 (4)	···	0	7 (2)	21 (6)	···	11 (5)	···	···
2300–2500 m	···	···	···	···	+ (+)	11 (5)	···	3 (1)	···	···
2500–2700 m	···	···	···	···	···	4 (2)	···	1 (1)	···	···
2700–2900 m	···	···	···	···	···	4 (3)	···	3 (+)	···	···
2900–3100 m	···	···	···	···	···	+ (+)	···	···	···	···
Habitat										
Ohia	48 (3)	61 (2)	4 (3)	4 (1)	14 (1)	···	88 (8)	78 (4)	34 (4)	42 (3)
Koa-ohia	83 (6)	78 (4)	···	66 (18)	22 (2)	···	···	100 (7)	···	···
Koa-mamane	···	3 (3)	···	5 (2)	17 (3)	···	···	···	···	···
Mamane-naio	···	···	···	···	12 (12)	25 (4)	···	···	···	···
Mamane	···	···	···	···	22 (3)	1 (1)	···	4 (4)	···	···
Other natives	···	31 (10)	···	7 (7)	15 (5)	···	···	31 (4)	···	+ (+)
Intro. trees	···	27 (8)	···	···	8 (2)	···	171 (12)	100 (13)	0	+ (+)
Treeless	0	1 (1)	0	15 (15)	+ (+)	···	···	8 (1)	+ (+)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

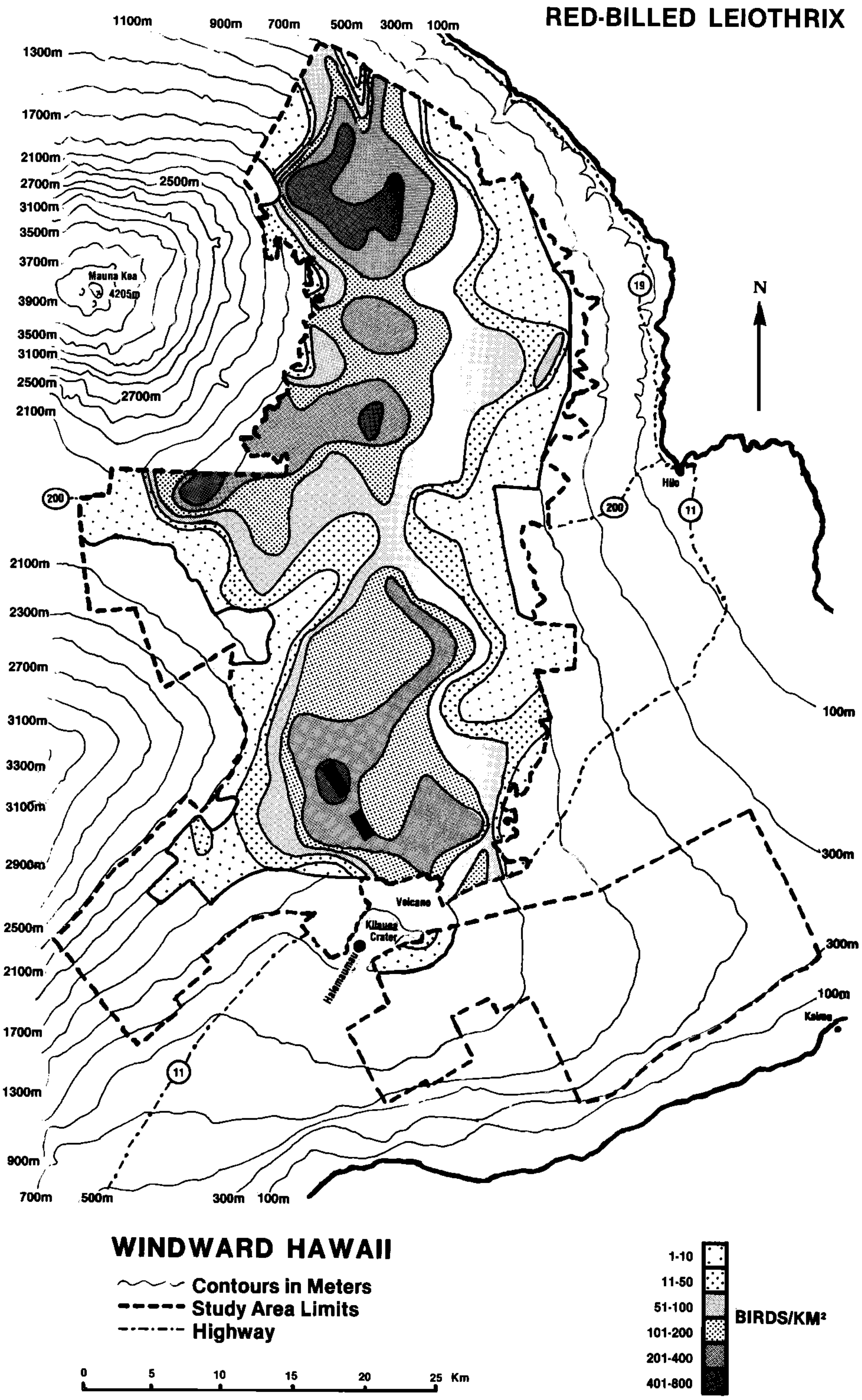


FIGURE 242. Distribution and abundance of the Red-billed Leiothrix in the windward Hawaii study areas.

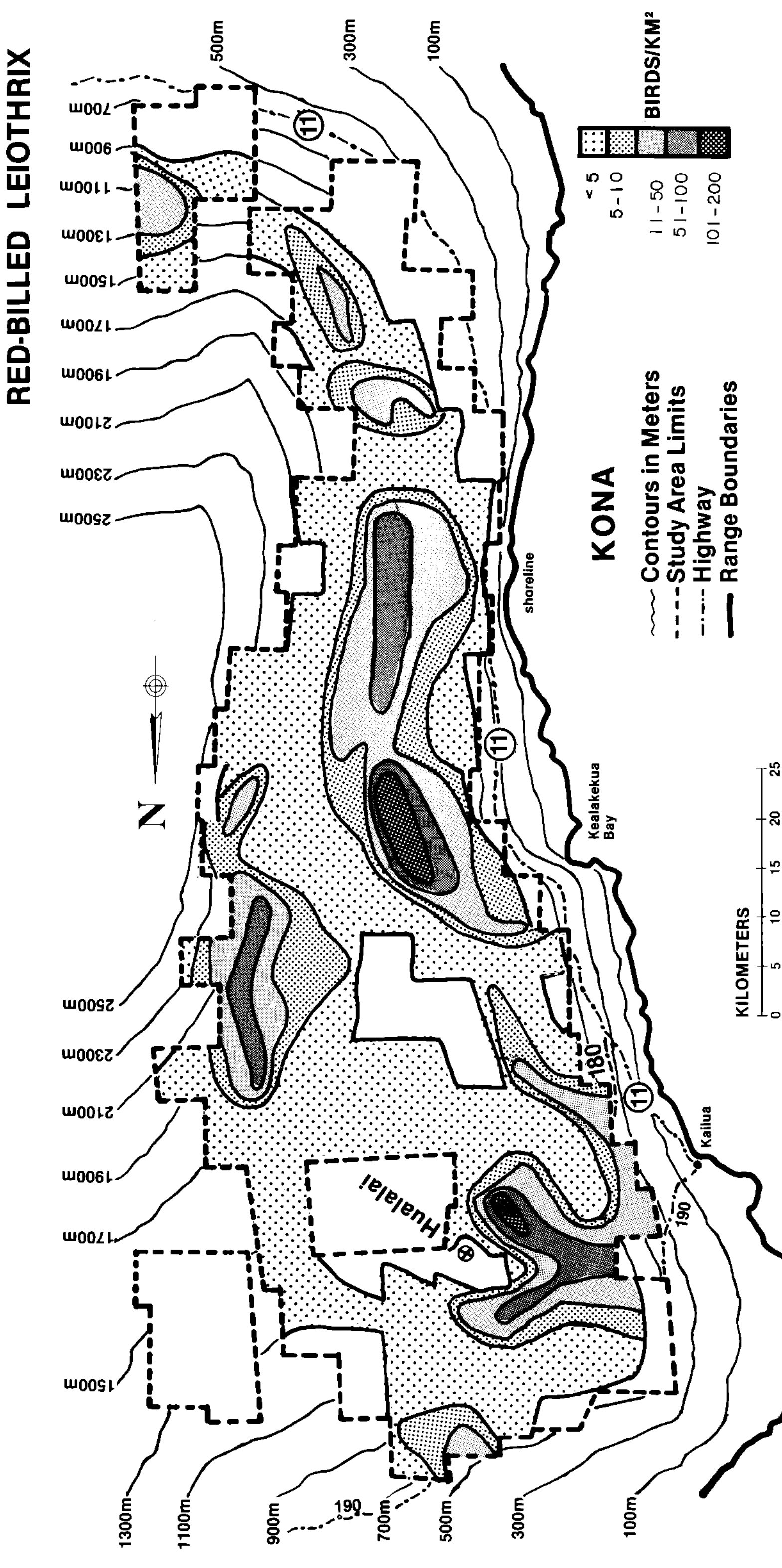


FIGURE 243. Distribution and abundance of the Red-billed Leiothrix in the Kona study area.

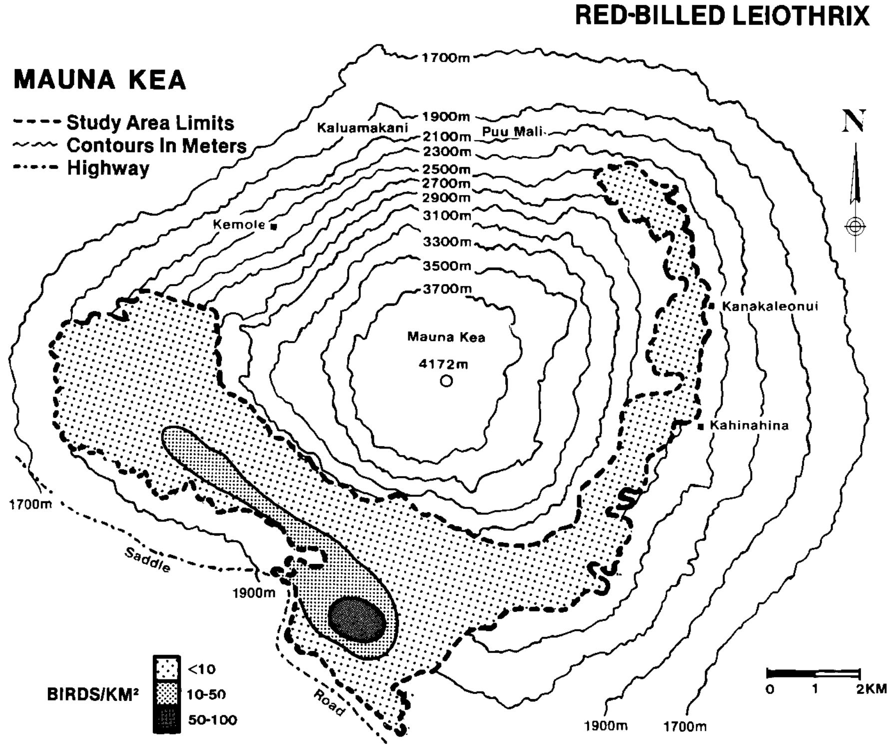


FIGURE 244. Distribution and abundance of the Red-billed Leiothrix in the Mauna Kea study area.

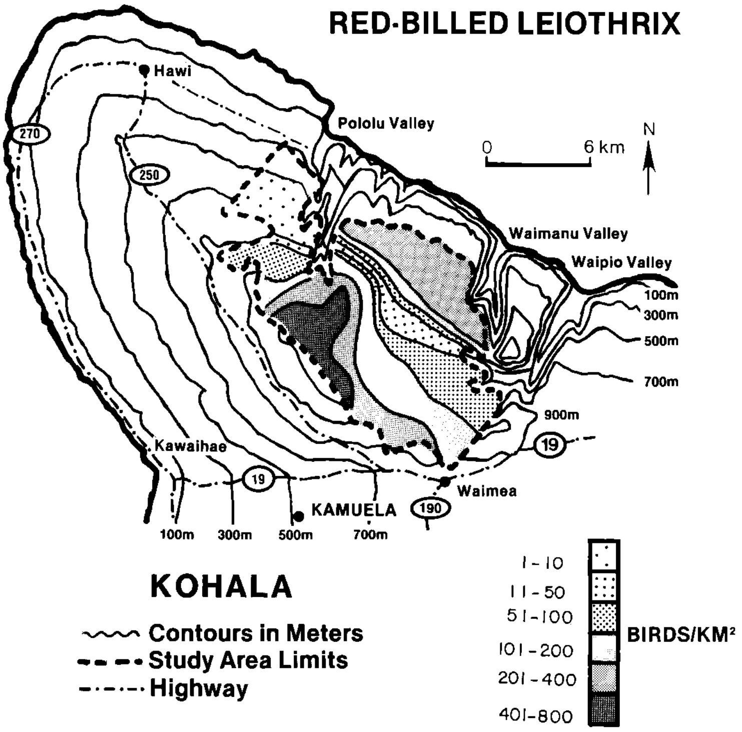


FIGURE 245. Distribution and abundance of the Red-billed Leiothrix in the Kohala study area.

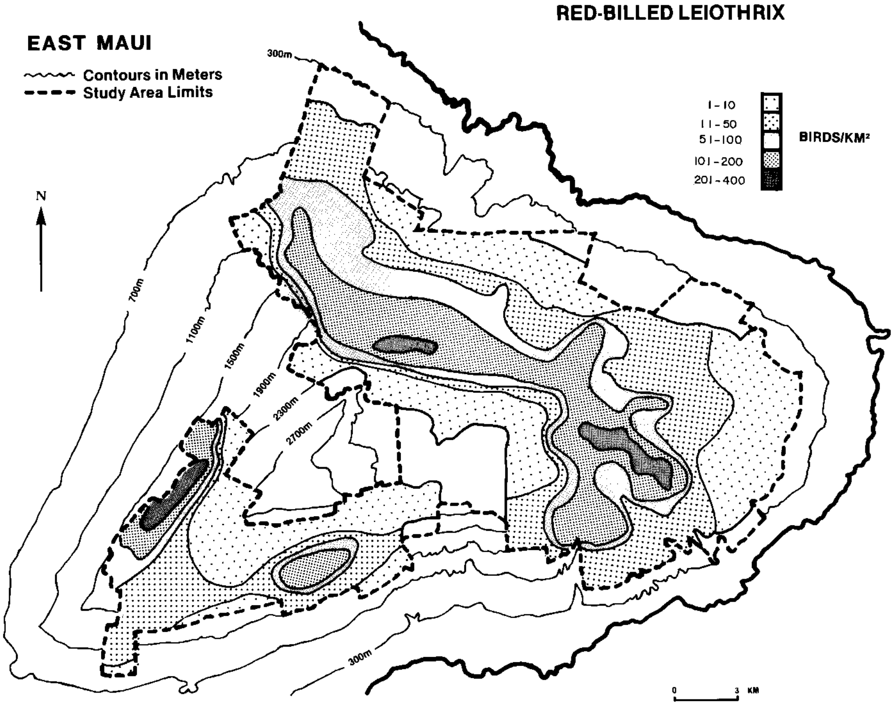


FIGURE 246. Distribution and abundance of the Red-billed Leothrix in the East Maui study area.

waii Volcanoes National Park, densities appear to have declined sharply in the 1940–1975 interval (Conant 1975, Banko and Banko 1980). S. Conant (1980) noted their absence in the Puna study area. They are also absent from deforested areas at the north edge of the Hamakua study area and on the Kapapala Tract. Birds are well distributed in Kau and Kona, except for open pasturelands. The species was well established in Kohala during our survey and the 1970–1972 study by van Riper (1982).

On East Maui an estimated 19,000 ± 1200 (95% CI) birds are widespread and common in areas with adequate water, although densities tend to be lower below 1000 m elevation on the windward side. Since 1977 birds have expanded greatly in range and numbers on northwest Haleakala in Kula as the expanding black wattle (*Acacia decurrens*) forest developed and provided suitable habitat (C. B. Kepler, pers. observ.). Densities are substantially lower on West Maui than on East Maui (Table 54), and there the population totals 800 ± 200 birds.

On Molokai 1800 ± 200 (95% CI) birds occur chiefly above 1000 m elevation on the Olokui Plateau, Puu Ohelo, Ohialele Plateau, and in the Kamakou Preserve. Scott et al. (1977) found this species common on Molokai above 1200 m elevation.

On Kauai we failed to find this species. For 1968–1973, Sincock et al. (1984) estimated 16 ± 30 (95% CI) birds for our study area and 2400 ± 2200 birds in native forests. Richardson and Bowles (1964) found this species restricted to areas above 1000 m elevation.

We found the Red-billed Leiothrix from 300 to 2900 m elevation on Hawaii, from 500 to 2900 m on Maui, and from 300 to 1500 m on Molokai; highest densities occurred at 900–1900 m on Hawaii, at 1100–1500 m on Molokai, and at 1300–2100 m on Maui. Fisher and Baldwin (1947) concluded that the upper distribution limit of 2400–2700 m elevation was determined by temperature. Our data suggest that the upper limit is not determined by thermoregulation, but by water requirements, as the distribution of densities > 10 birds/km² above 2500 m elevation on Mauna Kea closely corresponds with naio berries and gamebird watering sites.

Also intriguing is the lower elevational limit of about 1000 m in the Hawaiian Islands. In Burma, the Red-billed Leiothrix is distributed chiefly above 1500 m (Smythies 1953). We hypothesize that long-term survival of lowland populations is impeded by high temperatures, such as in the steamy lowlands of Burma or the more temperate lowlands of the Hawaiian Islands. This hypothesis would explain the absence

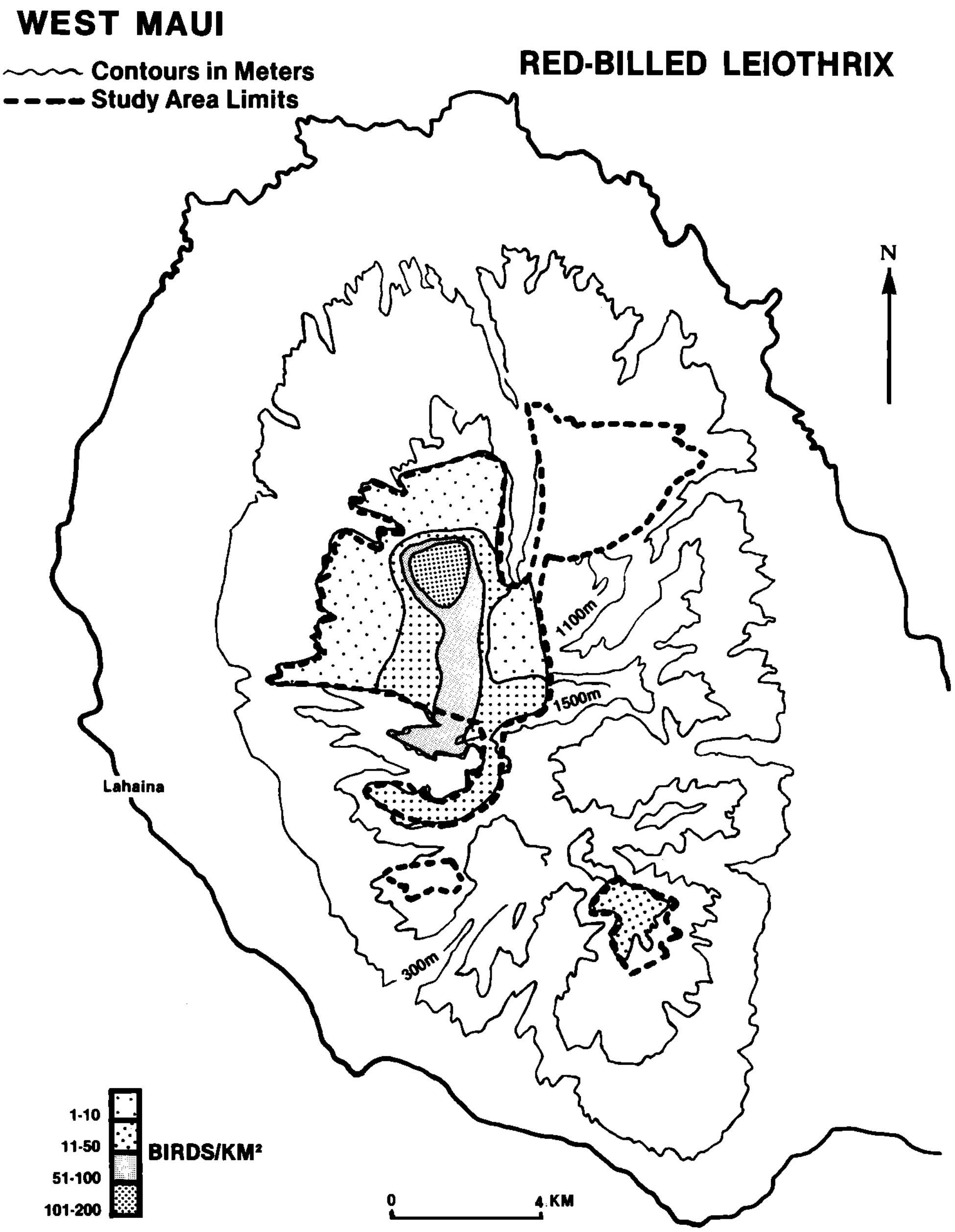


FIGURE 247. Disribution and abundance of the Red-billed Leiothrix in the West Maui study area.

or rarity of birds at lower elevations, and may also impart insight into the disappearance of birds on Oahu. As illustrated by annual Christmas Bird Counts, the Red-billed Leiothrix exhibited a drastic decline from about 100 birds per count before 1968 to 0–1 birds after 1969 (Anonymous 1974). Although birds were introduced and initially established large populations in lowland areas, they may have died off during periods of unfavorable climate. If they are in fact limited by climate to areas above 1000 m elevation in the Hawaiian Islands, then self-sustaining populations will occur only on islands with substantial areas above 1000 m such as Hawaii and Maui, and will eventually decline to sparse distributions on other islands such as Oahu and Kauai.

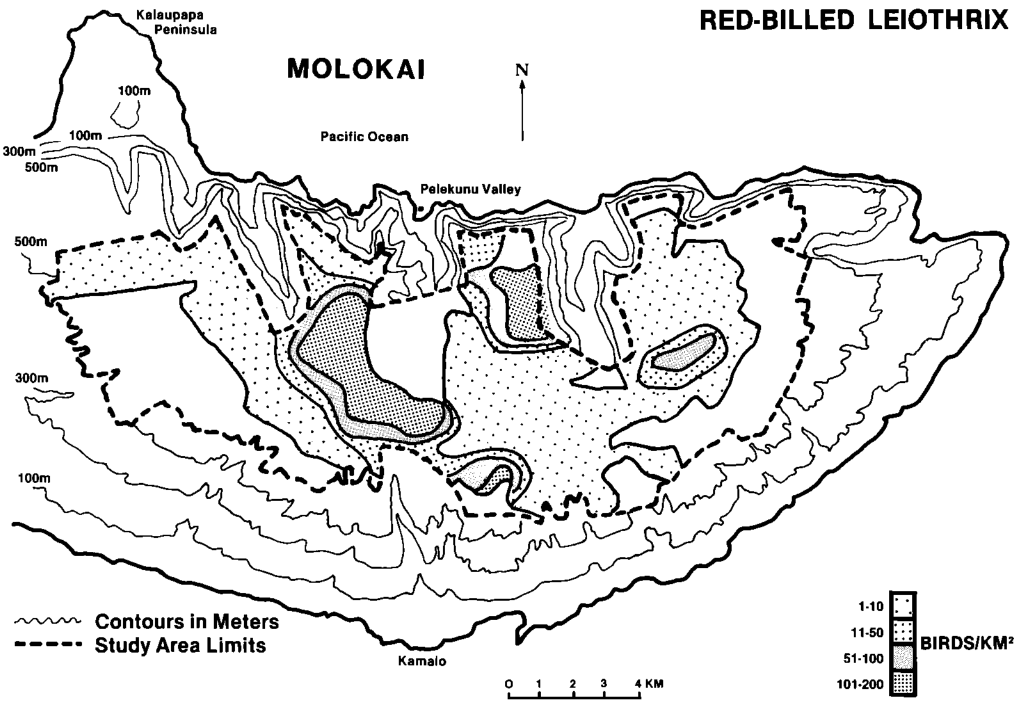


FIGURE 248. Distribution and abundance of the Red-billed Leiothrix in the Molokai study area.

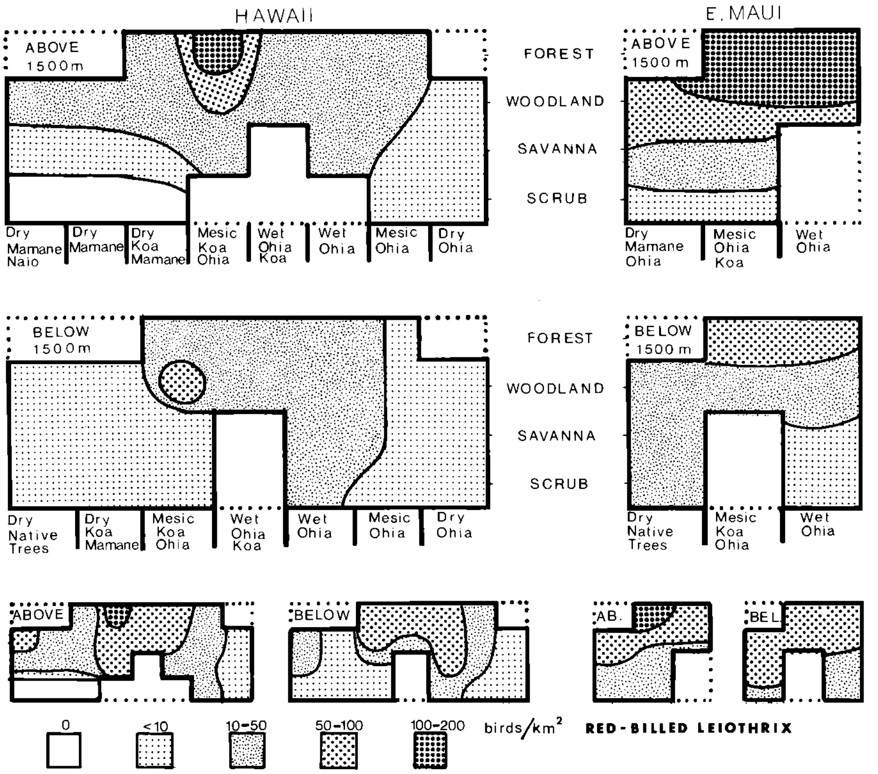


FIGURE 249. Habitat response graphs of the Red-billed Leiothrix. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 55
REGRESSION MODELS FOR HABITAT RESPONSE OF THE RED-BILLED LEIOTRHIX[a]

	Kau	Hamakua	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai
R^2	0.32*	0.45*	0.09*	0.34*	0.24*	0.35*	0.51*	0.62*
Moisture	···	8.8*	···	9.3*	X	X	···	···
Elevation	10.3*	13.2*	···	3.4*	−3.0	9.4*	14.4*	−7.4*
(Elevation)^2	−10.7*	−9.0*	···	···	2.6	···	−10.7*	10.6*
Tree biomass	5.5*	2.9	···	···	···	···	2.4	···
(Tree biomass)^2	···	···	4.7*	···	···	···	6.1*	···
Crown cover	−5.8*	−3.6*	···	3.7*	···	···	···	···
Canopy height	−5.0*	3.7*	···	2.3	···	···	−3.0	3.6*
Koa	···	3.6*	···	3.5*	X	X	···	X
Ohia	···	···	−3.7*	−9.1*	X	···	−3.2	···
Naio	X	X	···	4.6*	3.2	X	X	X
Mamane	X	−3.0	···	···	···	X	−4.3*	X
Intro. trees	X	···	X	···	X	···	···	−2.5
Shrub cover	···	−4.8*	···	···	3.7*	···	···	···
Ground cover	−6.3*	···	···	···	···	···	···	···
Native shrubs	···	6.7*	···	11.0*	X	···	···	···
Intro. shrubs	X	6.6*	···	···	X	···	···	···
Ground ferns	X	X	···	3.1	X	···	···	5.5*
Matted ferns	−2.7	−6.8*	···	−3.0	X	···	···	···
Tree ferns	···	X	X	8.2*	X	3.1	···	4.1*
Ieie	X	X	X	−8.2*	X	X	···	X
Passiflora	X	6.7*	X	6.0*	X	···	···	X
Native herbs	X	X	2.3	−3.3*	X	···	···	···
Intro. herbs	X	X	···	5.0*	···	···	3.9*	···
Native grasses	···	···	···	−5.9*	···	···	···	2.8
Intro. grasses	···	···	···	···	2.3	···	···	···
Ohia flowers	···	2.8	−3.6*	···	X	···	···	−3.4*
Olapa fruit	···	5.3*	···	8.6*	X	···	4.1*	3.7*
Mamane flowers	X	X	···	X	···	X	···	X
Mamane fruit	X	X	X	X	···	X	X	X
Naio fruit	X	X	X	X	···	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are *t* statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

The habitat response graphs show a widespread, well-established species that is more abundant in mesic forests and woodlands (Fig. 249). Tree biomass, crown cover, and canopy height terms tend to balance one another in most regression models (Table 55), indicating that some trees are essential, but that birds occur from open woodland to dense forests. Birds are virtually limited to areas of naio on Mauna Kea. The low density of fleshy fruits in mamane stands is reflected in the negative mamane terms. The association with koa probably reflects the occurrence of birds in open rather mesic forests at intermediate elevations. Relative to the response to other tree species, the negative terms for ohia may be due to lack of fleshy fruit on ohia.

Response to total ground or shrub cover is weak and indicates a wide range of occurrence. Fisher and Baldwin (1947) concluded that "a cover of dense vegetation near the ground is the major characteristic of the habitat" in order to explain the absence of this species in ironwood (*Casuarina equisetifolia*) and eucalyptus groves having barren understories. The models indicate that occupied habitat has the average understory of the study area. The average understory is considerably more dense than the understories of ironwood and eucalyptus groves. Positive responses to understory components occur for native shrubs, ground ferns, and introduced herbs. Matted ferns yield negative responses, probably because at high cover values they choke out other understory species, including berry plants. The association with passiflora indicates that the Red-billed Leiothrix is a potential dispersal agent for banana poka (Warshauer et al. 1983). The positive response to olapa fruit, reflecting occurrence in wet forest interiors, suggests local concentration at food sources. The association with fruit reflects the considerable quantity of fruit and berries in the diet (Fisher and Baldwin 1947).

NORTHERN MOCKINGBIRD
(*Mimus polyglottos*)

Native to North America, Northern Mockingbirds are largely insectivorous but also feed on

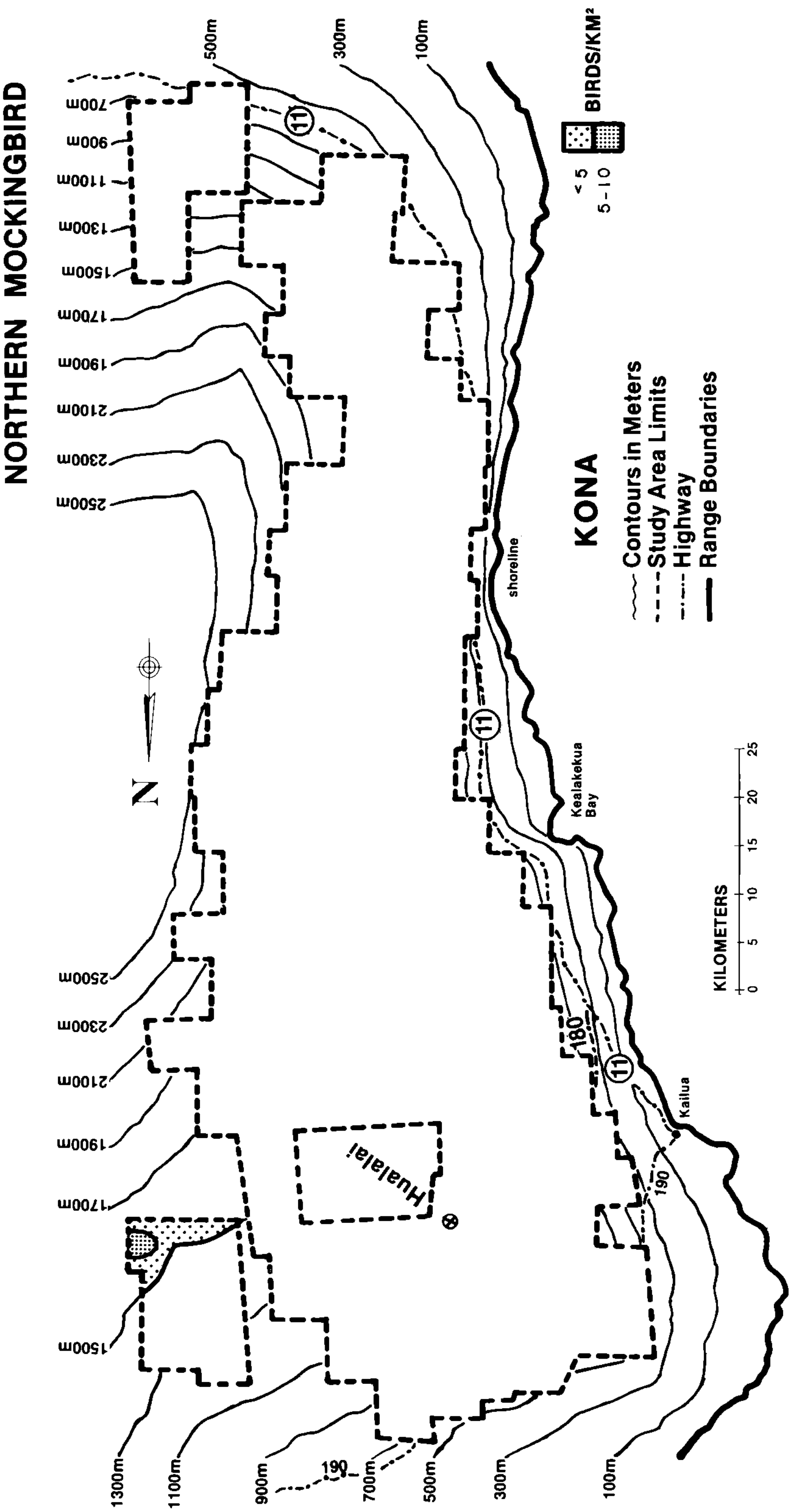


FIGURE 250. Distribution and abundance of the Northern Mockingbird in the Kona study area.

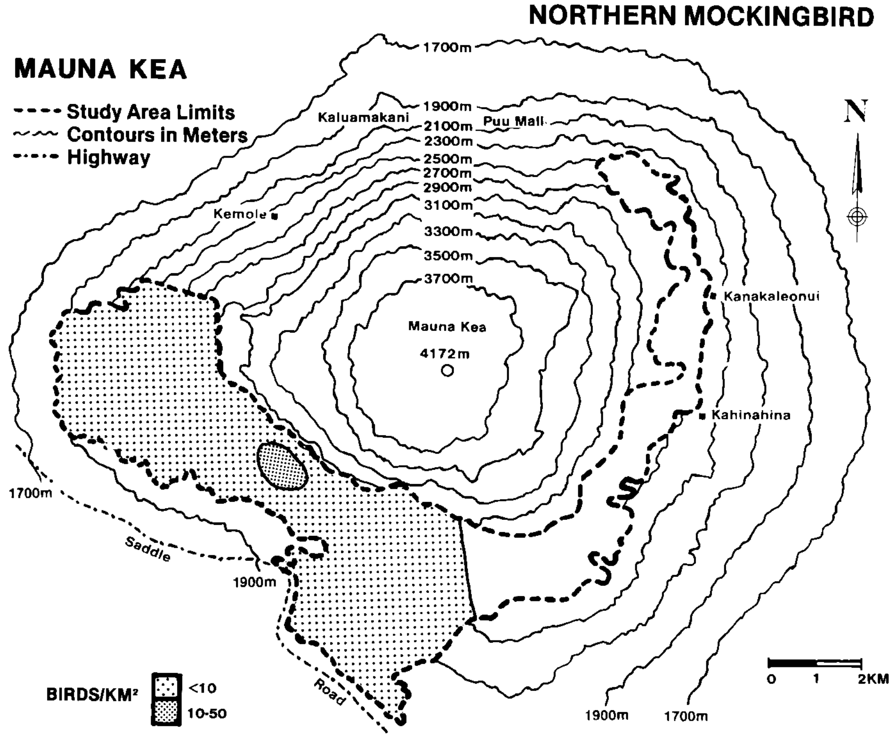


FIGURE 251. Distribution and abundance of the Northern Mockingbird in the Mauna Kea study area.

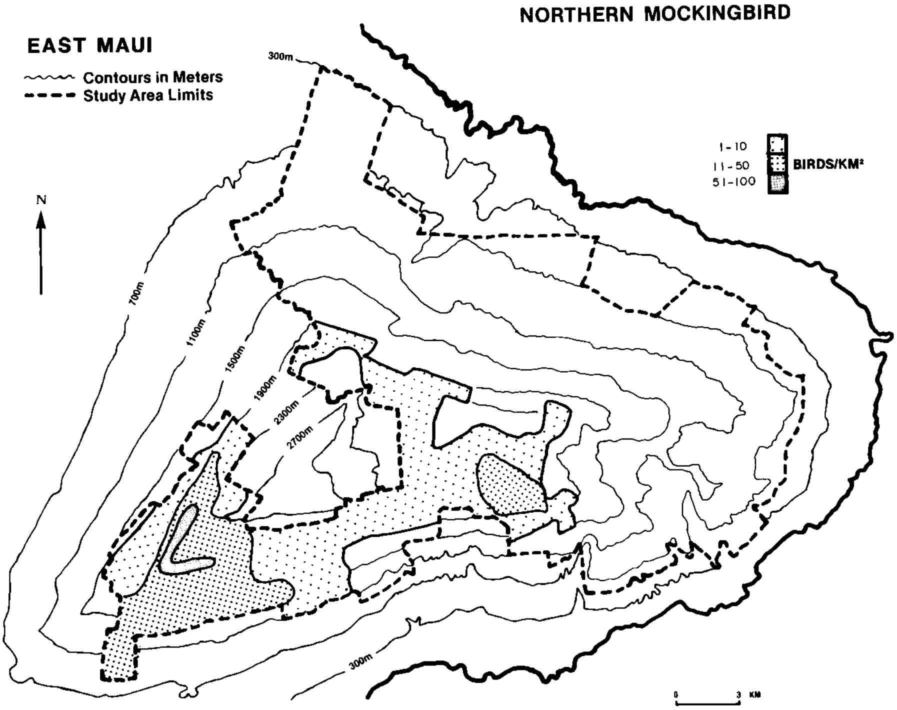


FIGURE 252. Distribution and abundance of the Northern Mockingbird in the East Maui study area.

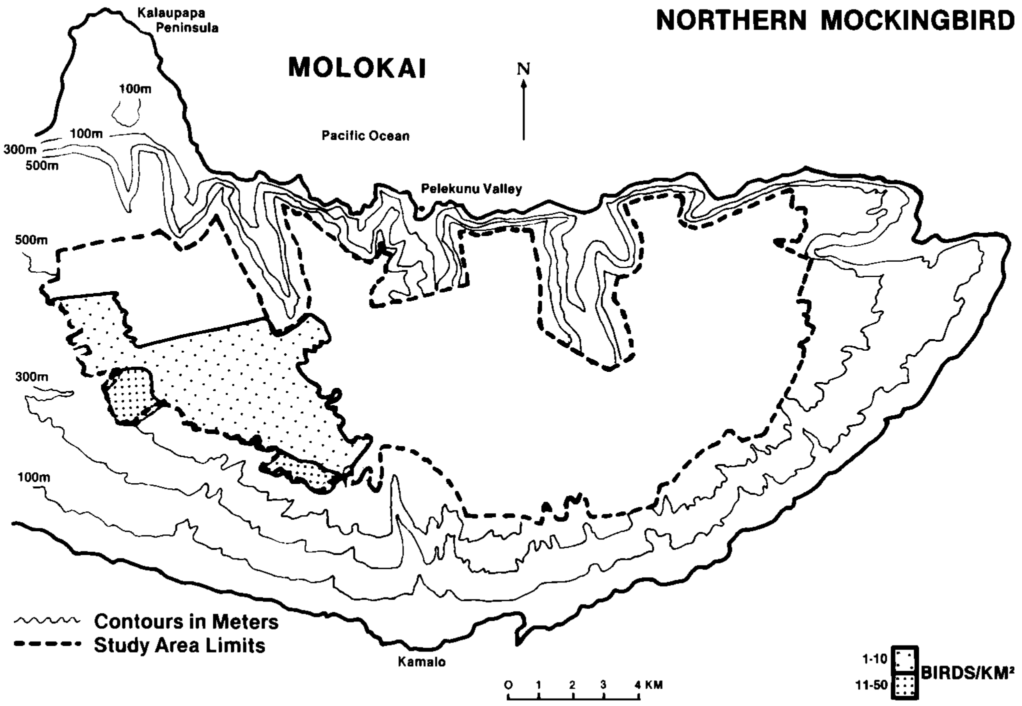


FIGURE 253. Distribution and abundance of the Northern Mockingbird in the Molokai study area.

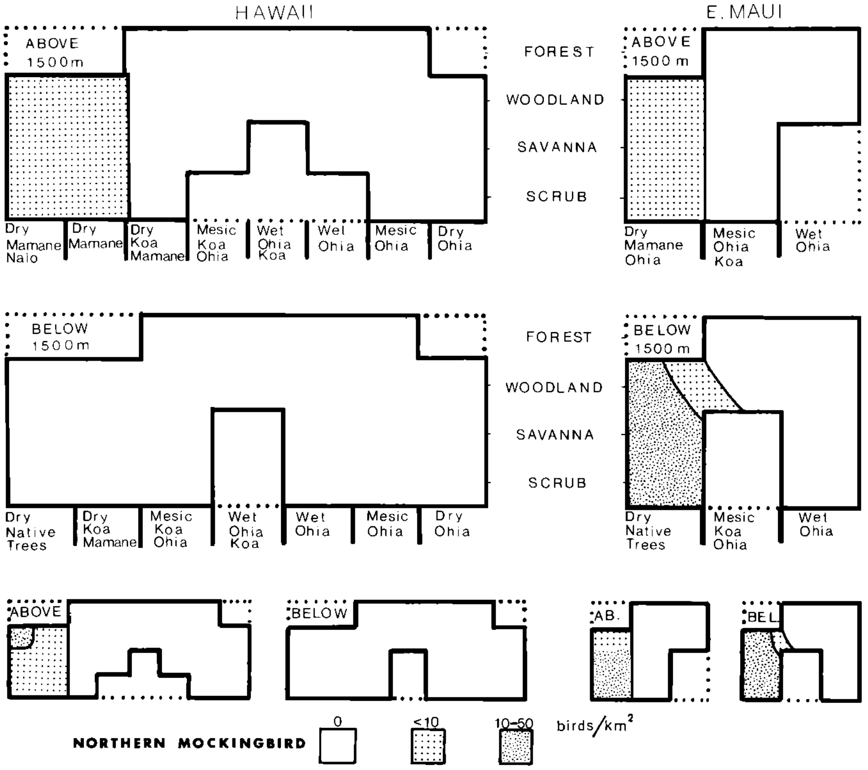


FIGURE 254. Habitat response graphs of the Northern Mockingbird. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 56

DENSITY [MEAN (SE)] OF THE COMMON MYNA BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	East Maui	Molokai	Lanai
Elevation									
100–300 m	···	···	···	···	···	···	···	7 (5)	···
300–500 m	···	0	0	···	+ (+)	···	0	+ (+)	···
500–700 m	+ (+)	0	0	···	6 (2)	···	0	30 (17)	3 (2)
700–900 m	9 (6)	7 (6)	22 (5)	···	14 (2)	···	8 (5)	1 (1)	+ (+)
900–1100 m	0	+ (+)	8 (7)	···	11 (3)	···	15 (3)	1 (1)	+ (+)
1100–1300 m	0	15 (3)	+ (+)	6 (2)	9 (2)	···	5 (3)	0	···
1300–1500 m	0	15 (5)	···	6 (2)	7 (1)	···	13 (7)	0	···
1500–1700 m	0	6 (2)	···	2 (1)	5 (1)	···	10 (5)	···	···
1700–1900 m	0	7 (2)	···	+ (+)	+ (+)	···	+ (+)	···	···
1900–2100 m	0	11 (2)	···	1 (+)	+ (+)	5 (4)	*	···	···
2100–2300 m	0	3 (2)	···	+ (+)	+ (+)	0	12 (12)	···	···
2300–2500 m	···	···	···	···	+ (+)	0	0	···	···
2500–2700 m	···	···	···	···	···	0	0	···	···
2700–2900 m	···	···	···	···	···	0	0	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···
Habitat									
Ohia	9 (6)	9 (2)	12 (3)	4 (1)	5 (1)	···	0	0	···
Koa-ohia	0	9 (3)	···	2 (1)	14 (2)	···	21 (8)	···	···
Koa-mamane	···	11 (2)	···	2 (1)	11 (2)	···	···	···	···
Mamane-naio	···	···	···	···	+ (+)	1 (1)	···	···	···
Mamane	···	···	···	···	2 (1)	+ (+)	0	···	···
Other natives	···	13 (2)	···	2 (1)	5 (1)	···	10 (2)	5 (5)	+ (+)
Intro. trees	···	2 (2)	···	···	8 (3)	···	5 (2)	14 (9)	1 (+)
Treeless	0	+ (+)	+ (+)	+ (+)	+ (+)	···	0	+ (+)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area; * indicates stratum was not sampled in range but was sampled elsewhere in study area.

fruits, especially during winter (Sprunt 1948). They occur in open forest, woodland, and scrub habitats throughout the southern United States and into Mexico (Grinnell and Miller 1944, Sprunt 1948).

Northern Mockingbirds were first released on Oahu in 1931 and on Maui in 1933 (Anonymous 1961). Berger (1981) found them well established in dry woodland areas on Hawaii, Maui, Molokai, Lanai, Oahu, and Kauai. Details of the distribution on Maui were given by Udvardy (1961), on Lanai by Hirai (1978), and on Kauai by Richardson and Bowles (1964). Birds were first reported on Hawaii in 1959 (Dunmire 1961), and have become well established in dry areas along the leeward coast.

We found Northern Mockingbirds in five study areas (Tables 33, 34, 51, Figs. 250–253), with highest densities on the crater and leeward slopes of Haleakala. The population on Mauna Kea became established after 1978, when birds were noted at Mauna Kea State Park. Occurrence in the Kona and West Maui study areas appears to be marginal. Birds occur on the dry southwest side of the Molokai study area, but are more abundant in the lowlands (Berger 1981).

Northern Mockingbirds occur over a wide range of elevations and vegetation types (Table 51). The habitat response graphs show a strong association with dry habitat types on Hawaii and Maui (Fig. 254). Only the populations on Mauna Kea and Maui were sufficiently sampled to construct regression models. Those models (Table 50) show that highest densities occur in naio forest on Mauna Kea and in dry open mamane forest on Maui.

Udvardy (1961) found this species to be very common on Maui from sea level to 1000 m in dry mesquite woodlands. The negative tree biomass and positive crown cover terms in the Maui model indicate occurrence in sparse, open woodland, a physiognomy characteristic of both mamane and mesquite woodlands. The negative terms for other tree species indicate that birds did not occur with these trees in the study area.

Among understory components, the only strong response is towards passiflora. In North America wild fruit totals 43% of the diet (Beal et al. 1916). Northern Mockingbirds are potential dispersal agents for banana poka (Warshauer et al. 1983), particularly as the population expands on Hawaii.

The habitat response of Northern Mockingbirds in the Hawaiian Islands is similar to that

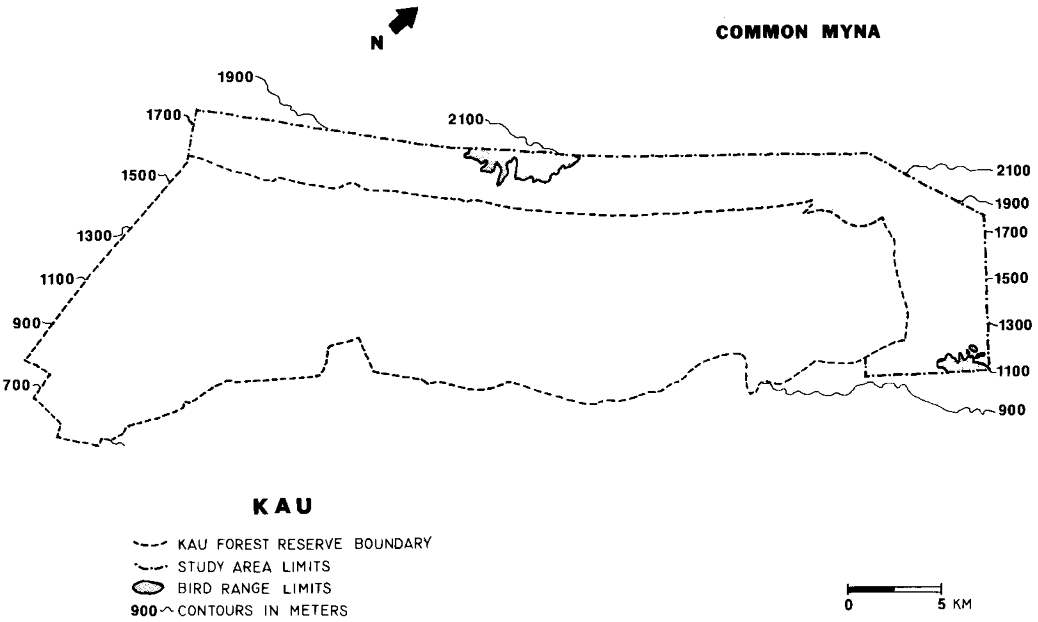


FIGURE 255. Distribution and abundance of the Common Myna in the Kau study area. (Density within range is less than 10 birds/km².)

shown by populations in the western United States, where high densities occur in scattered brush or very open woodland with variety of plants yielding fruits and berries (Grinnell and Miller 1944). Populations in the eastern United States tend to favor open woodland edges, pastures, and open brushland, as well as the more closed forests of "moss-bannered live oaks and towering magnolias" (Sprunt 1948).

COMMON MYNA (*Acridotheres tristis*)

Common Mynas, introduced from India in 1865 (Caum 1933), are common to abundant in most lowland areas except forest interiors. They are common residents of drier open forests from sea level to 1500 m in India (Ali and Ripley 1972), and are primarily terrestrial omnivores (Caum 1933, Berger 1981).

In the 1890s Common Mynas were widespread and common even in the deepest forests (W. A. Bryan and Seale 1901, Perkins 1903). This was a temporary situation, as E. H. Bryan (1940) later indicated that they seldom came into contact with native birds. Common Mynas occur in nine study areas (Tables 33, 34, 56, Figs. 255–259), always in association with forest edges, pastures, and other disturbed areas. On Hawaii 4500 ± 400 (95% CI) birds occur in the study areas; on Maui, 180 ± 90; on Molokai, 140 ± 150; and on Lanai, 20 ± 20. Although neither we nor Sincock et al. (1984) found birds in the Alakai Swamp, birds occurred on the summit of Waialeale in 1900 (Bryan and Seale 1901).

Common Mynas occur from sea level to 2300 m. Broad habitat preferences are seen in the habitat response graphs for Hawaii (Fig. 260), but occurrence in a habitat usually depends on the presence of water troughs or domestic stock. We found no birds in closed canopy forests. The regression models (Table 57) show that birds are most common in dry woodlands and partly open forests with low shrub cover at low elevations. There were too few sightings in the Maui, Molokai, and Lanai study areas to construct models; however, Common Mynas are common in dry open forest at low elevations in those areas.

Birds were associated with drier areas in every regression model. Bird density in three of the four models is associated with lower elevations, higher tree biomass, or lower shrub cover. The response to canopy height is positive and to crown cover negative, indicating association with open to scattered canopies of tall trees. Perhaps because of its height and open foliage, koa tends to generate positive responses, but ohia, which usually attains greatest biomass in wet forest interiors, generates negative ones. Common Mynas are not attracted to passiflora infestations, which mainly occur at higher elevations, nor to fern understories, which are probably too dense for foraging and are usually characteristic of wet forest interiors. In Hamakua the negative response

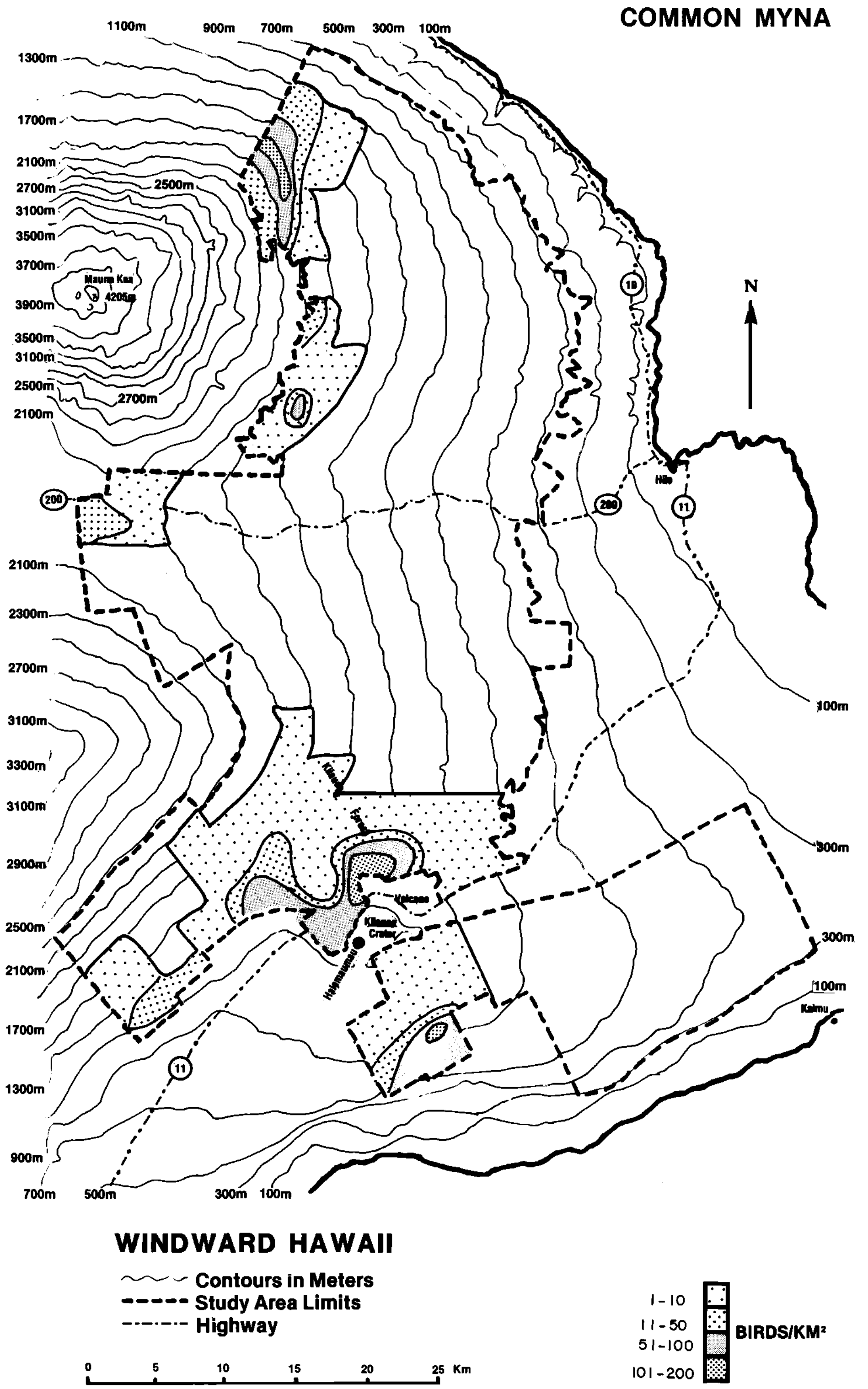


FIGURE 256. Distribution and abundance of the Common Myna in the windward Hawaii study areas.

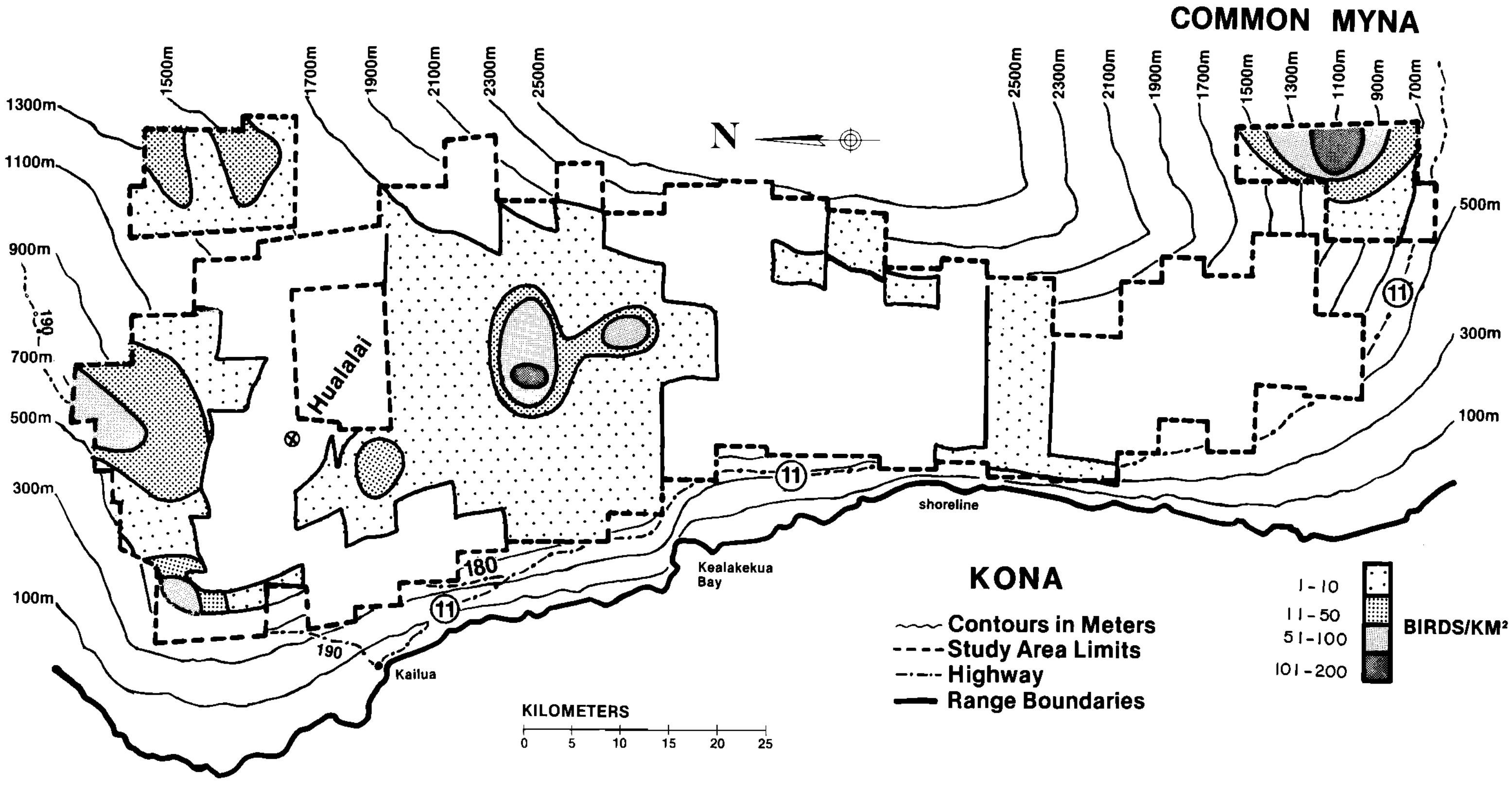


FIGURE 257. Distribution and abundance of the Common Myna in the Kona study area.

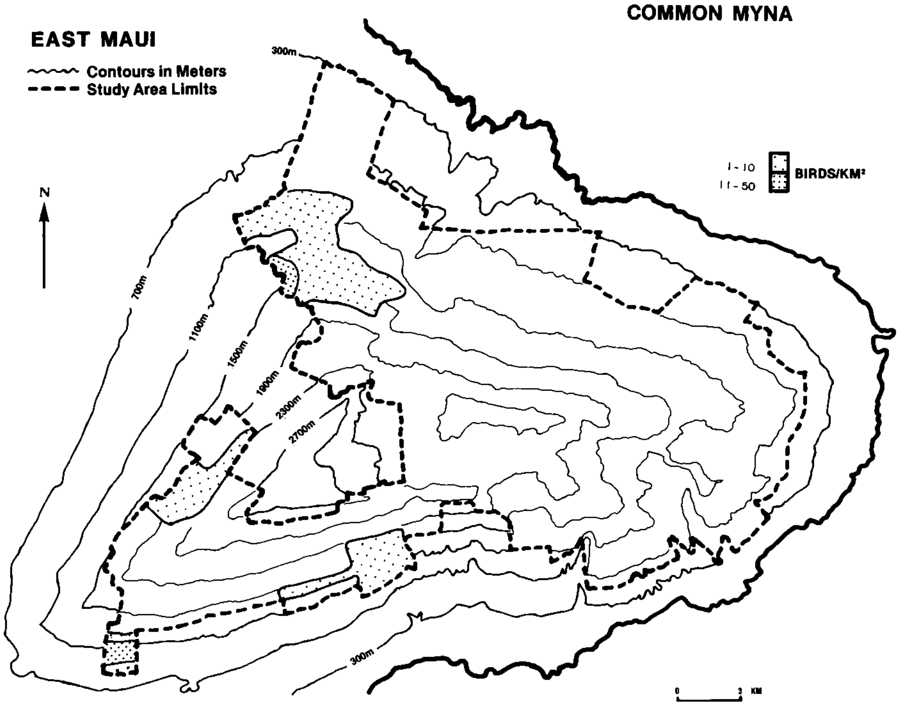


FIGURE 258. Distribution and abundance of the Common Myna in the East Maui study area.

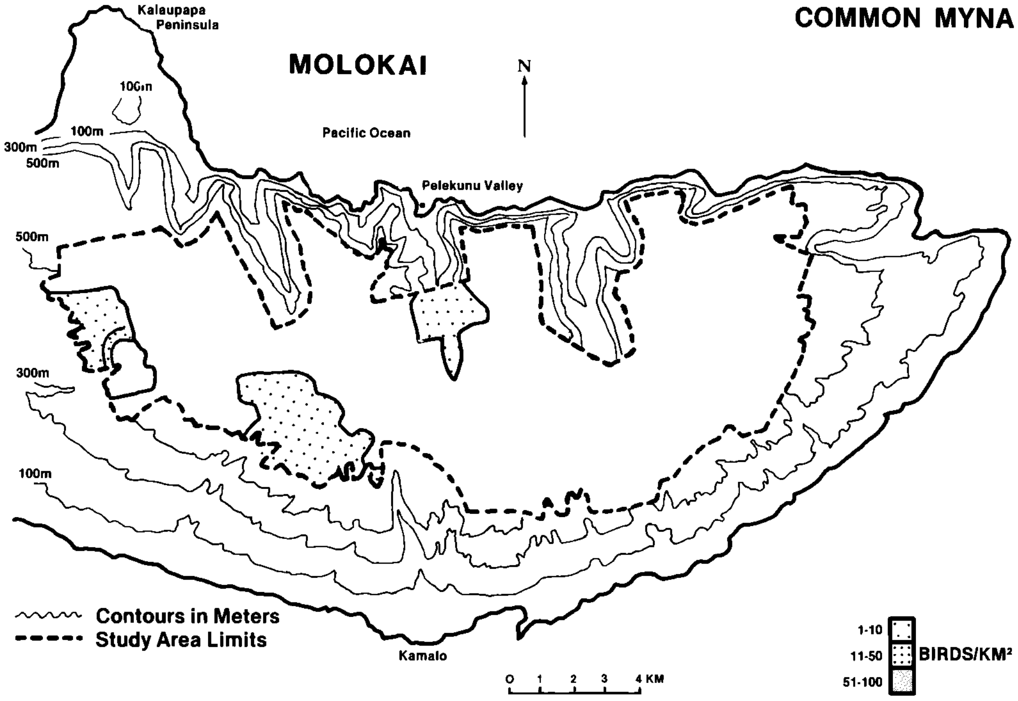


FIGURE 259. Distribution and abundance of the Common Myna in the Molokai study area.

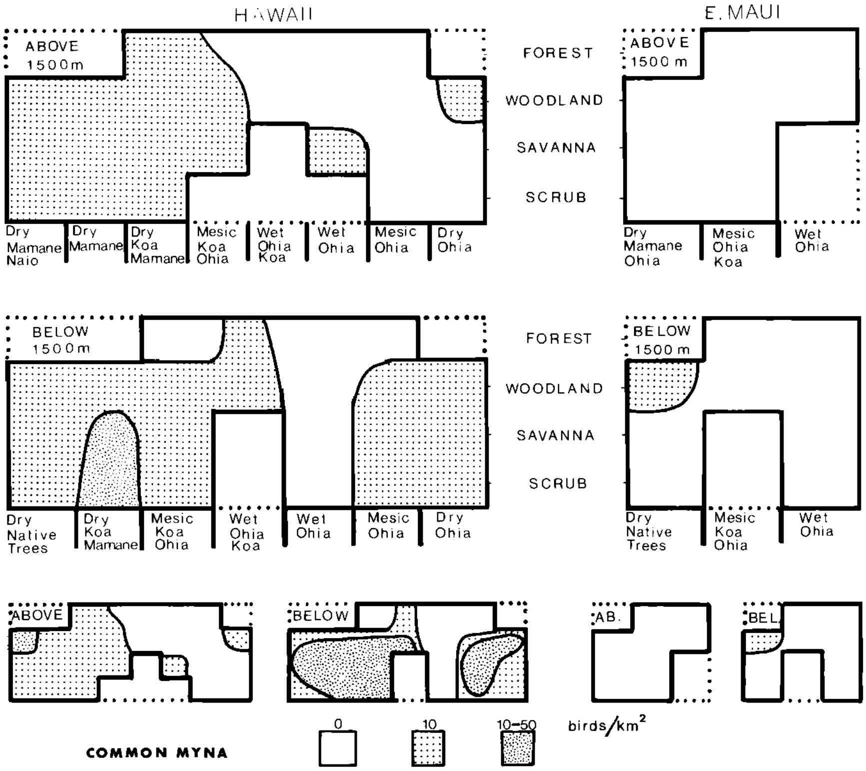


FIGURE 260. Habitat response graphs of the Common Myna. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

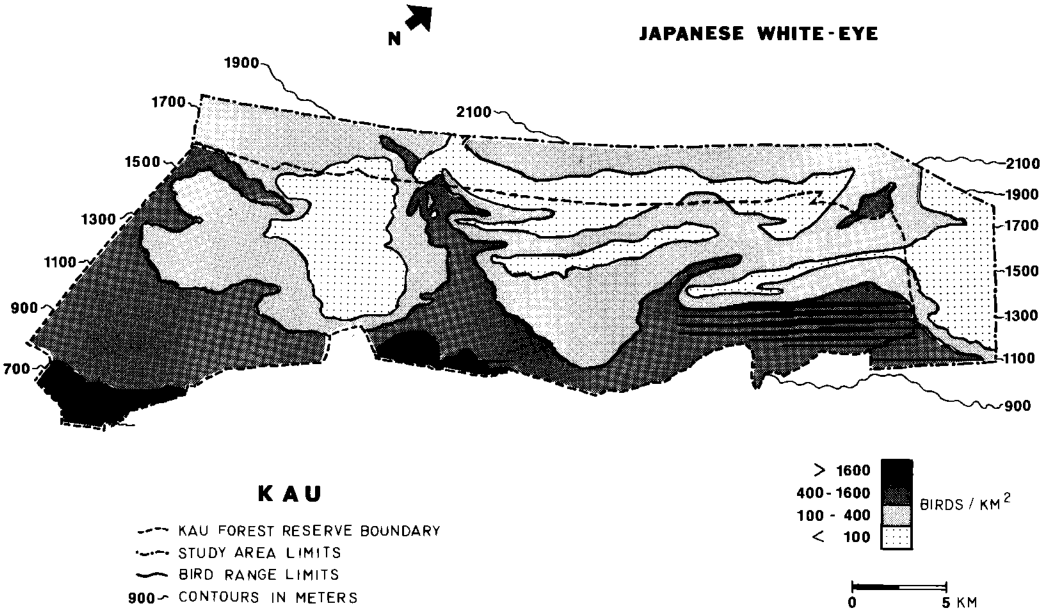


FIGURE 261. Distribution and abundance of the Japanese White-eye in the Kau study area.

TABLE 57
Regression Models for Habitat Response of the Common Myna, Saffron Finch, and Yellow-fronted Canary[a]

	Common Myna				Saffron Finch	Yellow-fronted Canary
	Hamakua	Puna	Kipukas	Kona	Kona	Kona
R^2	0.51*	0.26*	0.39*	0.23*	0.17*	0.13*
Moisture	−6.1*	−3.5*	−5.0*	−5.7*	−3.4*	−9.7*
Elevation	···	4.5*	−7.3*	···	−8.8*	−6.1*
$(\text{Elevation})^2$	···	−4.8*	6.7*	−9.1*	···	3.5*
Tree biomass	3.6*	5.8*	···	6.2*	···	···
$(\text{Tree biomass})^2$	···	···	···	···	−6.1*	−3.2
Crown cover	···	−5.1*	···	−6.7*	···	···
Canopy height	4.2*	···	2.7	···	4.2*	···
Koa	−2.2	X	3.7*	8.3*	···	···
Ohia	−8.5*	···	···	−4.6*	···	6.0*
Naio	X	X	···	−6.1*	−3.9*	···
Mamane	···	4.7*	···	···	4.4*	5.3*
Intro. trees	−6.4*	···	X	2.6	13.7*	5.7*
Shrub cover	−7.7*	···	−4.3*	−4.1*	−4.0*	···
Ground cover	−9.8*	···	4.8*	8.2*	4.2*	7.0*
Native shrubs	−2.7	2.9	−3.6*	···	···	−2.5
Intro. shrubs	···	···	−2.7	−2.7	−3.6*	−3.9*
Ground ferns	X	···	···	−10.8*	···	···
Matted ferns	−3.1	···	···	−2.5	···	···
Tree ferns	X	−3.0	X	···	···	···
Ieie	X	···	X	···	···	···
Passiflora	−3.0	X	X	···	···	3.3
Native herbs	X	···	···	···	···	···
Intro. herbs	X	···	···	···	···	−3.6*
Native grasses	···	···	−2.6	−2.3	···	···
Intro. grasses	···	···	−3.5*	−4.2*	···	···
Ohia flowers	−2.4	···	···	2.5	···	···
Olapa fruit	···	···	···	3.7*	···	···
Mamane flowers	X	X	···	X	X	X
Mamane fruit	X	X	X	X	X	X
Naio fruit	X	X	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

to ground cover mainly represents low numbers in high elevation pastures.

Although common and widespread in many communities, Common Mynas seldom enter the higher-elevation forests where native bird densities are greatest. This suggests support for the hypothesis that Common Mynas had little involvement in the drastic decline of native birds at the turn of the century (Caum 1933, Munro 1944, Berger 1981); however, mynas are cavity-nesters and during their tenure in the montane forests in the 1890s, they may have been competitors with the Hawaii Oo, Kauai Oo, and other native cavity-nesters that began to decline in numbers thereafter. Common Mynas may also have been sources and reservoirs for avian diseases in remote areas during that era.

Japanese White-eye
(*Zosterops japonicus*)

Japanese White-eyes, also known as Mejiro, are the most abundant land birds in the Hawaiian Islands. They were first introduced from Japan in 1929 to Oahu (Caum 1933), with an introduction to Hawaii in 1937 (Berger 1981). They occur from sea level to tree line, in very dry to very wet habitat on all the islands (Berger 1981). They are omnivores, feeding mostly on fruit, nectar, and insects from understory sites (Guest 1973, Conant 1975). In Hawaii Volcanoes National Park, Baldwin (1953) noted that the average frequency of this species on his plots increased from 23% in 1940–1944 to 50% in 1948–1949; by the 1970s, Conant (1975) and Banko

TABLE 58
DENSITY [MEAN (SE)] OF THE JAPANESE WHITE-EYE BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevation												
100–300 m	···	···	···	···	···	···	···	···	···	1386 (174)	···	···
300–500 m	···	603 (55)	719 (26)	···	526 (51)	···	174 (174)	187 (64)	···	1269 (120)	···	···
500–700 m	1608 (92)	716 (30)	671 (26)	···	344 (24)	···	1157 (156)	386 (51)	473 (107)	1147 (95)	741 (280)	···
700–900 m	1384 (124)	770 (22)	542 (23)	···	431 (17)	···	1289 (147)	389 (41)	658 (87)	820 (70)	491 (58)	···
900–1100 m	768 (45)	816 (24)	671 (31)	···	431 (16)	···	675 (72)	480 (34)	366 (58)	884 (66)	641 (103)	···
1100–1300 m	523 (43)	682 (24)	357 (58)	608 (72)	385 (16)	···	296 (39)	426 (34)	406 (52)	759 (52)	···	707 (38)
1300–1500 m	163 (16)	489 (22)	···	195 (33)	233 (9)	···	176 (31)	426 (34)	338 (61)	522 (140)	···	356 (33)
1500–1700 m	213 (24)	408 (24)	···	137 (17)	148 (7)	···	163 (77)	338 (24)	348 (61)	···	···	···
1700–1900 m	137 (20)	436 (36)	···	49 (8)	100 (8)	···	···	321 (31)	442 (79)	···	···	···
1900–2100 m	108 (23)	177 (29)	···	35 (9)	62 (7)	291 (48)	···	214 (26)	···	···	···	···
2100–2300 m	119 (119)	372 (90)	···	45 (16)	17 (3)	280 (42)	···	91 (14)	···	···	···	···
2300–2500 m	···	···	···	···	+ (+)	326 (41)	···	41 (12)	···	···	···	···
2500–2700 m	···	···	···	···	···	171 (28)	···	16 (10)	···	···	···	···
2700–2900 m	···	···	···	···	···	240 (53)	···	+ (+)	···	···	···	···
2900–3100 m	···	···	···	···	···	410 (200)	···	···	···	···	···	···
Habitat												
Ohia	469 (26)	555 (12)	654 (13)	56 (6)	259 (7)	···	459 (36)	360 (15)	473 (33)	816 (36)	···	547 (29)
Koa-ohia	319 (25)	774 (17)	···	388 (50)	344 (11)	···	···	555 (37)	···	···	···	···
Koa-mamane	···	341 (53)	···	124 (20)	186 (11)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	95 (18)	396 (27)	···	···	···	···	···	···
Mamane	···	···	···	···	116 (11)	115 (24)	···	59 (35)	···	···	···	···
Other natives	···	301 (31)	···	133 (32)	195 (22)	···	···	296 (26)	···	711 (87)	660 (172)	···
Intro. trees	···	523 (32)	···	···	398 (40)	···	809 (285)	352 (38)	845 (846)	1471 (96)	571 (70)	···
Treeless	107 (71)	101 (22)	138 (55)	20 (14)	25 (6)	···	···	99 (15)	292 (70)	477 (131)	400 (175)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

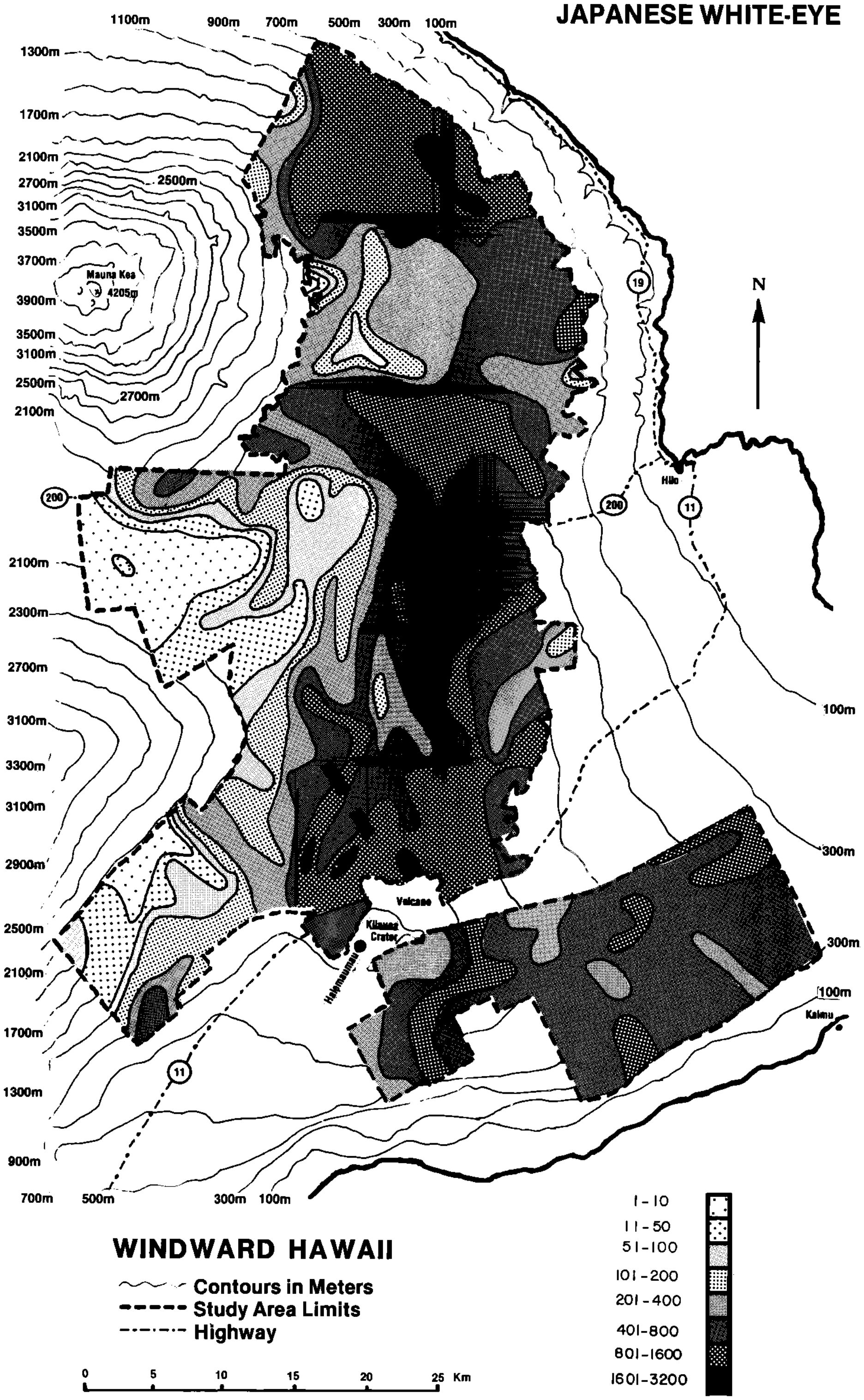


FIGURE 262. Distibution and abundance of the Japanese White-eye in the windward Hawaii study areas.

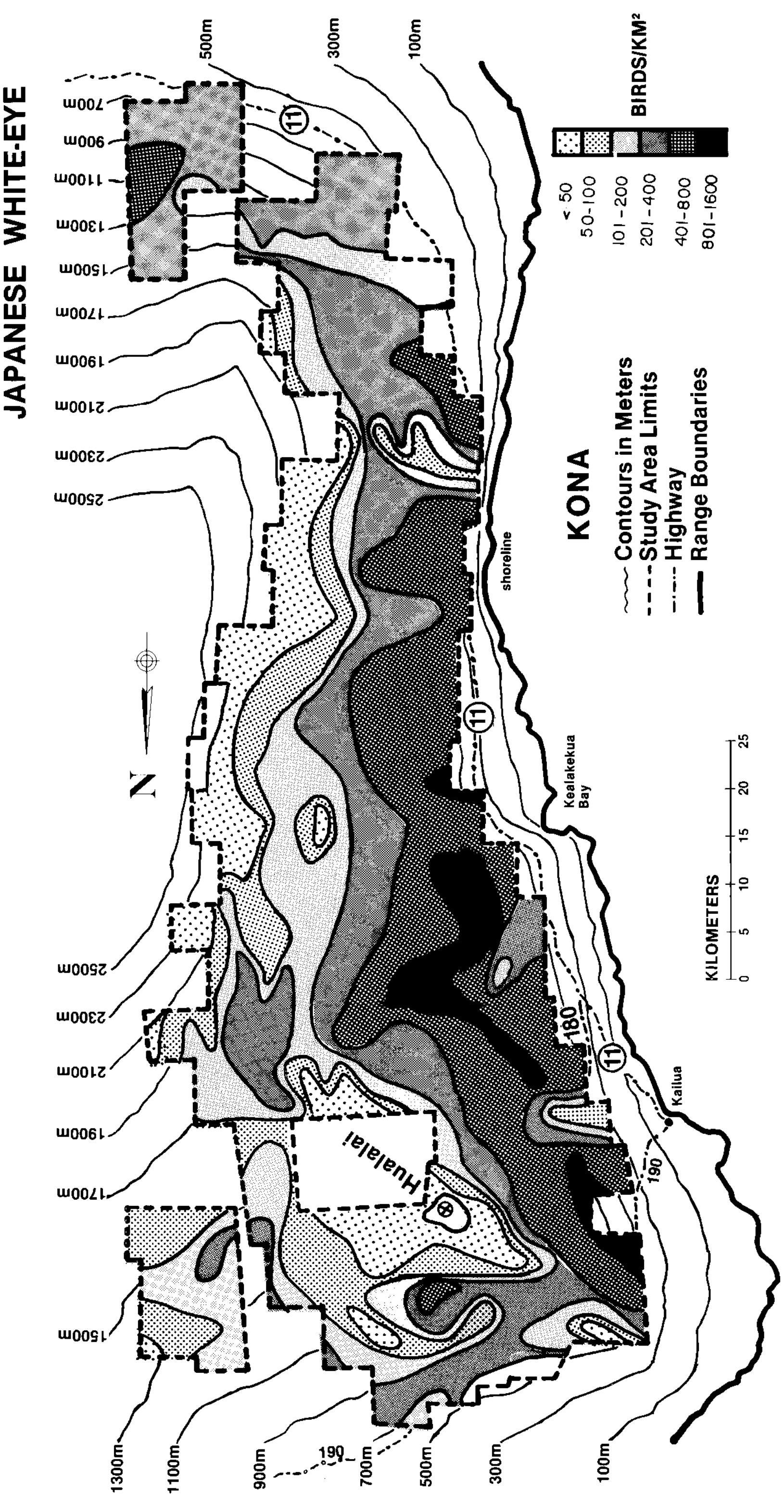


FIGURE 263. Distribution and abundance of the Japanese White-eye in the Kona study area.

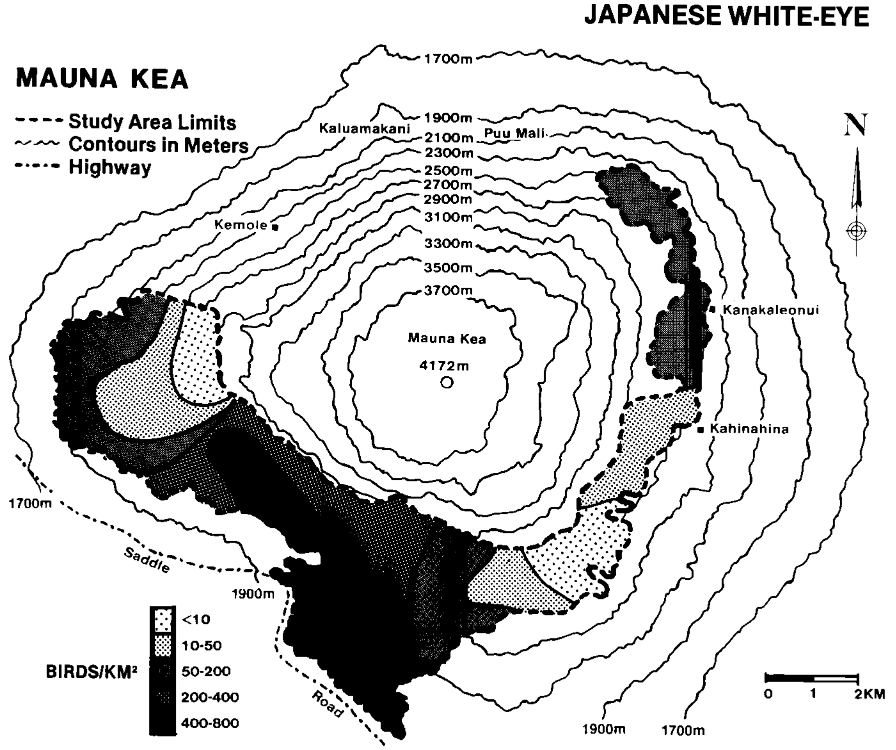


FIGURE 264. Distribution and abundance of the Japanese White-eye in the Mauna Kea study area.

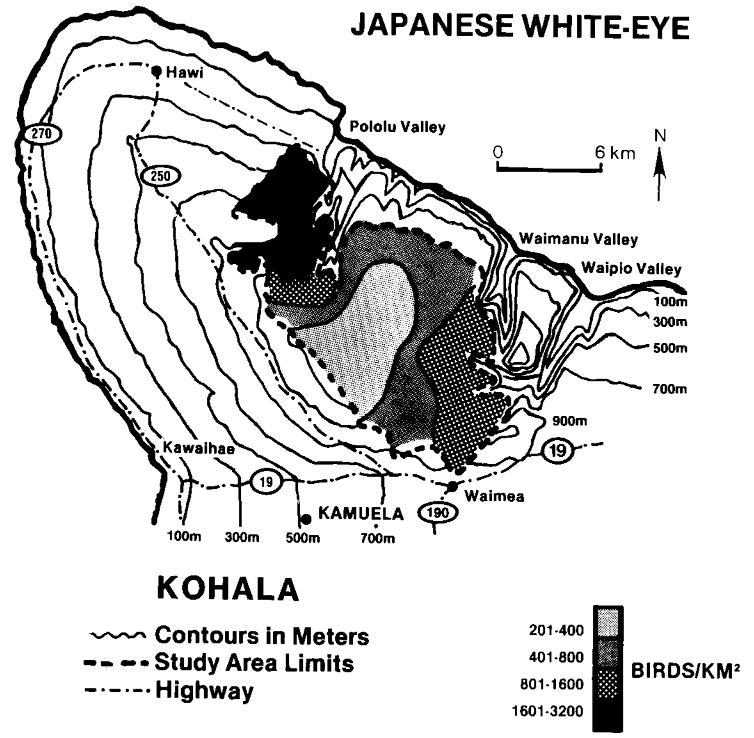


FIGURE 265. Distribution and abundance of the Japanese White-eye in the Kohala study area.

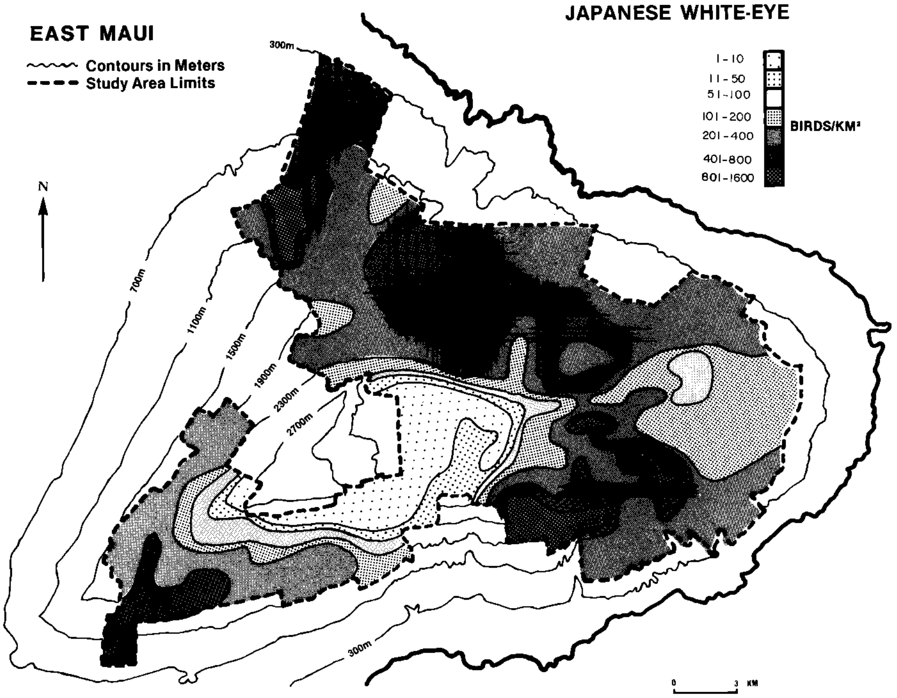


FIGURE 266. Distribution and abundance of the Japanese White-eye in the East Maui study area.

and Banko (1980) found frequencies approaching 100%.

Japanese White-eyes are ubiquitous in our study areas (Tables 33, 34, 58, Figs. 261–270). An estimated 1,300,000 ± 25,000 (95% CI) birds occupy the seven study areas on Hawaii, with the largest percentage (48%) in the Hamakua study area. Within our study areas we estimated 114,000 ± 7000 birds on East Maui, 19,000 ± 2000 on West Maui, 120,000 ± 9000 on Molokai, 11,000 ± 4000 on Lanai, and 15,000 ± 1400 on Kauai. For 1968–1973 Sincock et al. (1984) estimated 12,000 ± 6000 birds in our study area and a total of 256,000 ± 37,000 in native forests on Kauai.

Japanese White-eyes occur from sea level to 3100 m on Hawaii and 2700 m on Maui. Densities above 500 birds/km^2 occur below 1300 m on Hawaii and Kauai, and at all elevations sampled on Molokai and Lanai. Densities on Maui are lower than in other study areas, and reach 500 birds/km^2 only in one elevational stratum on West Maui. Distributional patterns on Hawaii, Maui, Molokai, and Kauai suggest the advance of lowland populations into montane forests. Japanese White-eyes tend to be more common along broad forest edges than within forest interiors, although habitat responses obscure this pattern somewhat. On Mauna Kea (Fig. 264) densities are lower in the middle of the mamane forest at Puu Laau than along the lower edges of the study area that border on pasture. In Kona (Fig. 263) densities are greater in the broken koa and mamane forest at Puu Lehua (25 km southeast of Kailua) than in the unbroken koa forests on north Hualalai (5 km north of the summit) and in central Kona (20 km east of Kealakekua Bay). Densities in Kohala (Fig. 265) are greater along the forests of the northwest margins than in the forest interior. Windward Hawaii densities (Fig. 262) are much greater in koa-ohia and ohia forests in the northernmost sixth of the Hamakua study area lying along rangeland than in the forest interior of the next sixth south. Densities on East Maui (Fig. 266) are much greater along the northwest edge of the wet forest than at the same elevation in the forest interior. Japanese White-eye are widespread and common on West Maui. On Molokai (Fig. 268) densities are lowest in the interior Olokui plateau that is well buffered from forest edges. On Lanai, Japanese White-eyes are abundant throughout the study area. On Kauai (Fig. 270) densities decline towards the interior of the Alakai Swamp. Forest edges seem to act as avenues along which Japanese White-eyes disperse toward more remote areas.

The habitat response graphs indicate well-es-

FIGURE 267. Distribution and abundance of the Japanese White-eye in the West Maui study area.

tablished populations with greatest densities in mesic koa-ohia forests (Fig. 271). Unlike most native and many introduced passerines, Japanese White-eyes maintain densities above 200 birds/km^2 in woodland, savanna, and even some scrub habitats. Rainforest interiors above 1500 m elevation have lower densities.

Compared with the regression models of other common species, Japanese White-eyes (Table 59) have fewer significant variables than the norm, indicating a habitat generalist. They are most common at low-elevation sites with some trees and introduced ground cover.

Japanese White-eyes occur across a broad range of moisture regimes and in most regression models show no response to moisture. Koa, naio,

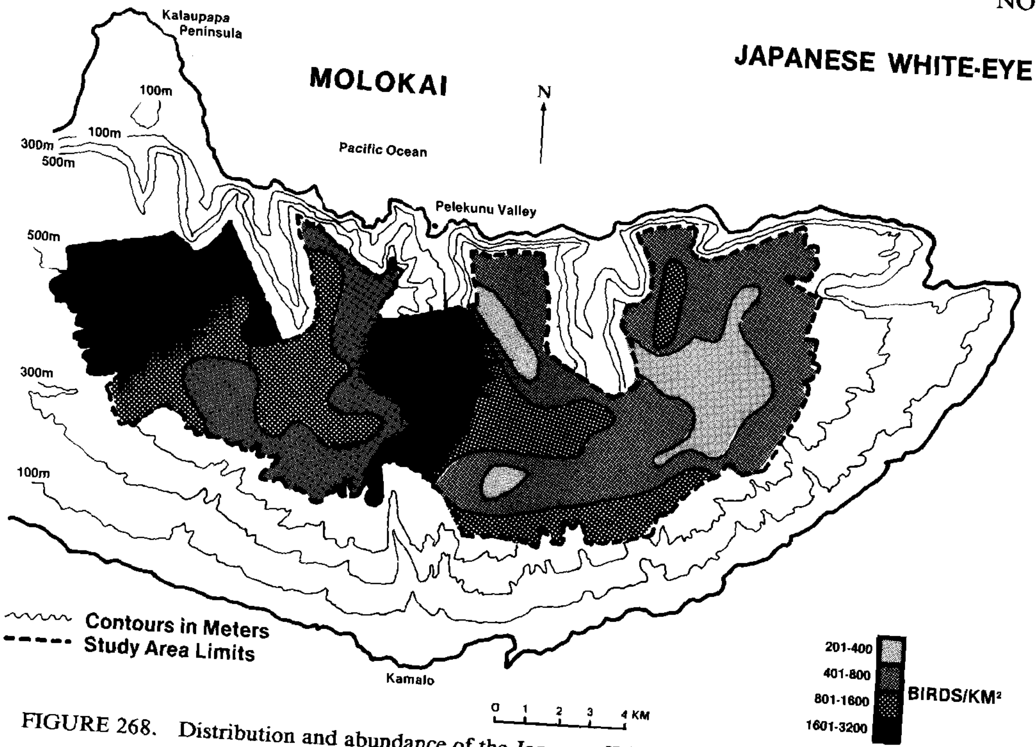


FIGURE 268. Distribution and abundance of the Japanese White-eye in the Molokai study area.

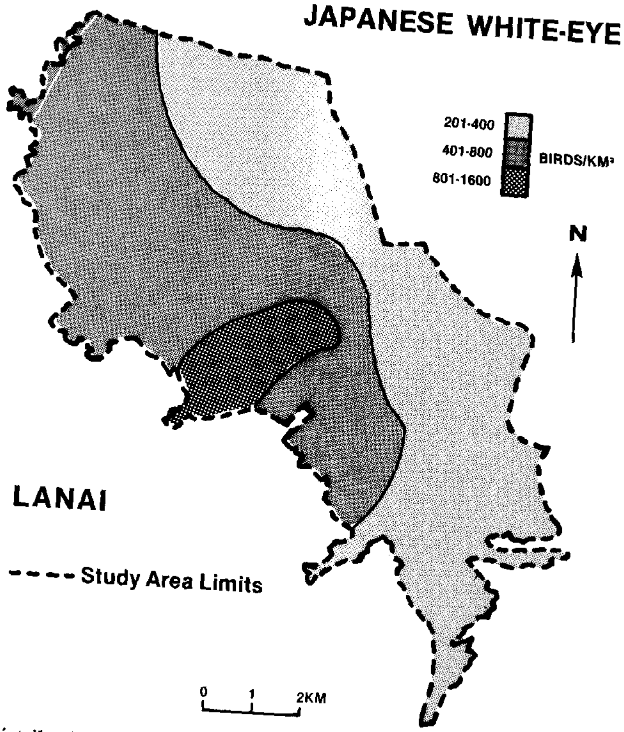


FIGURE 269. Distribution and abundance of the Japanese White-eye in the Lanai study area.

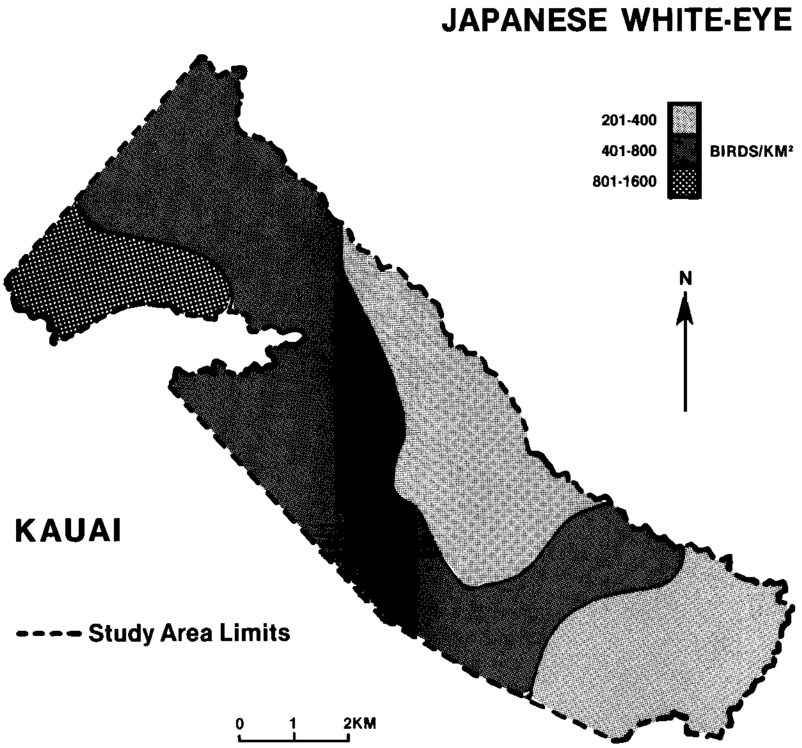


FIGURE 270. Distribution and abundance of the Japanese White-eye in the Kauai study area.

and mamane generate positive terms; ohia, usually negative terms. The two models with positive ohia terms are anomalous: Puna has a negative tree biomass correction term (here ohia is the main forest species and indexes forest development), and Molokai has a negative moisture term (indicating that ohia rainforest interiors are avoided). Responses to introduced trees, shrubs, and ferns are undistinguished.

Japanese White-eyes tend to occupy sites with introduced species dominating the ground cover. Response is positive to introduced herbs in four models and to passiflora and introduced grasses in one each. Native grasses have negative terms in two models. In the case of passiflora, birds are attracted to the nectar and fruit of banana poka (Warshauer et al. 1983). Introduced ground covers often indicate disturbance by grazing cattle or feral animals, and birds may enter forest interiors more rapidly via disturbed areas rather than through unbroken native forests. This is to be expected in view of the white-eye's recent introduction and its understory foraging zone, and was supported by anecdotal literature references. Dunmire (1962) noted that Japanese White-eye numbers "exploded" in Hawaii Volcanoes National Park in the 1940–1961 period, representing the arriving wave of a highly successful, booming population. Scott and Sincock (1977) noted very few Japanese White-eyes in the upper Koolau Forest Reserve on Maui in 1975, and the 1967 Kipahulu Valley expedition found few birds at upper elevations (Warner 1967). During our 1980 survey on Maui, however, fairly high densities were found in these areas, suggesting a recent (around 1975–1980), substantial increase in numbers on windward Maui above 1500 m elevation. Since the habitat and regional distribution of Japanese White-eyes have not yet stabilized, the response to disturbed ground cover may indicate the "route of least resistance" for range expansion. Our analysis of interspecific competition suggests that Japanese White-eyes have negative impacts on native passerines, particularly on species that feed on similar foods, such as Elepaio, Common Amakihi, and Hawaii Creeper (Mountainspring and Scott 1985). This species also appears to have a negative impact on other introduced birds in lowland areas (Moulton and Pimm 1983).

NORTHERN CARDINAL
(*Cardinalis cardinalis*)

Northern Cardinals were introduced to the Hawaiian Islands in 1929 (Caum 1933) and are well established in introduced and disturbed na-

TABLE 59

Regression Models for Habitat Response of the Japanese White-eye[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Lanai	Kauai
R^2	0.34*	0.25*	0.12*	0.44*	0.39*	0.24*	0.43*	0.31*	0.33*	0.18*	0.20*
Moisture	···	···	···	···	9.0*	X	X	···	−8.1*	···	X
Elevation	−6.3*	···	−5.5*	−7.2*	5.3*	···	···	4.3*	3.2	···	−5.9*
(Elevation)^2	4.1*	−19.5*	···	6.0*	−10.0*	···	−6.6*	−4.9*	−4.0*	···	···
Tree biomass	−2.2	···	···	···	6.4*	···	···	7.4*	9.9*	3.9*	···
(Tree biomass)^2	···	···	−2.9	···	−3.8*	···	···	−3.5*	···	···	···
Crown cover	···	···	···	···	···	···	···	···	···	···	···
Canopy height	···	4.3*	···	···	···	···	···	···	···	···	···
Koa	···	4.2*	X	···	···	X	X	···	X	X	X
Ohia	···	−5.5*	5.3*	···	−3.9*	X	···	−3.2	5.3*	···	X
Naio	X	X	X	2.3	3.5*	8.9*	X	X	X	X	X
Mamane	X	2.3	···	4.8*	···	···	X	···	X	X	X
Intro. trees	X	−2.8	···	X	···	X	···	···	···	···	X
Shrub cover	···	···	···	···	···	···	···	6.5*	···	···	···
Ground cover	···	3.4*	···	···	···	···	···	−3.6*	···	···	···
Native shrubs	···	···	···	···	−2.2	X	···	···	···	···	···
Intro. shrubs	X	···	···	···	···	X	···	···	···	···	···
Ground ferns	X	X	···	···	−2.8	X	···	···	−2.5	X	···
Matted ferns	···	···	···	···	−6.0*	X	···	···	···	···	···
Tree ferns	2.3	X	···	X	···	X	···	−2.3	···	X	···
Ieie	X	X	···	X	···	X	X	···	X	X	···
Passiflora	X	6.5*	X	X	···	X	···	···	X	X	X
Native herbs	X	X	···	···	···	X	···	4.4*	···	X	···
Intro. herbs	X	X	···	···	3.8*	2.8	4.6*	4.9*	···	X	···
Native grasses	···	−5.0*	···	···	−5.0*	···	···	···	···	X	···
Intro. grasses	···	···	···	···	···	···	3.5*	···	···	···	···
Ohia flowers	5.8*	10.6*	···	···	6.3*	X	···	2.4	···	···	···
Olapa fruit	···	4.3*	···	···	···	X	···	···	···	···	···
Mamane flowers	X	X	X	···	X	···	X	−3.6*	X	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

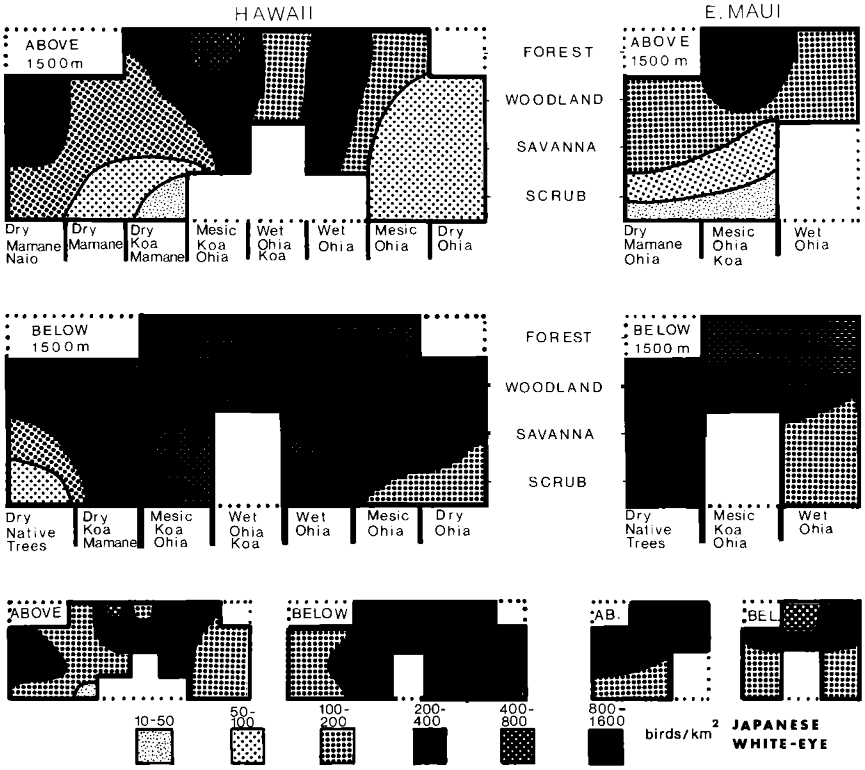


FIGURE 271. Habitat response graphs of the Japanese White-eye. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

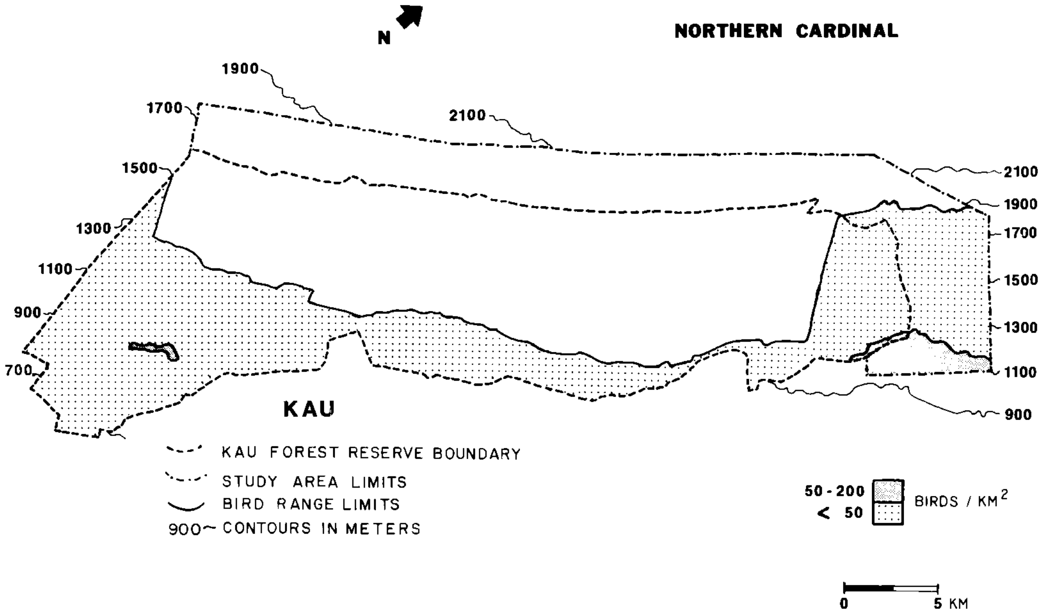


FIGURE 272. Distribution and abundance of the Northern Cardinal in the Kau study area.

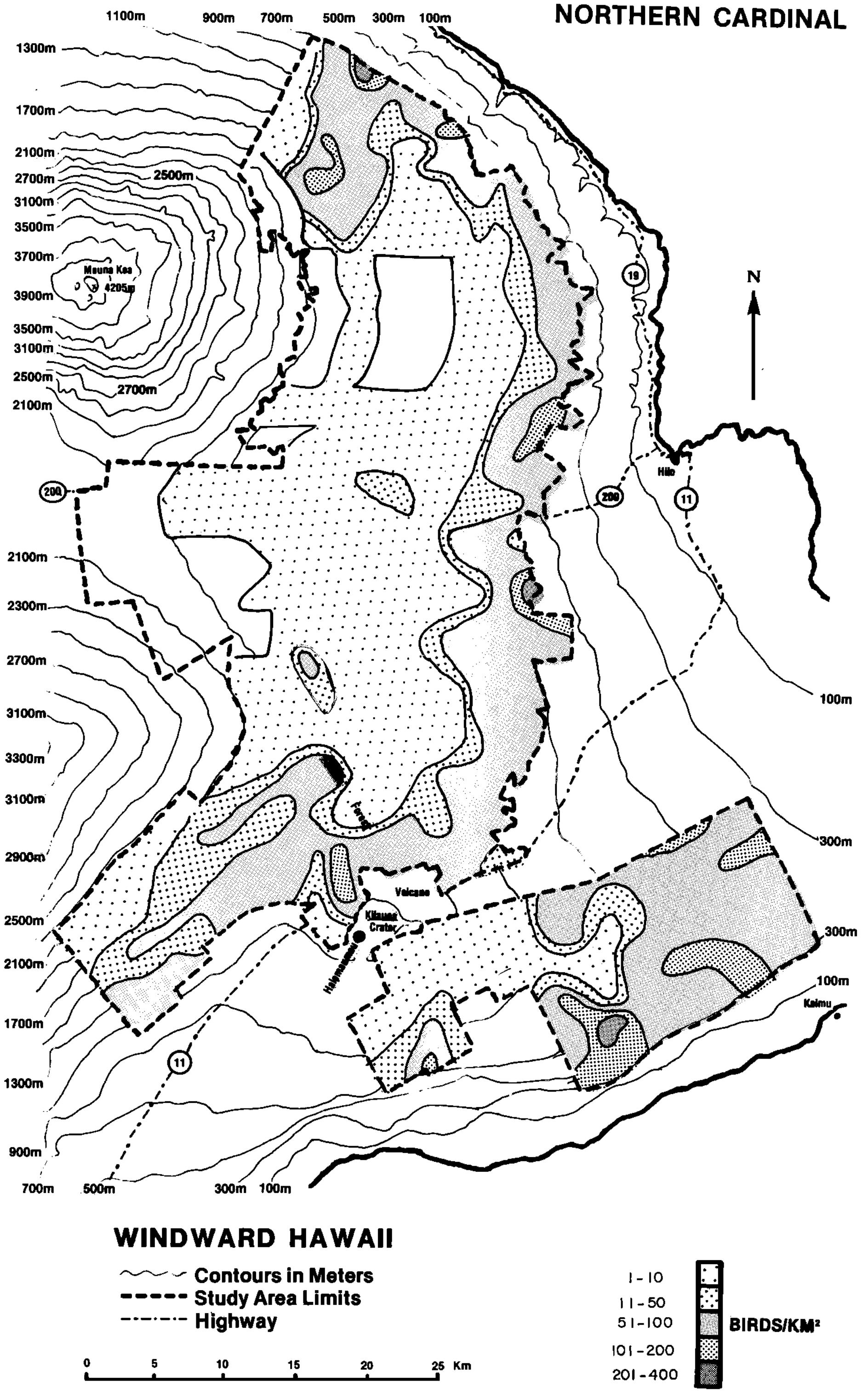


FIGURE 273. Distribution and abundance of the Northern Cardinal in the windward Hawaii study areas.

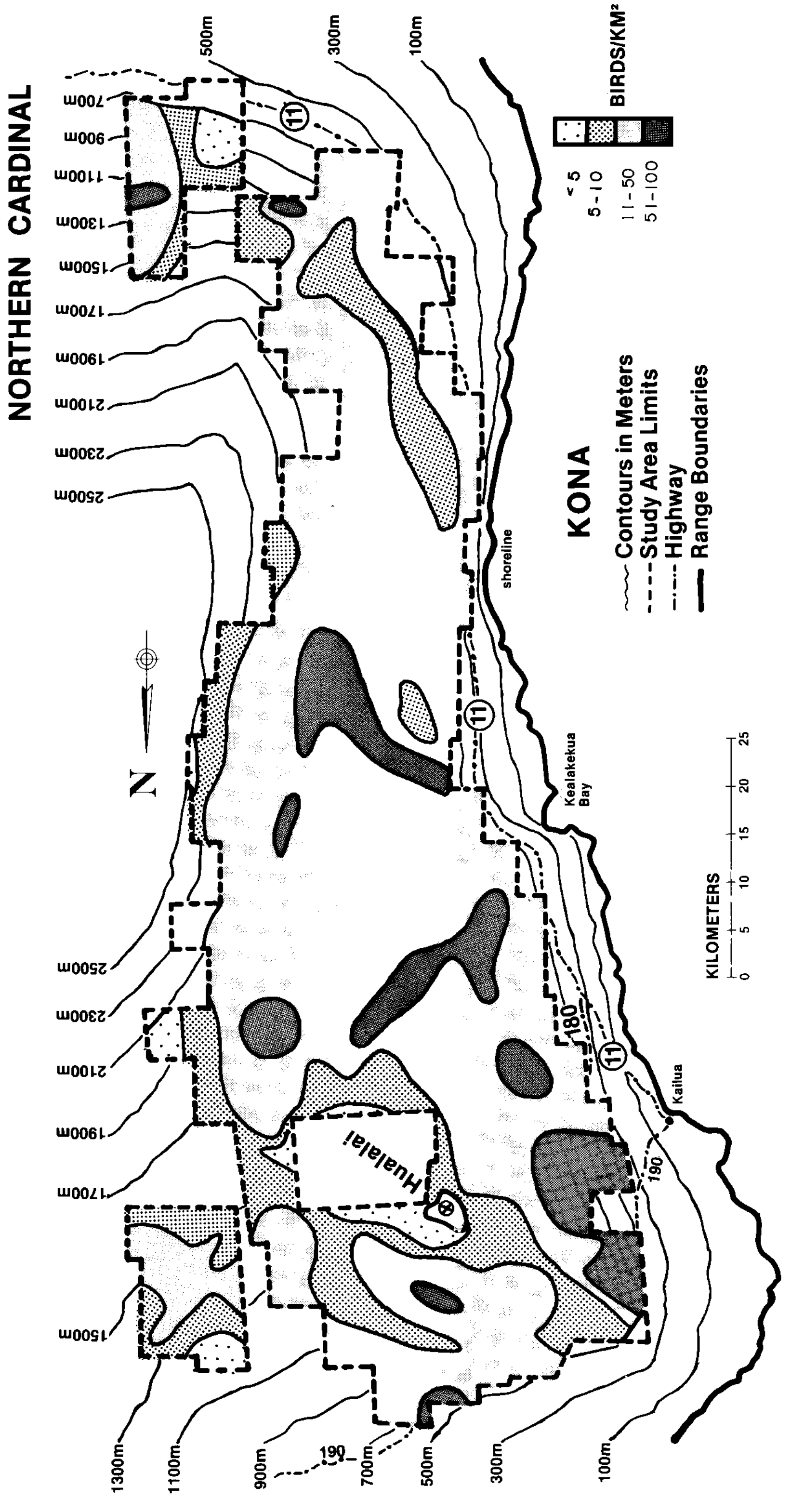


FIGURE 274. Distribution and abundance of the Northern Cardinal in the Kona study area.

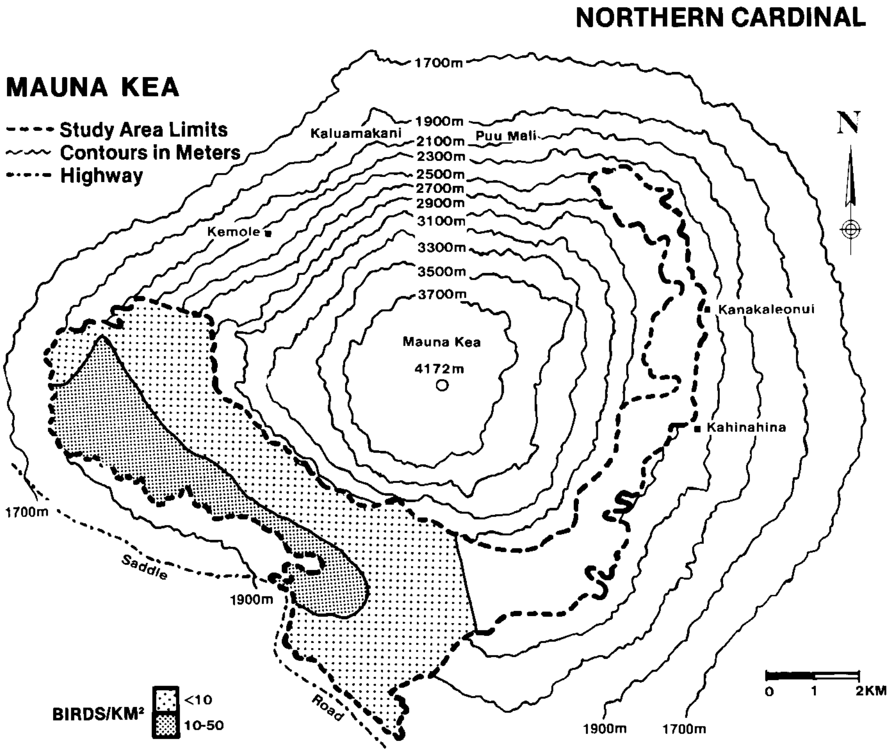


FIGURE 275. Distribution and abundance of the Northern Cardinal in the Mauna Kea study area.

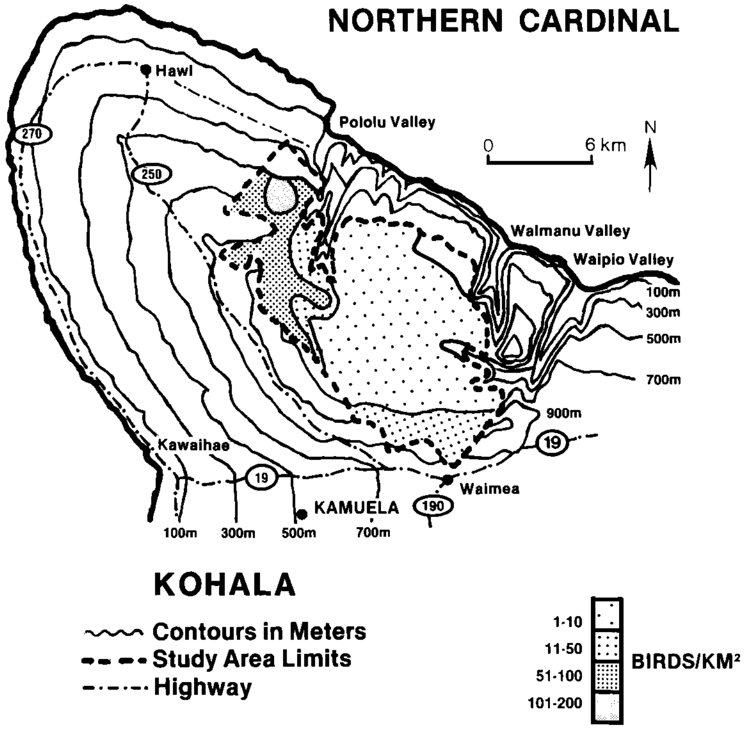


FIGURE 276. Distribution and abundance of the Northern Cardinal in the Kohala study area.

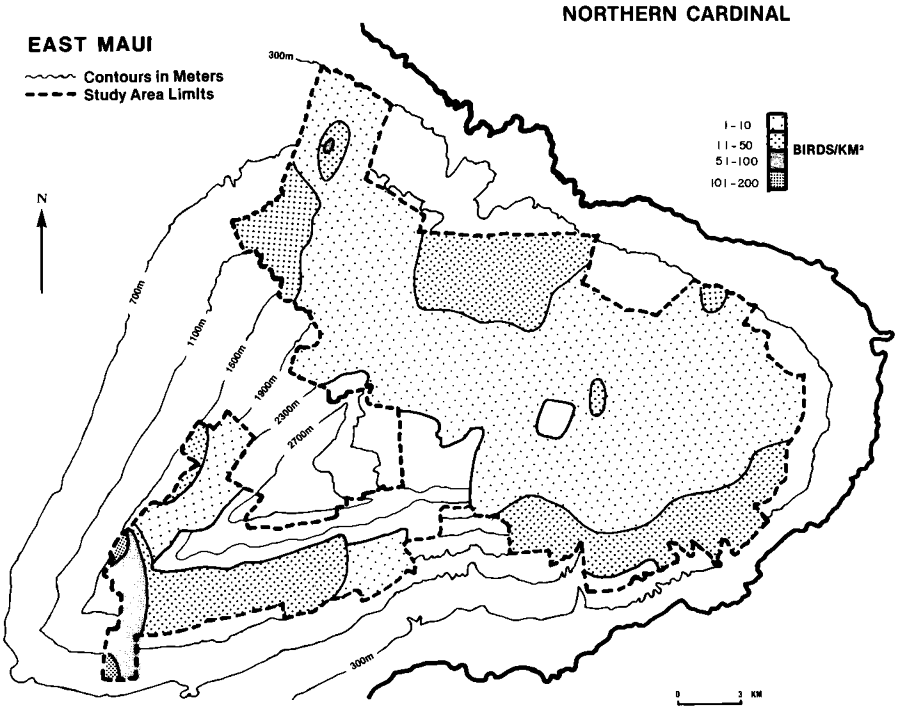


FIGURE 277. Distribution and abundance of the Northern Cardinal in the East Maui study area.

tive forests throughout the islands (Berger 1981). They are natives of North America that frequent hedges, thickets, and open woodlands and feed on seeds, fruits, and insects (Bent 1968). They are also known as Cardinals, Red Cardinals, American Cardinals, and Kentucky Cardinals, in contrast to the Red-crested or Brazilian Cardinal (*Paroaria coronata*) and the Yellow-billed Cardinal (*P. capitata*) of dry lowland areas, which were introduced from South America.

Northern Cardinals occur in all study areas (Figs. 272–281), but nowhere do they reach the densities of Japanese White-eyes (Tables 33, 34, 60). On Hawaii, 48,000 ± 1500 (95% CI) birds occur in the study areas. The distributional patterns for Hamakua and Kona indicate they inhabit forest edges and broken habitats rather than forest interiors. Their absence on the eastern Mauna Kea study area may be due to low food diversity, as this area has mamane trees but very little understory and no naio trees. Northern Cardinals feed on naio berries and may depend on them for water on Mauna Kea. Birds infiltrate most of the closed forest in the Puna study area. This is facilitated by three factors. First, the Puna forest has extensive edges with disturbed habitat along its north, east, and south boundaries. Second, an active volcanic rift zone runs through the middle of the forest and supports disturbed habitat. And third, widespread localized marijuana (*Cannabis sativa* and *indica*) cultivation by feral man throughout the forest interior creates numerous canopy openings and provides seeds for the diet. In Hawaii Volcanoes National Park, Northern Cardinals were very rare in the 1940s (Baldwin 1953), but by the 1970s they were abundant at Kipuka Puaulu (Conant 1975, Banko and Banko 1980) and widespread elsewhere.

An estimated 3000 ± 400 (95% CI) birds occupy our study areas on Maui, 1700 ± 300 on Molokai, 1100 ± 300 on Lanai, and 110 ± 40 on Kauai. On these islands, forests are less extensive geographically than on Hawaii, and Northern Cardinals penetrate deeper into the forest as a result of the increased edge. On Molokai the only areas lacking birds are the high interior forest plateaux and the devastated habitat of east Molokai. On Kauai, birds are rare in the Alakai Swamp, and showed no statistical difference from the 50 ± 55 birds estimated for that area by Sincock et al. (1984). Richardson and Bowles (1964) found birds sparse at the edges of the Alakai, as our survey suggested, and more common elsewhere. Sincock et al. (1984) estimated a total of 8500 ± 2900 birds for native forests on Kauai.

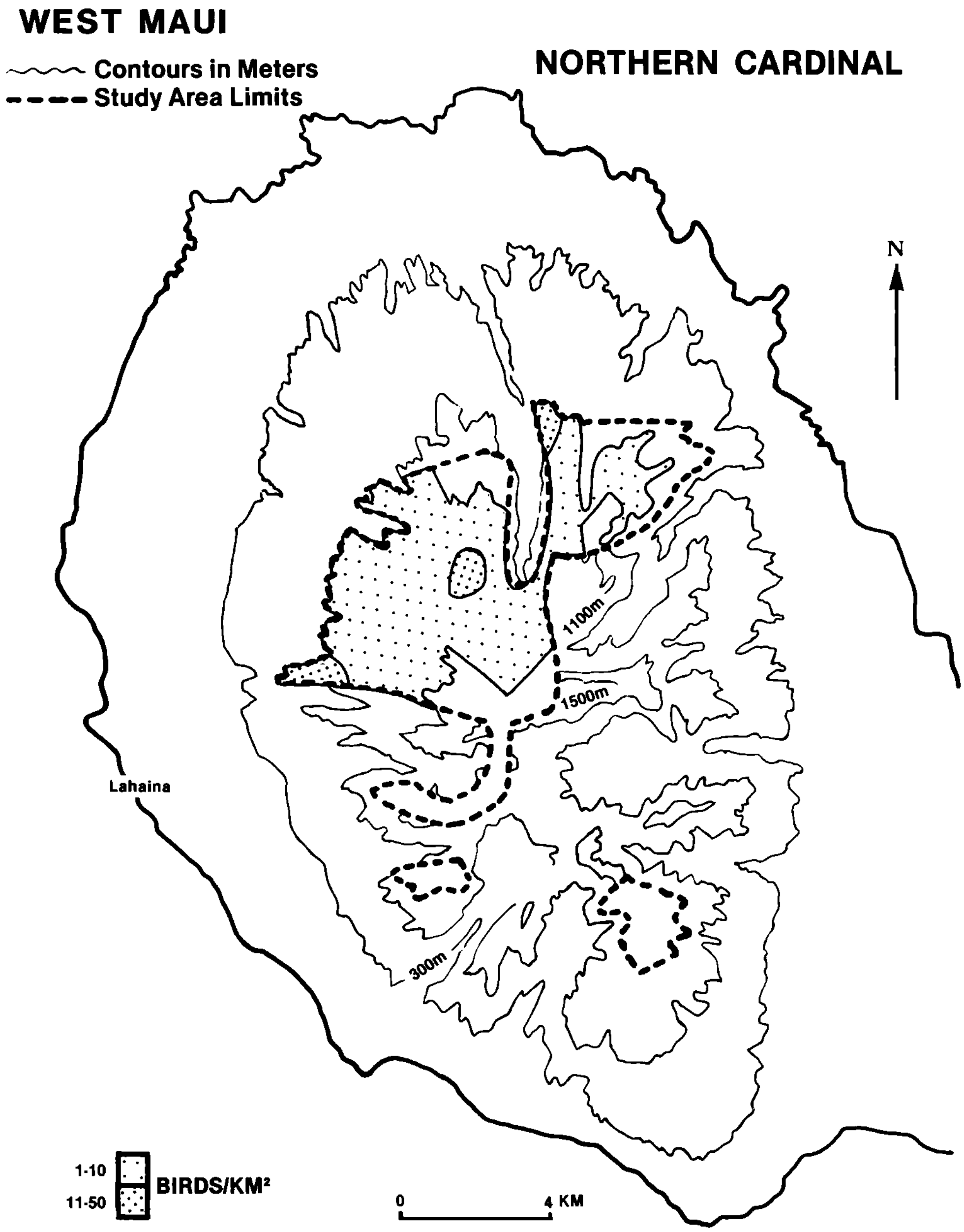


FIGURE 278. Distribution and abundance of the Northern Cardinal in the West Maui study area.

Northern Cardinals show remarkably uniform densities across all habitats, especially at lower elevations on Hawaii (Fig. 282). The regression models indicate that they are generally associated with dry, open forests at low elevations with understories of introduced shrubs and introduced grasses (Table 61). Although densities increase with tree biomass, crown cover, or canopy height in most models, the modest significance of these terms and the frequency of negative correction terms indicates avoidance of dense forest and preference for more open and brushy situations. Response is positive to introduced shrubs in four models, to passiflora in two, and to introduced grasses in five. Negative responses appear for matted ferns and usually native grasses. The low significance and inconsistency between models for other understory components sug-

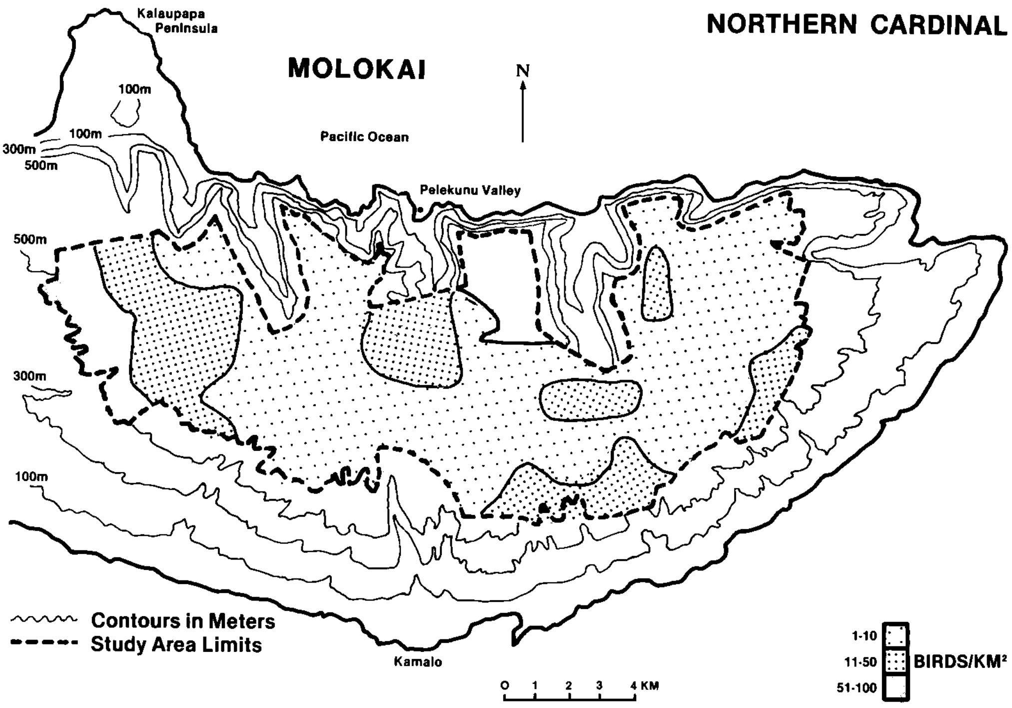


FIGURE 279. Distribution and abundance of the Northern Cardinal in the Molokai study area.

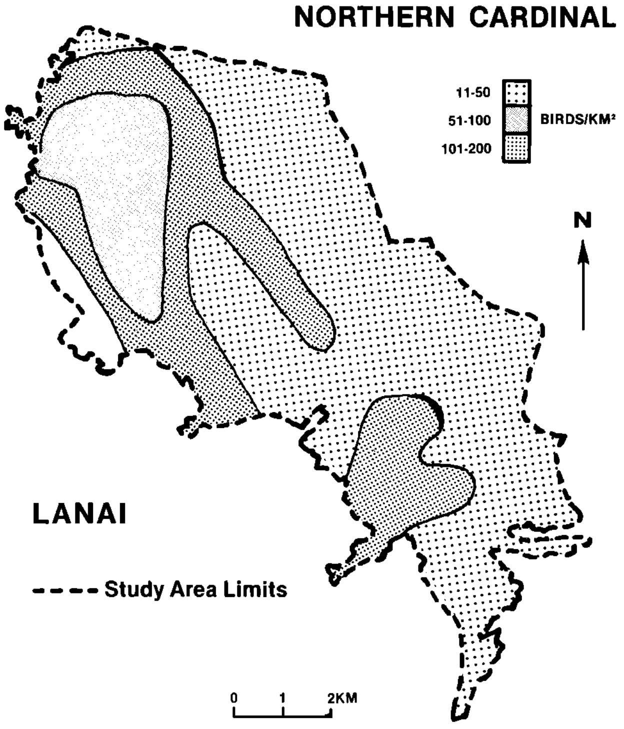


FIGURE 280. Distribution and abundance of the Northern Cardinal in the Lanai study area.

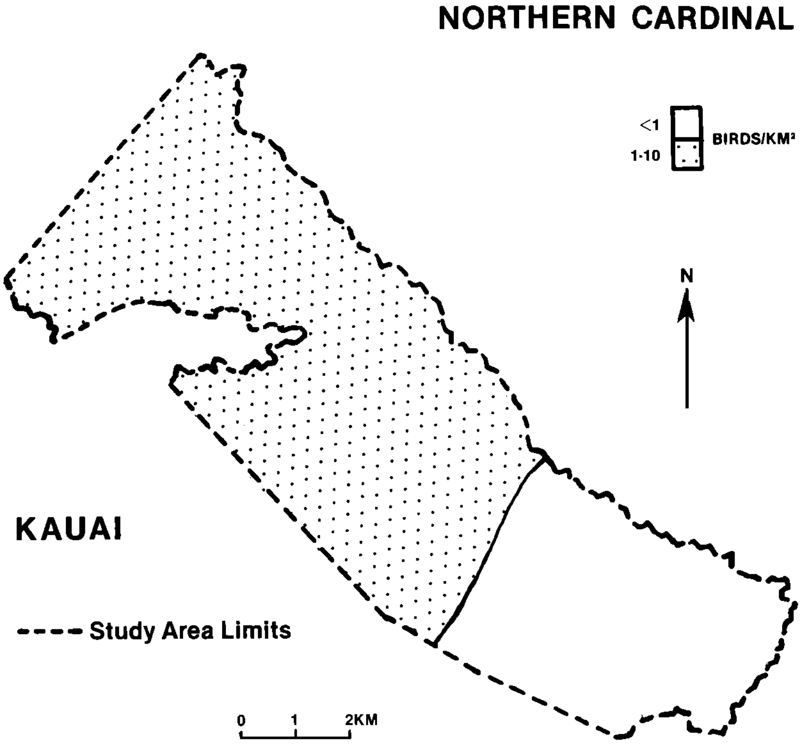


FIGURE 281. Distribution and abundance of the Northern Cardinal in the Kauai study area.

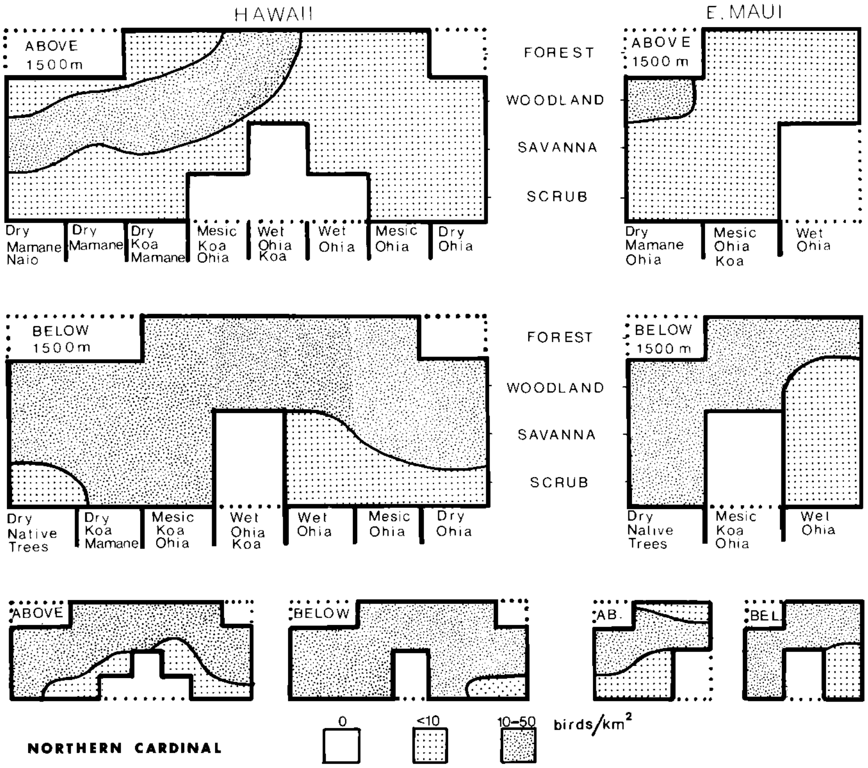


FIGURE 282. Habitat response graphs of the Northern Cardinal. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

TABLE 60
Density [mean (se)] of the Northern Cardinal by Elevation, Habitat, and Study Area[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevation												
100–300 m	...	...	...	...	...	...	...	...	...	29 (9)	...	...
300–500 m	...	28 (6)	37 (2)	...	25 (5)	...	...	11 (6)	...	25 (4)	...	...
500–700 m	13 (8)	25 (3)	42 (3)	...	30 (2)	...	44 (9)	15 (3)	20 (20)	26 (4)	104 (22)	...
700–900 m	8 (3)	18 (2)	12 (2)	...	32 (2)	...	16 (10)	11 (2)	8 (3)	9 (2)	38 (6)	...
900–1100 m	23 (4)	10 (1)	2 (1)	...	22 (1)	...	10 (3)	18 (3)	1 (1)	11 (3)	63 (11)	...
1100–1300 m	7 (2)	7 (1)	+ (+)	32 (6)	25 (1)	...	8 (2)	7 (1)	4 (2)	1 (+)	...	6 (1)
1300–1500 m	4 (2)	6 (1)	...	14 (1)	24 (1)	...	1 (1)	8 (2)	+ (+)	+ (+)	...	1 (1)
1500–1700 m	3 (2)	12 (2)	...	11 (2)	27 (1)	...	+ (+)	9 (2)	+ (+)	...	...	...
1700–1900 m	2 (2)	13 (2)	...	5 (1)	26 (1)	...	...	11 (2)	+ (+)	...	...	...
1900–2100 m	21 (21)	+ (+)	...	1 (1)	18 (1)	13 (4)	...	7 (2)	...	...	...	...
2100–2300 m	0	0	...	+ (+)	9 (1)	9 (3)	...	4 (2)	...	...	...	...
2300–2500 m	...	...	...	...	4 (1)	4 (2)	...	1 (1)	...	...	...	...
2500–2700 m	...	...	...	...	...	1 (1)	...	+ (+)	...	...	...	...
2700–2900 m	...	...	...	...	...	+ (+)	...	0	...	...	...	...
2900–3100 m	...	...	...	...	...	+ (+)	...	...	...	...	...	...
Habitat												
Ohia	11 (2)	5 (+)	24 (1)	4 (1)	20 (1)	...	8 (2)	6 (1)	4 (1)	6 (1)	...	4 (1)
Koa-ohia	16 (4)	20 (1)	...	23 (1)	32 (1)	...	...	15 (2)	...	...	...	...
Koa-mamane	...	+ (+)	...	10 (2)	38 (2)	...	...	...	...	...	...	...
Mamane-naio	...	...	...	...	16 (3)	6 (1)	...	...	...	...	...	...
Mamane	...	...	...	...	23 (2)	2 (1)	...	4 (4)	...	...	...	...
Other natives	...	6 (2)	...	19 (4)	22 (2)	...	...	19 (3)	...	7 (2)	46 (13)	...
Intro. trees	...	22 (2)	...	...	39 (4)	...	30 (11)	22 (3)	20 (20)	42 (5)	61 (7)	...
Treeless	0	+ (+)	+ (+)	1 (+)	5 (1)	...	...	7 (2)	+ (+)	5 (3)	31 (19)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

TABLE 61
Regression Models for Habitat Response of the Northern Cardinal[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Lanai	Kauai
R^2	0.27*	0.34*	0.53*	0.60*	0.23*	0.17*	0.31*	0.23*	0.41*	0.23*	0.10*
Moisture	−6.0*	−2.2	···	···	···	X	X	−9.3*	−12.4*	···	X
Elevation	···	−14.3*	···	−3.8*	···	···	−3.1	−5.2*	−12.0*	···	−3.9*
(Elevation)^2	−9.8*	···	−20.4*	2.9	···	···	···	···	···	···	···
Tree biomass	2.6	−3.5*	···	4.8*	···	···	···	···	9.0*	···	···
(Tree biomass)^2	···	···	···	···	···	···	···	···	···	4.4*	···
Crown cover	···	3.0	···	···	8.4*	···	···	9.6*	···	···	···
Canopy height	···	3.5*	···	···	···	···	3.5*	···	···	···	···
Koa	···	4.9*	X	···	7.1*	X	X	···	X	X	X
Ohia	···	···	···	−5.8*	···	X	−2.6	···	···	···	X
Naio	X	X	X	−4.0*	···	···	X	X	X	X	X
Mamane	X	···	···	···	5.0*	···	X	···	X	X	X
Intro. trees	X	···	···	X	···	X	···	5.5*	···	···	X
Shrub cover	···	4.2*	2.3	···	···	−3.7*	···	···	···	···	···
Ground cover	−5.0*	−3.9*	···	···	···	···	···	···	···	···	···
Native shrubs	···	···	···	···	···	X	−2.5	···	···	···	···
Intro. shrubs	X	14.2*	5.8*	···	9.8*	X	3.6*	···	···	···	···
Ground ferns	X	X	···	···	−5.0*	X	···	···	···	X	···
Matted ferns	···	−2.0	···	···	−4.9*	X	···	−2.8	···	···	···
Tree ferns	···	X	···	X	···	X	···	···	···	X	···
Ieie	X	X	···	X	···	X	X	···	X	X	···
Passiflora	X	15.6*	X	X	2.8	X	···	···	X	X	X
Native herbs	X	X	···	···	···	X	···	−2.2	···	X	···
Intro. herbs	X	X	−3.2	3.1	4.3*	···	···	···	···	X	···
Native grasses	···	3.7*	−4.4*	···	−4.5*	···	···	−2.1	···	X	···
Intro. grasses	5.4*	4.0*	···	4.5*	7.8*	···	···	2.3	···	···	···
Ohia flowers	···	5.5*	···	···	−4.8*	X	···	···	···	···	···
Olapa fruit	···	···	···	···	3.1	X	···	···	···	···	···
Mamane flowers	X	X	X	···	X	···	X	···	X	X	X
Mamane fruit	X	X	X	X	X	2.2	X	X	X	X	X
Naio fruit	X	X	X	X	X	5.4*	X	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

TABLE 62

DENSITY [MEAN (SE)] OF THE SAFFRON FINCH, YELLOW-FRONTED CANARY, RED-CHEEKED CORDONBLEU, LAVENDER WAXBILL, AND WARBLING SILVERBILL BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Saffron Finch	Yellow-fronted Canary	Red-cheeked Cordonbleu	Lavender Waxbill	Warbling Silverbill	
	Kona	Kona	Kona	Kona	Kona	Mauna Kea
Elevation						
100–300 m	···	···	···	···	···	···
300–500 m	0	0	0	0	0	···
500–700 m	27 (9)	121 (41)	2 (2)	3 (3)	51 (15)	···
700–900 m	58 (11)	131 (30)	6 (6)	15 (9)	12 (7)	···
900–1100 m	44 (11)	44 (11)	0	31 (31)	+ (+)	···
1100–1300 m	16 (5)	23 (8)	+ (+)	+ (+)	+ (+)	···
1300–1500 m	2 (1)	3 (2)	0	0	0	···
1500–1700 m	+ (+)	+ (+)	0	0	0	···
1700–1900 m	0	+ (+)	0	0	0	···
1900–2100 m	0	0	0	0	0	+ (+)
2100–2300 m	0	0	0	0	0	+ (+)
2300–2500 m	0	0	0	0	0	14 (14)
2500–2700 m	···	···	···	···	···	+ (+)
2700–2900 m	···	···	···	···	···	+ (+)
2900–3100 m	···	···	···	···	···	+ (+)
Habitat						
Ohia	22 (4)	84 (16)	4 (4)	6 (4)	15 (3)	···
Koa-ohia	14 (7)	48 (16)	0	0	2 (1)	···
Koa-mamane	0	0	0	0	0	···
Mamane-naio	+ (+)	+ (+)	0	0	15 (15)	7 (7)
Mamane	30 (7)	5 (2)	0	0	7 (4)	+ (+)
Other natives	13 (6)	12 (4)	2 (2)	3 (3)	47 (12)	···
Intro. trees	89 (25)	30 (15)	+ (+)	103 (51)	38 (26)	···
Treeless	+ (+)	+ (+)	+ (+)	+ (+)	+ (+)	···

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

gests a minor role in determining habitat response.

Northern Cardinals occupy a diversity of habitats in North America and the Hawaiian Islands. On Kauai, Richardson and Bowles (1964) found them from arid scrub near sea level to wet montane forest in the Alakai Swamp. In eastern North America they are usually found in dense thickets and tangles near open areas, field edges, woodland borders, and swamps (Pough 1949), and in Arizona, in tall dense brush (Phillips et al. 1964). Dow (1968) found that Northern Cardinals are associated with dense shrubs and vines in Tennessee. The habitat response patterns we found in this study are in remarkable agreement, particularly the preferences for introduced shrub and passiflora understories that form dense tangled thickets.

The bill of this species is well adapted to feeding on large seeds. To a certain degree cardinals occupy the seed-eating niche left vacant by extinct finch-billed honeycreepers. Northern Cardinals regularly feed on koa, naio, and mamane seeds; at one site near Puu Lehua in Kona, 40–60% of the nearly mature sandalwood fruit had been cut in half and the seed removed by cardinals (F. R. Warshauer, pers. observ.). In an extensive study of the food habits of this species, McAtee (1908) found that they feed primarily on almost all kinds of wild fruit and weed seed. The occurrence of birds in introduced grasslands and introduced shrub understories (often dominated by two prolific fruit-bearers, guava and Christmas-berry), probably reflects high food levels. Birds may have low densities in native grasslands because the seeds of the dominant native grass *D. australis* are too tiny to serve as a staple in the diet. On Mauna Kea, food resources may explain the association with mamane pods and naio berries in the regression model.

SAFFRON FINCH (*Sicalis flaveola*)

Saffron Finches were first recorded in the Hawaiian Islands on Oahu in 1965 and on Hawaii in 1966 (Berger 1981). These emberizine finches are native to South America.

In our study areas this species occurs only in the Puu Waawaa area of leeward Hawaii, where 2400 ± 600 (95% CI) birds occupy eight general habitat types (Tables 33, 62, Fig. 283). The range

TABLE 63
DENSITY [MEAN (SE)] OF THE HOUSE FINCH BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevation												
100–300 m	...	...	...	...	...	...	...	...	...	119 (45)	...	...
300–500 m	...	19 (19)	10 (3)	...	45 (18)	...	10 (10)	0	...	97 (29)	...	...
500–700 m	+ (+)	16 (8)	6 (2)	...	63 (7)	...	+ (+)	0	13 (8)	72 (13)	90 (29)	...
700–900 m	11 (11)	0	33 (8)	...	75 (8)	...	19 (8)	19 (11)	5 (3)	30 (11)	4 (3)	...
900–1100 m	0	0	120 (13)	...	53 (5)	...	+ (+)	67 (18)	1 (1)	38 (7)	+ (+)	...
1100–1300 m	0	34 (11)	150 (36)	94 (15)	71 (4)	...	1 (1)	175 (29)	5 (3)	14 (4)	...	1 (1)
1300–1500 m	0	68 (11)	...	51 (7)	84 (4)	...	3 (2)	96 (29)	+ (+)	5 (5)	...	+ (+)
1500–1700 m	0	40 (7)	...	41 (6)	59 (4)	...	8 (8)	118 (37)	+ (+)	...	...	...
1700–1900 m	+ (+)	99 (15)	...	27 (7)	35 (3)	...	...	74 (18)	+ (+)	...	...	...
1900–2100 m	+ (+)	102 (30)	...	41 (5)	24 (3)	246 (32)	...	33 (9)	...	...	...	...
2100–2300 m	0	157 (54)	...	1 (1)	15 (2)	140 (22)	...	19 (6)	...	...	...	...
2300–2500 m	...	...	...	...	7 (2)	158 (16)	...	+ (+)	...	...	...	...
2500–2700 m	...	...	...	...	...	102 (17)	...	+ (+)	...	...	...	...
2700–2900 m	...	...	...	...	...	200 (48)	...	0	...	...	...	...
2900–3100 m	...	...	...	...	...	611 (362)	...	...	...	...	...	...
Habitat												
Ohia	3 (3)	15 (3)	30 (3)	30 (3)	60 (2)	...	4 (1)	1 (1)	4 (2)	26 (5)	...	1 (1)
Koa-ohia	0	73 (9)	...	83 (12)	52 (4)	...	...	103 (34)	...	...	...	...
Koa-mamane	...	118 (14)	...	30 (5)	54 (4)	...	...	...	...	...	...	...
Mamane-naio	...	...	...	...	61 (11)	217 (29)	...	...	...	...	...	...
Mamane	...	...	...	...	74 (7)	135 (21)	...	11 (11)	...	...	...	...
Other natives	...	208 (30)	...	70 (11)	139 (10)	...	...	77 (8)	...	55 (10)	8 (8)	...
Intro. trees	...	142 (38)	...	...	75 (15)	...	15 (15)	209 (33)	27 (27)	112 (19)	12 (6)	...
Treeless	0	+ (+)	+ (+)	4 (4)	12 (4)	...	...	4 (1)	9 (9)	13 (8)	42 (34)	+ (+)

[a] Densities are given in birds/km^2; + indicates stratum was in the species range but density <0.5 birds/km^2; 0 indicates stratum was outside range but was sampled; ... indicates stratum was not sampled in study area.

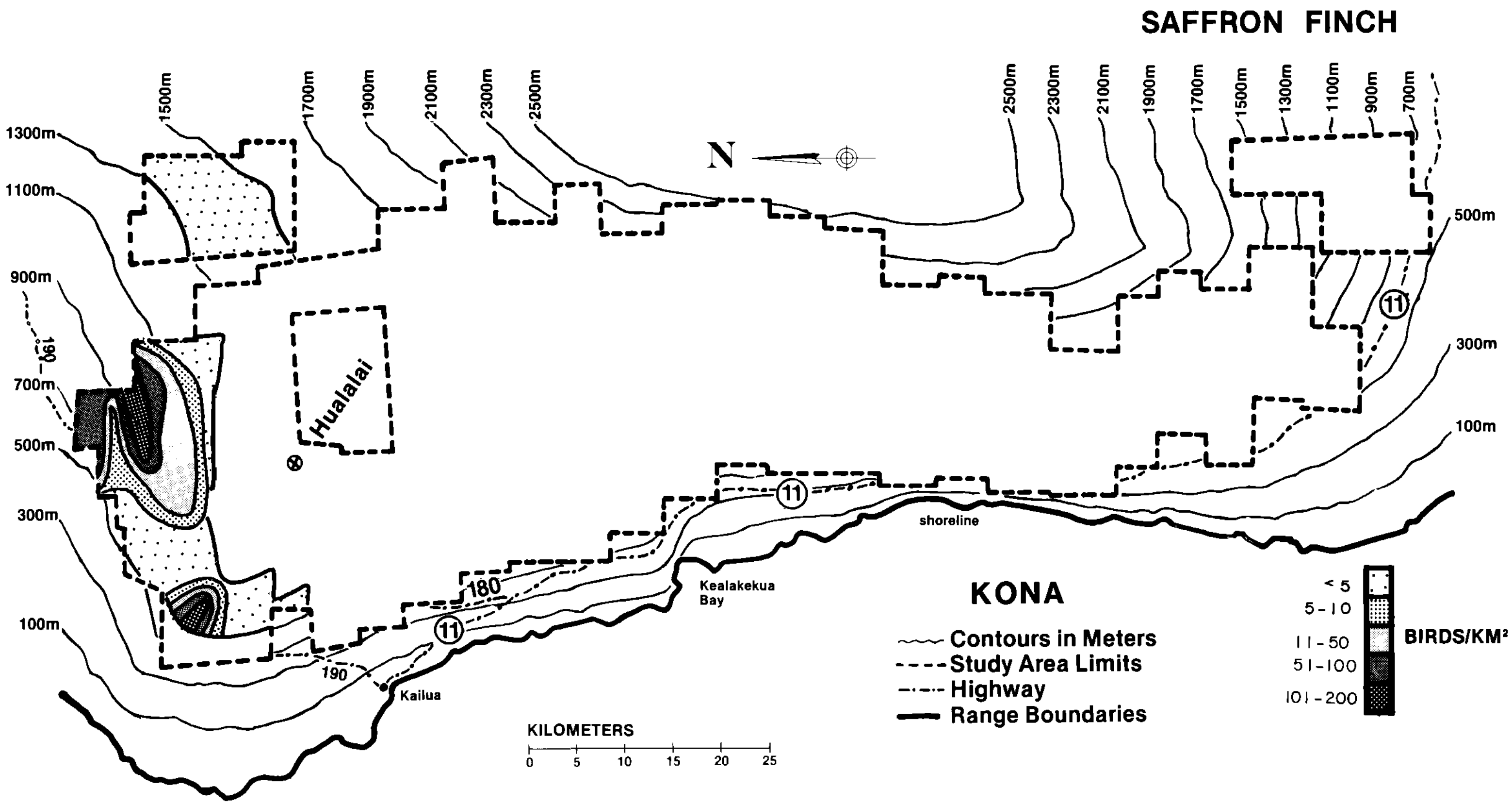


FIGURE 283. Distribution and abundance of the Saffron Finch in the Kona study area.

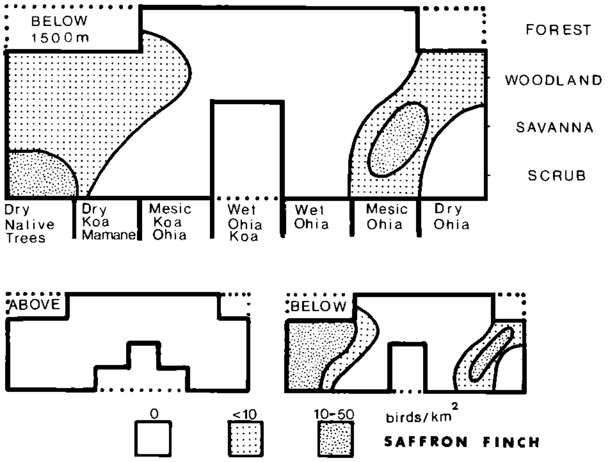


FIGURE 284. Habitat response graphs of the Saffron Finch. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

was fairly limited in 1978 but since then has expanded along the Kona coast (J. M. Scott, S. Mountainspring, pers. observ.).

Saffron Finches occur in dry to mesic areas at lower elevations with scattered trees and little shrub cover (Table 57, Fig. 284). Highest densities occur in habitats dominated by introduced trees, but most of the population is in ohia. The negative quadratic term for tree biomass in the regression model indicates fairly high densities over a range of very scattered to very open habitats. Birds tend to be more common in mamane than in naio.

In South America, Saffron Finches inhabit gardens, shrublands, palm groves, savanna-like grasslands, open woodland, and second growth forests (Meyer de Schauensee 1976, Meyer de Schauensee and Phelps 1978). Their habitat response in Kona is similar, and they occur in coconut groves at Hapuna Bay and Kailua Bay along the Kona coast (S. Mountainspring, pers. observ.).

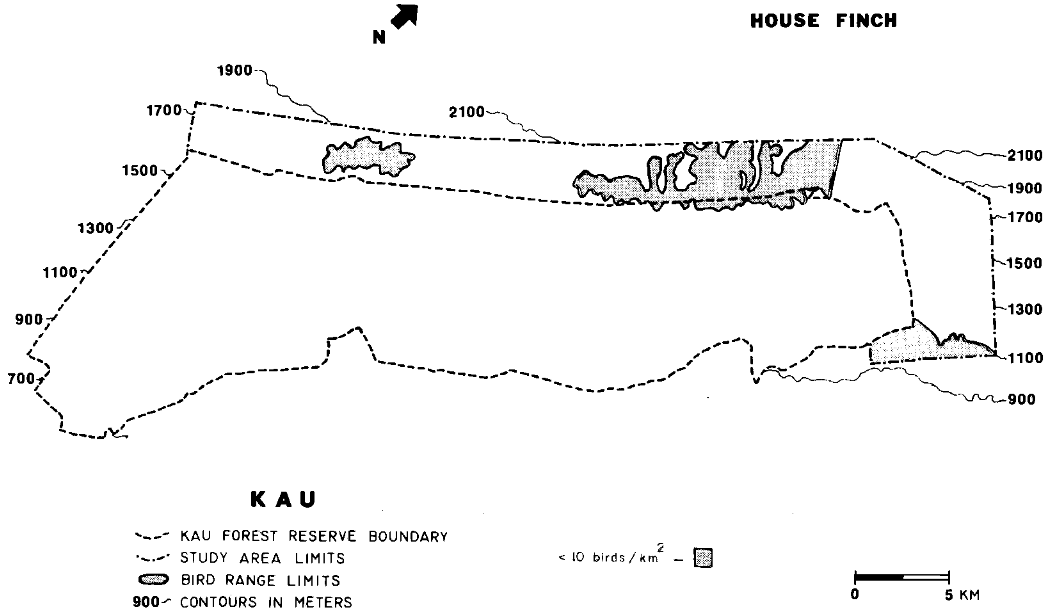


FIGURE 285. Distribution and abundance of the House Finch in the Kau study area.

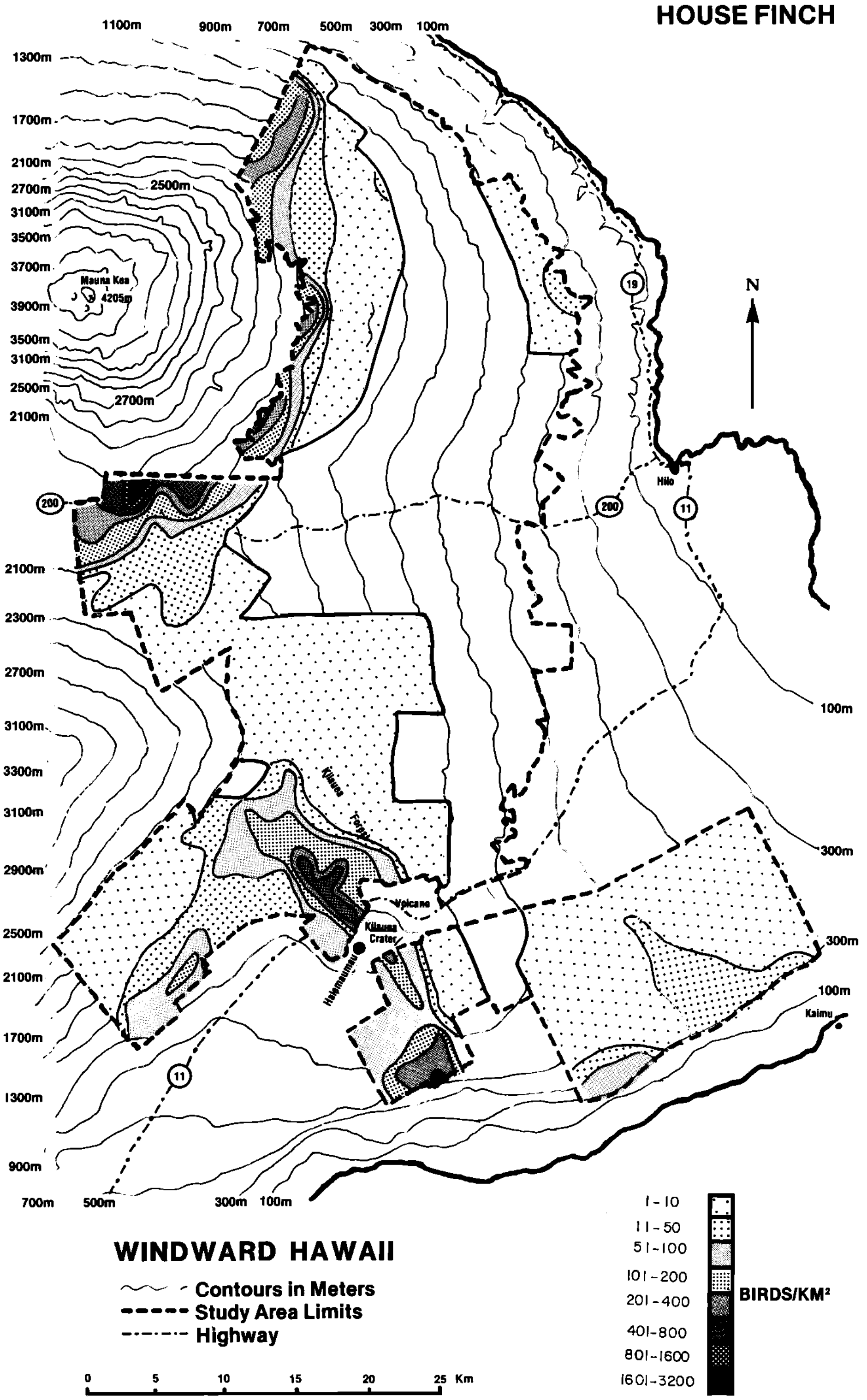


FIGURE 286. Distribution and abundance of the House Finch in the windward Hawaii study areas.

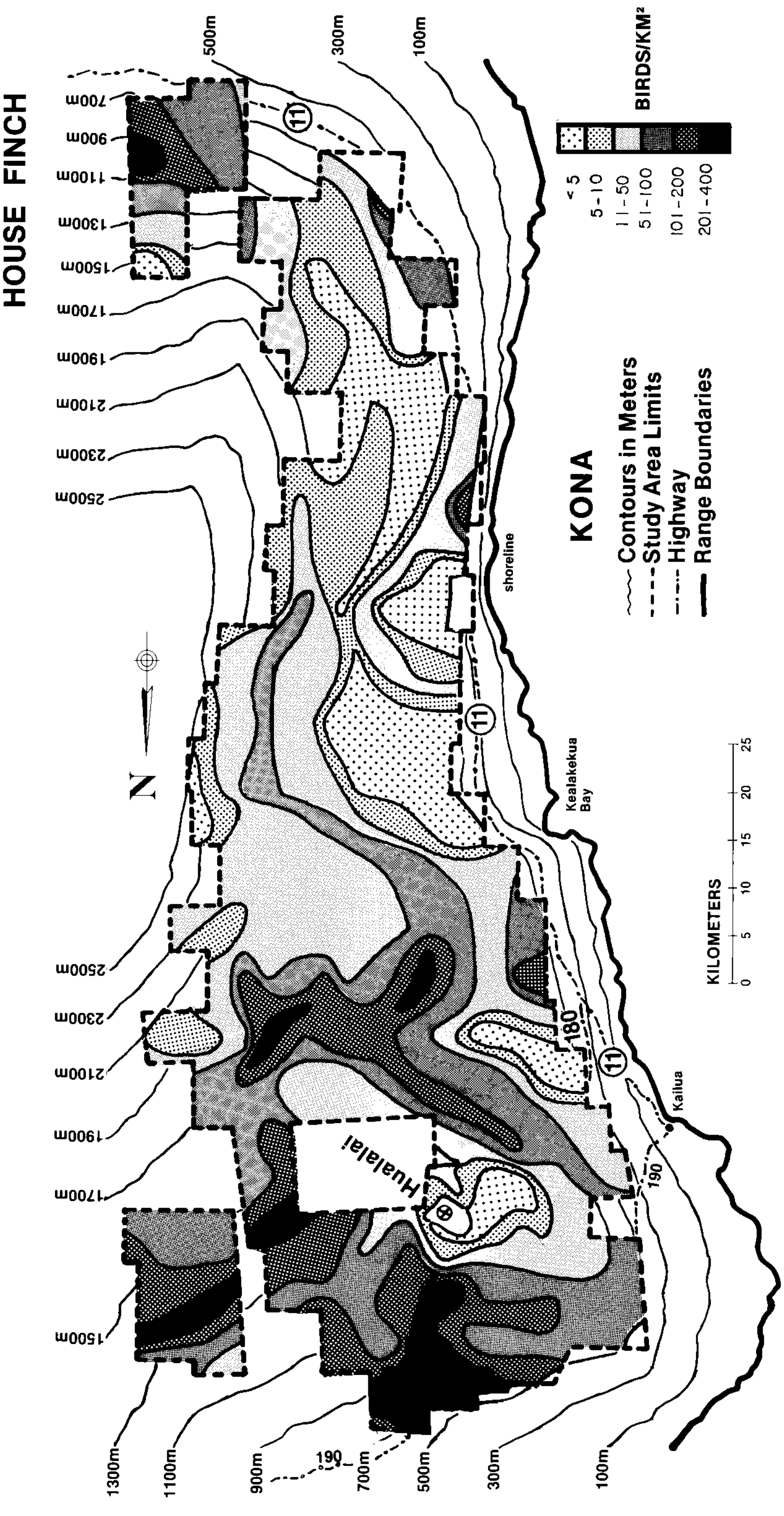


FIGURE 287. Distribution and abundance of the House Finch in the Kona study area.

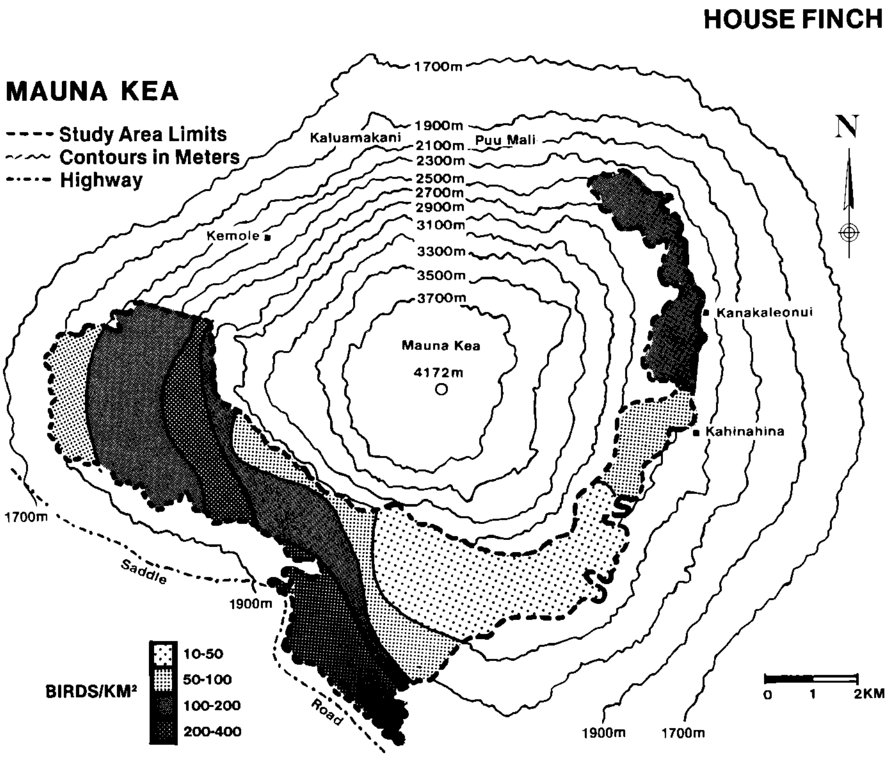


FIGURE 288. Distribution and abundance of the House Finch in the Mauna Kea study area.

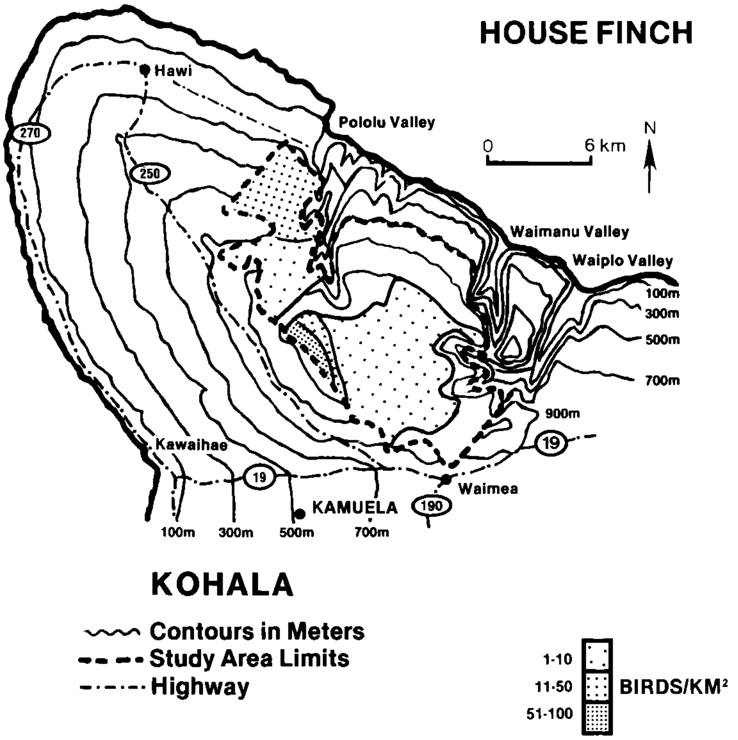


FIGURE 289. Distribution and abundance of the House Finch in the Kohala study area.

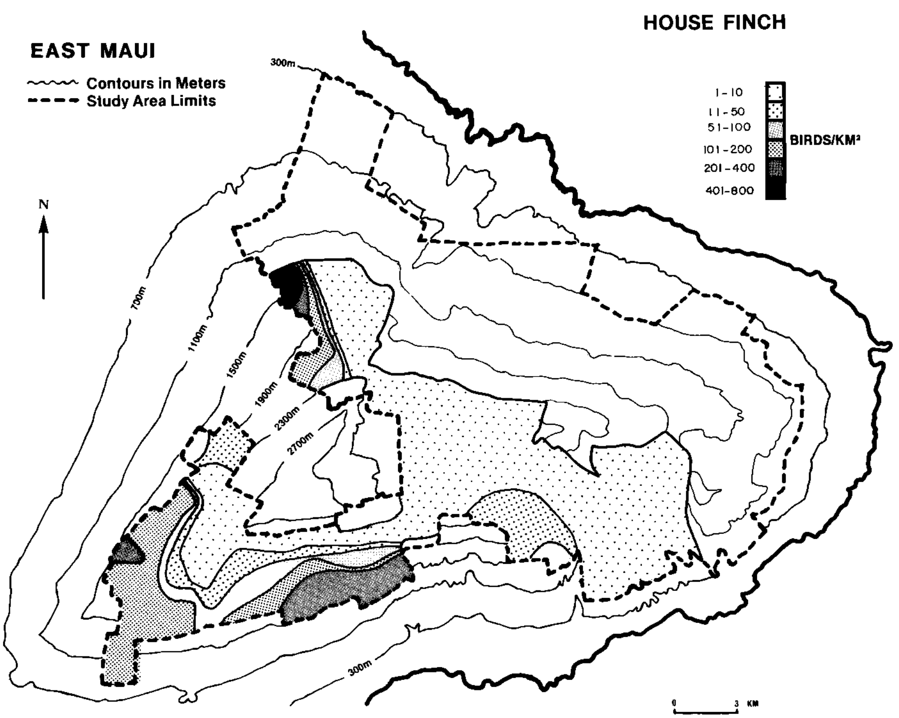


FIGURE 290. Distribution and abundance of the House Finch in the East Maui study area.

Apparently suitable habitat for this species is abundant in leeward Hawaii. It seems likely that Saffron Finches will expand in range north and south of Hualalai and up the drier slopes of Mauna Loa and Mauna Kea. Observers should be alert for possible range expansions to windward Hawaii and Maui.

HOUSE FINCH (*Carpodacus mexicanus*)

House Finches were introduced to the Hawaiian Islands before 1870, probably from San Francisco (Caum 1933, Berger 1975a). Munro (1944) found them well established on all the islands. This species is native to North America and widely distributed over the western half of the continent (Bent 1968). Known locally as papaya birds from the habit of feeding on papaya fruit, House Finches are omnivorous and feed extensively on seed, buds, and fruit. In the Hawaiian Islands, they are common in cities, towns, wet and dry agricultural areas, high-elevation ranchlands, mamane-naio woodland on Mauna Kea, and cutover wet forest (Berger 1981).

We found House Finches in all the study areas (Tables 33, 34, 63, Figs. 285–293). On Hawaii, 127,000 ± 7000 (95% CI) birds occur in the study areas; on Maui, 8000 ± 1000; on Molokai, 5300 ± 1300; on Lanai, 600 ± 400; and on Kauai, 20 ± 40. They occur in low densities at upper elevations in Kau and Hamakua, but are more uniformly distributed in Puna. In Hawaii Volcanoes National Park a general increase in frequency occurred over the 1940–1975 interval from 32% of plot counts to 51% (Baldwin 1953, Banko and Banko 1980). On Mauna Kea, House Finches have low densities in the Hale Pohaku area and reach greatest numbers in naio woodlands and areas with available water. In our study areas House Finches chiefly inhabit forest edges, pastures, open woodland, and scrub. They are widespread and abundant on Molokai, absent only on the heavily forested Olokui Plateau. One straggler occurred on a drier ridge top in the Alakai Swamp, where they are also generally absent. The fragmented forests of Kona appear to constitute ideal habitat.

This species occupies a broad range of habitats and is most common over a range of elevations in dry woodlands and savannas (Fig. 294). In most regression models an association appears with open woodlands having introduced grass and herb understories (Table 64). The models for Kohala and Lanai have no significant response to any variable. Response to elevation tends to be bell-shaped. The negative relation to elevation in the Kipukas reflects the high elevation of the area, and the positive relation in Hamakua reflects the absence of dry habitat at

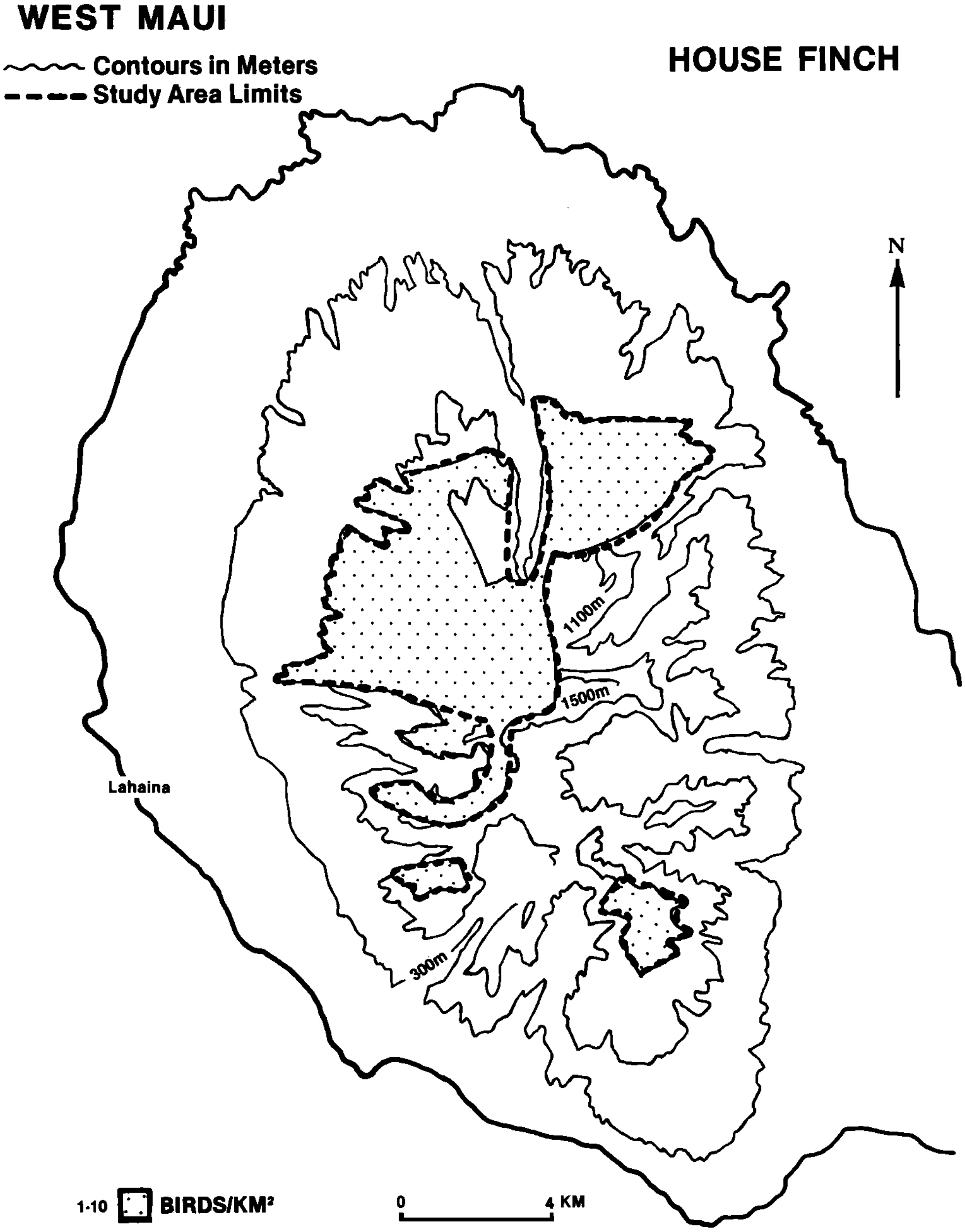


FIGURE 291. Distribution and abundance of the House Finch in the West Maui study area.

low elevations. Use of fruits and berries is reflected in the association with passiflora, and House Finches may actively disperse banana poka (Warshauer et al. 1983).

Grinnell and Miller (1944) found that the habitat requirements of House Finches include water in some form within a fairly wide cruising radius, open ground for growth of low stature seed-producing plants, fruits and berries during part of the year, and cliffs or other structures for nesting and roosting. Water from cattle troughs on ranches and gamebird waterers on game management areas is readily available in most dry areas where House Finches occur in the Hawaiian Islands, but lack of water may limit populations on lava flows and above timberline on

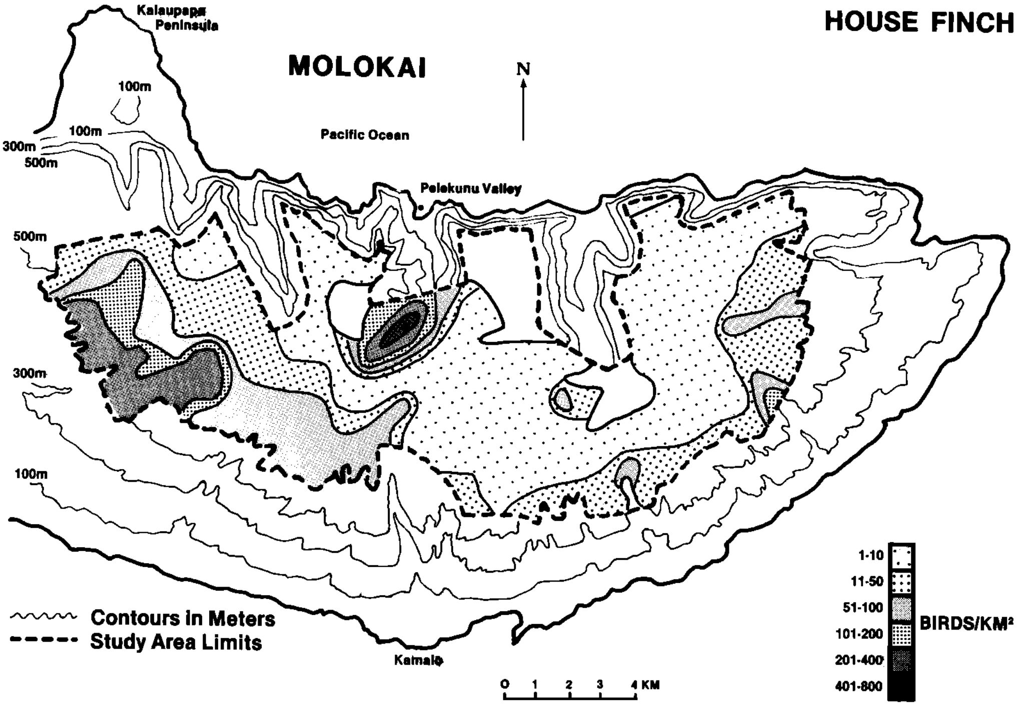


FIGURE 292. Distribution and abundance of the House Finch in the Molokai study area.

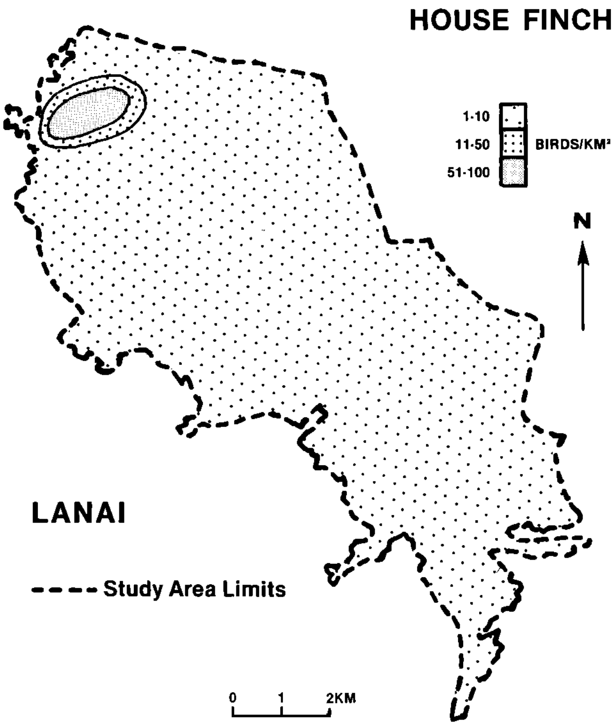


FIGURE 293. Distribution and abundance of the House Finch in the Lanai study area.

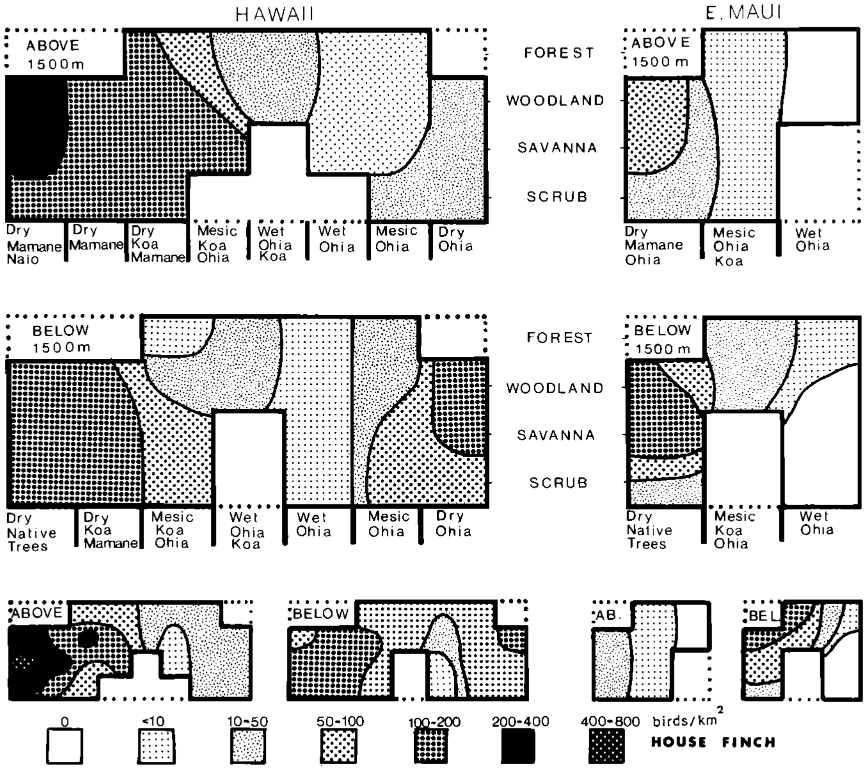


FIGURE 294. Habitat response graphs of the House Finch. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

Hawaii and in native grasslands and the crater desert on Maui. The abundance of this species on Hawaii was largely due to the spread of ranching (van Riper 1976). The highest densities on Mauna Kea are associated with water seeps at timberline. In dry woodland and open scrub, the fruit requirement is met by *Styphelia, Coprosma, Vaccinium,* lama, and naio.

YELLOW-FRONTED CANARY (*Serinus mozambicus*)

Yellow-fronted Canaries were first reported from the Hawaiian Islands on Oahu in June 1964, where they have since become frequent breeders (Berger 1977). They were first recorded from Hawaii in December 1977 on the upper slopes of Mauna Kea by van Riper (1978b), who speculated that they were released at Puu Waawaa, without documenting their occurrence there.

We found Yellow-fronted Canaries only on leeward Hawaii, concentrated in the Puu Waawaa area (Tables 33, 62, Fig. 295). They occur in five of eight general habitat types, most commonly in ohia forests below 1500 m elevation, although during winter, numbers occur in mamane and naio woodlands as high as 2800 m (van Riper 1978b). An estimated 4500 ± 800 (95% CI) birds occur in the Kona study area.

In the habitat analysis, Yellow-fronted Canaries are associated with dry woodland savannas (Fig. 296) with a light cover of ohia, mamane, or introduced trees (Table 57). The negative term for tree biomass in the regression model balances positive terms of three tree species, indicating fairly open forests.

Yellow-fronted Canaries feed mainly on seeds (Berger 1981) and in Africa occur in lightly wooded country, savanna, brush, and cultivated areas (Williams 1963). The woodlands on the north slopes of Hualalai and at higher elevations on Mauna Kea are fairly close to this description. The distribution and abundance of this species in Kona and recent observations well outside that area (Paton 1981) suggest that the range is expanding.

HOUSE SPARROW (*Passer domesticus*)

House Sparrows were first introduced to Oahu in 1871 and quickly became established (Caum 1933). They are presently found on all the islands, especially in urban and agricultural areas (Berger 1981). We found them in the Hamakua,

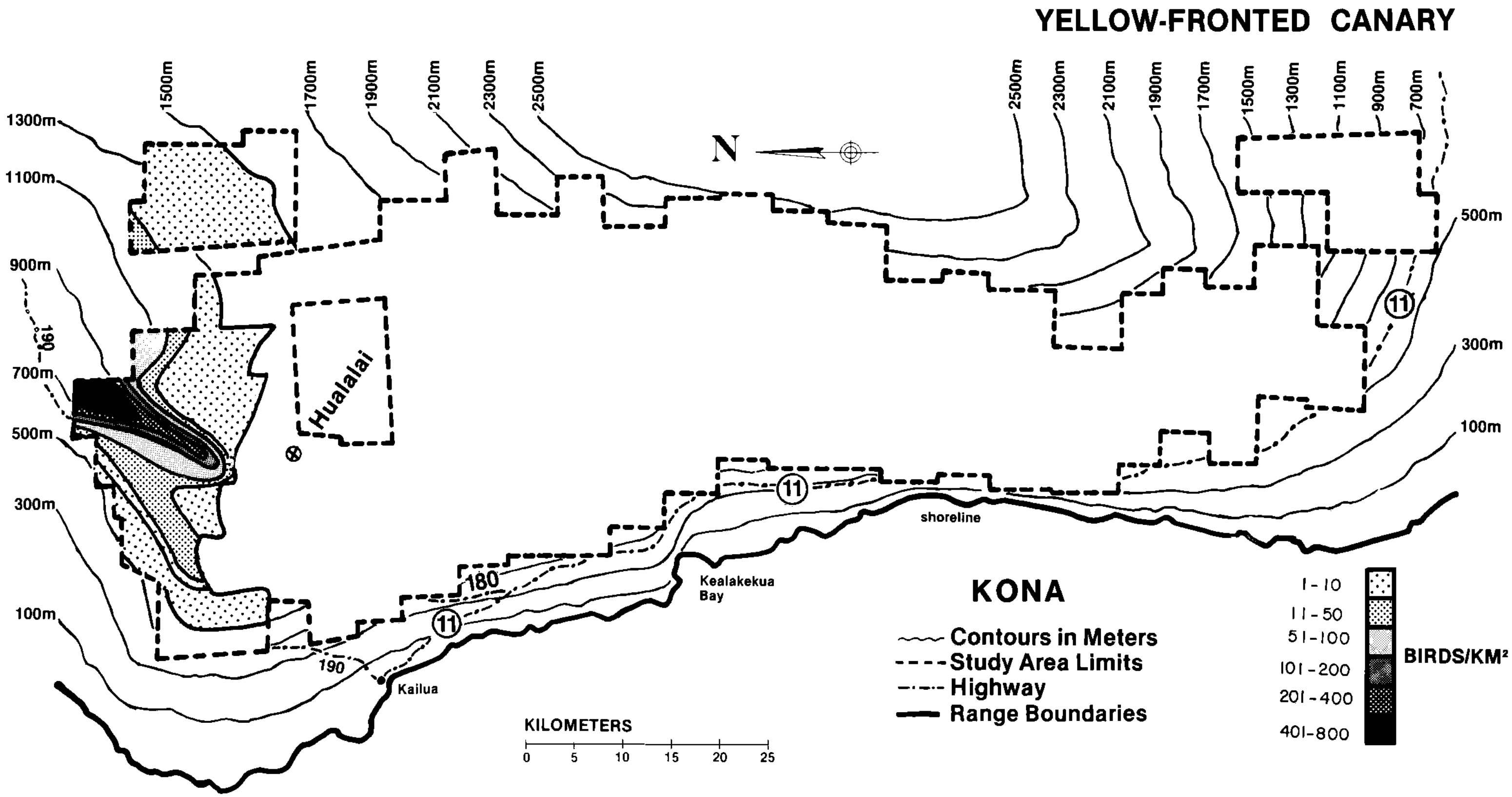


FIGURE 295. Distribution and abundance of the Yellow-fronted Canary in the Kona study area.

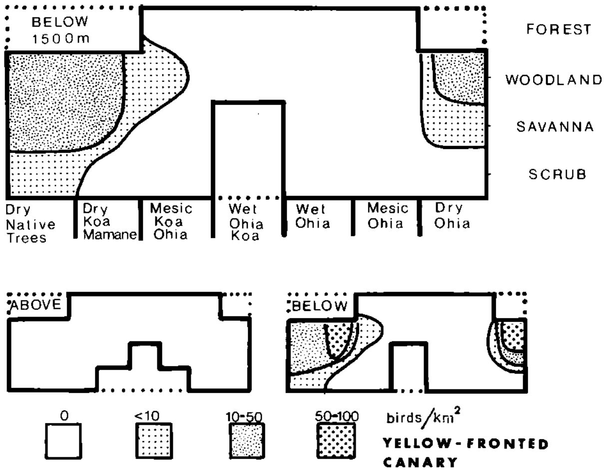


FIGURE 296. Habitat response graphs of the Yellow-fronted Canary. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

TABLE 64
Regression Models for Habitat Response of the House Finch[a]

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Maui	Molokai
R^2	0.52*	0.64*	0.44*	0.39*	0.13*	0.54*	0.30*
Moisture	−8.5*	−12.0*	−4.4*	−18.8*	X	−14.1*	−6.8*
Elevation	···	···	−6.8*	9.4*	···	10.5*	−3.1
(Elevation)^2	5.9*	···	···	−12.9*	···	−10.4*	2.2
Tree biomass	6.2*	5.7*	···	6.8*	···	5.4*	···
(Tree biomass)^2	−3.1	···	···	−3.3*	···	−2.7	···
Crown cover	−3.4*	−5.8*	···	−6.7*	···	···	···
Canopy height	···	−2.5	5.2*	···	6.9*	···	···
Koa	···	X	···	−3.6*	X	···	X
Ohia	−12.6*	···	···	3.2	X	−2.8	···
Naio	X	X	···	···	···	X	X
Mamane	···	···	···	4.8*	···	3.5*	X
Intro. trees	−4.5*	···	X	···	X	4.2*	···
Shrub cover	···	···	···	−5.4*	···	−6.2*	···
Ground cover	−7.8*	···	···	···	···	6.3*	···
Native shrubs	−8.0*	···	···	···	X	···	···
Intro. shrubs	···	···	···	···	X	···	···
Ground ferns	X	···	···	−5.1*	X	−3.1	···
Matted ferns	···	−4.8*	···	−5.1*	X	···	···
Tree ferns	X	−3.1	X	···	X	···	−3.1
Ieie	X	···	X	···	X	···	X
Passiflora	···	X	X	2.3	X	3.3	X
Native herbs	X	···	3.9*	···	X	−3.1	···
Intro. herbs	X	···	4.4*	5.0*	···	−3.4*	···
Native grasses	···	−4.6*	−8.1*	···	···	−6.7*	···
Intro. grasses	8.0*	···	···	4.3*	···	4.6*	···
Ohia flowers	···	···	4.8*	···	X	···	···
Olapa fruit	···	···	···	···	X	···	···
Mamane flowers	X	X	2.9	X	···	−3.7*	X
Mamane fruit	X	X	X	X	···	X	X
Naio fruit	X	X	X	X	···	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

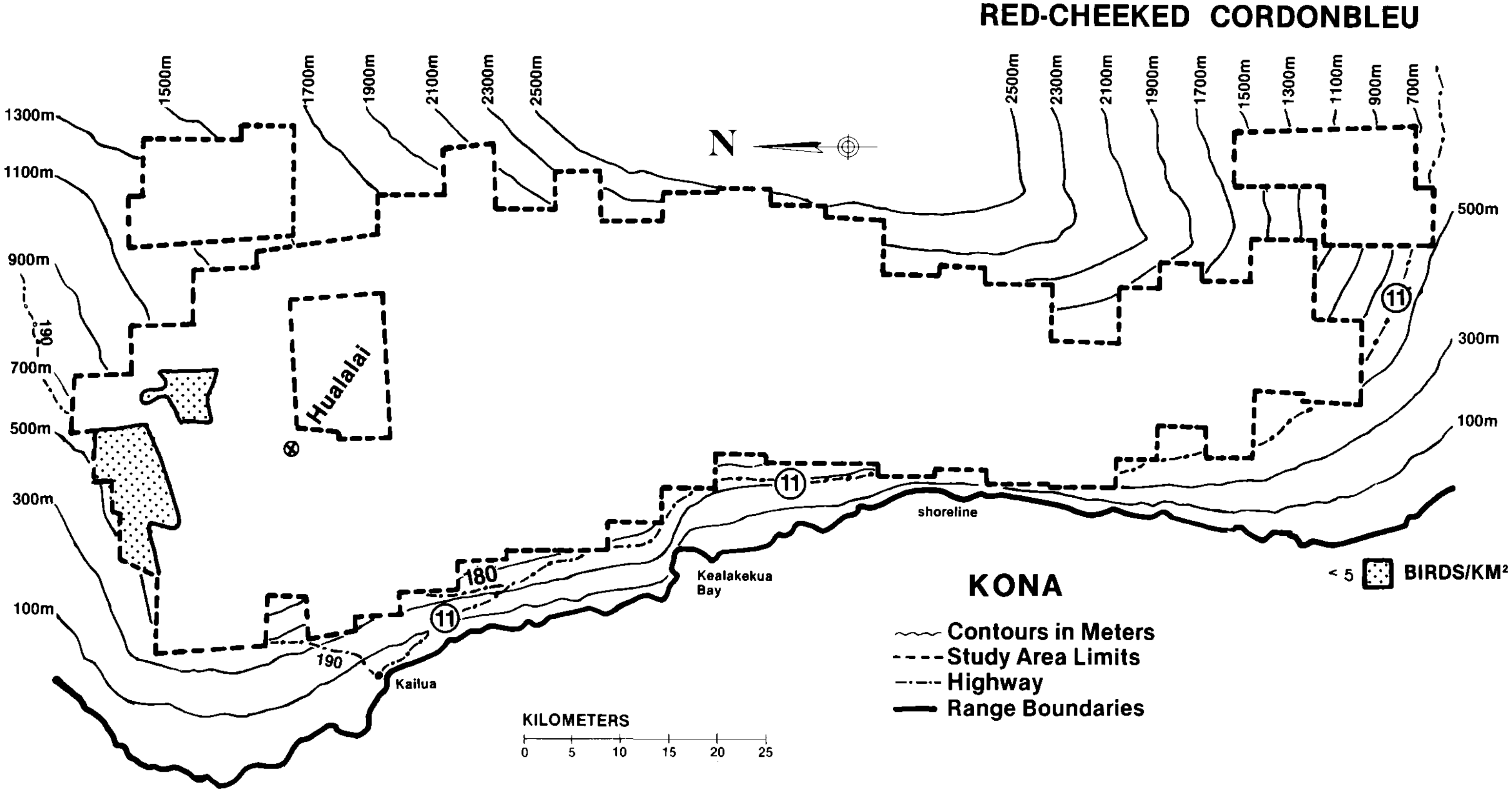


FIGURE 297. Distribution and abundance of the Red-cheeked Cordonbleu in the Kona study area.

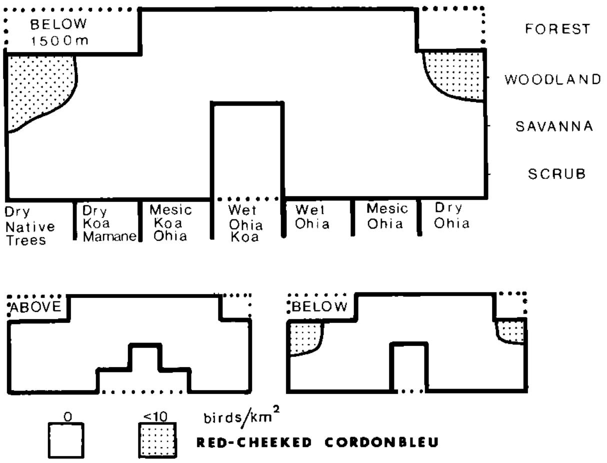


FIGURE 298. Habitat response graphs of the Red-cheeked Cordonbleu. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

Kona, Mauna Kea, Kipukas, and East Maui study areas (Tables 33, 34), always in association with human disturbance (inhabitations, ranch paddocks, feedlots, campgrounds). A large concentration occurs at Mauna Kea State Park in the Mauna Kea study area. Because of their close association with man, limited distribution, and small numbers, we did not calculate the distribution.

Red-cheeked Cordonbleu

(*Uraeginthus bengalus*)

The Red-cheeked Cordonbleu is native to tropical Africa, where it inhabits thorn shrub, savanna, dry woodland, and cultivated areas, and feeds on grass seeds and small invertebrates (Goodwin 1982).

The species was first introduced to the Hawaiian Islands in the 1960s on Oahu, and later released on the north slopes of Hualalai on Hawaii (Berger 1981). We found very low densities (Tables 33, 62, Fig. 297) on Puu Waawaa Ranch below 1100 m elevation. An estimated 30 ± 50 (95% CI) birds occur in the study area, mostly in dry lama-ohia woodlands with introduced grass understories (Fig. 298). It remains to be seen whether this species will become established on Hawaii. Observers should be alert for range expansion.

Lavender Waxbill

(*Estrilda caerulescens*)

Lavender Waxbills are native to tropical western Africa where they inhabit semi-arid savannas, woodlands, and brushlands, as well as gardens and cultivated areas. They feed on seeds, small fruits, and insects (Goodwin 1982). Lavender Waxbills were first reported from the Hawaiian Islands on Oahu in 1965 (Berger 1981). During the HFBS, birds were discovered on Hawaii, the only other island of known occurrence (Ashman and Pyle 1979).

We found Lavender Waxbills only on the northern slopes of Hualalai on leeward Hawaii (Fig. 299) where they are uncommon below 1100 m elevation in dry lama-ohia woodlands and savannas (Tables 33, 62, Fig. 300). An estimated 230 ± 120 (95% CI) birds occur in the study area.

The range of the Lavender Waxbill is centered on Puu Waawaa Ranch, an area where large numbers of introduced species have been released (Lewin 1971; van Riper 1973a, 1978b). This species may have been introduced there along with other estrildid finches. Unlike Saffron Finches and Yellow-fronted Canaries, Lavender Waxbills have not expanded their range to other parts of the island.

Warbling Silverbill

(*Lonchura malabrica*)

Warbling Silverbills are drab estrildid finches from Africa that were first collected from the Hawaiian Islands in 1972 on Hawaii (Berger 1975a) and have since spread to dry low habitat on Maui (Walters 1979), Lanai (Hirai 1980), Kahoolawe (Conant 1983), and Oahu (Conant 1984). Below our study areas on Hawaii and Maui, they are common in coastal mesquite woodlands with introduced grass and shrub understories.

An estimated 4000 ± 1700 (95% CI) birds occupy our study areas (Tables 33, 62, Fig. 301). Flocks of over 200 birds occur on Puu Waawaa Ranch north of Hualalai in Kona and smaller

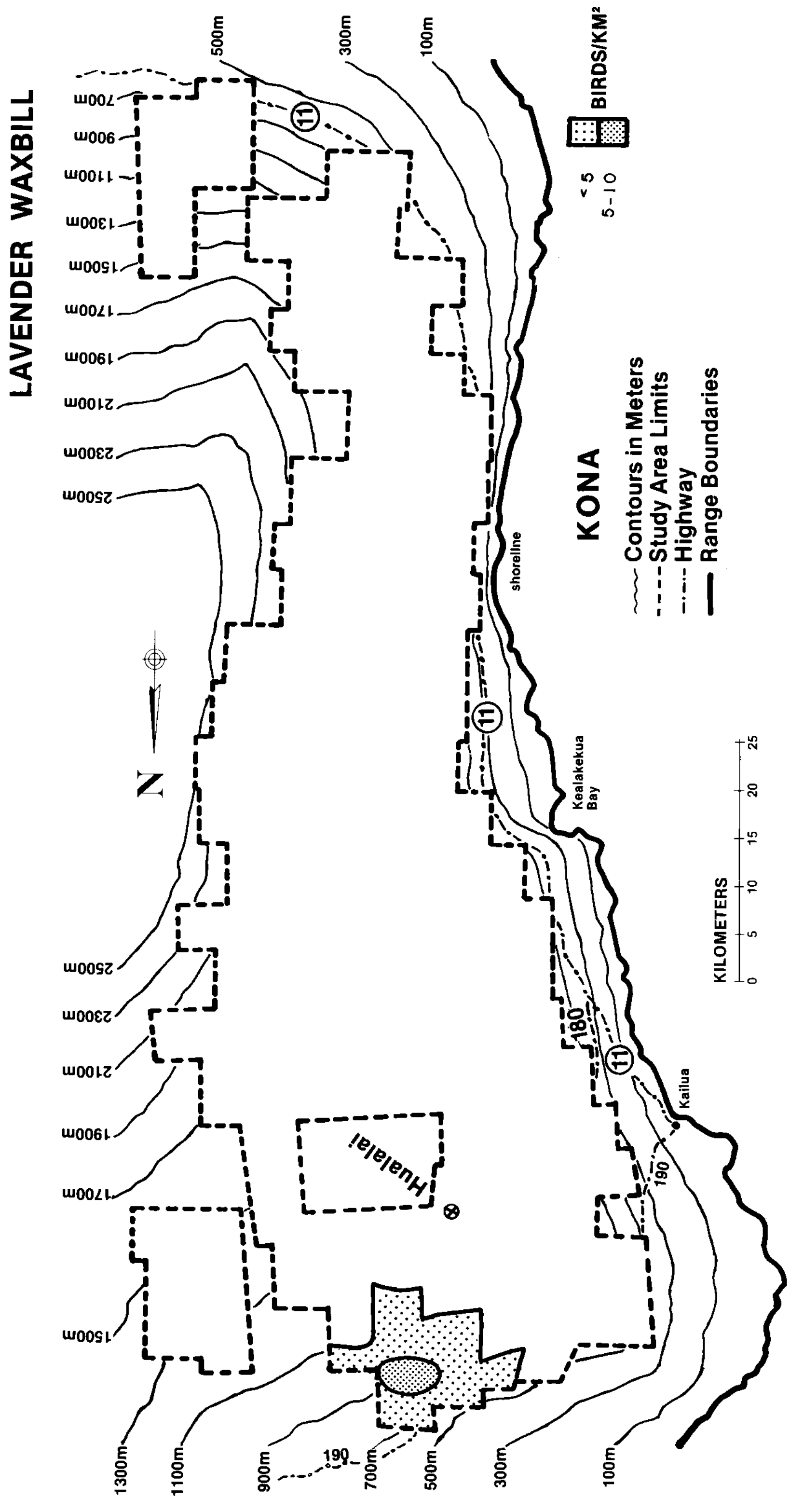


FIGURE 299. Distribution and abundance of the Lavender Waxbill in the Kona study area.

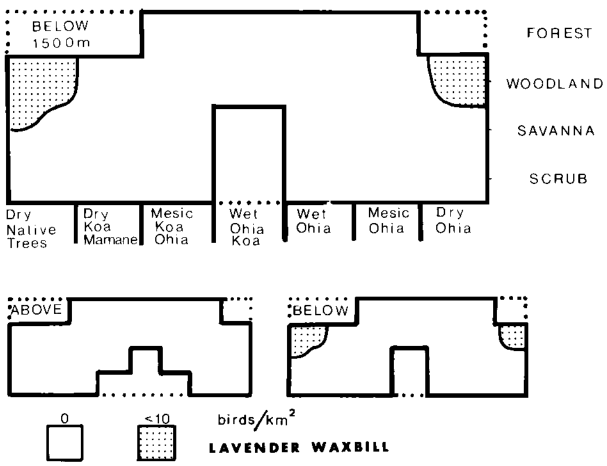


FIGURE 300. Habitat response graphs of the Lavender Waxbill. (Graphs give mean density below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

TABLE 65
Regression Models for Habitat Response of the Warbling Silverbill and Nutmeg Mannikin[a]

	Warbling Silverbill	Nutmeg Mannikin						
	Kona	Hamakua	Puna	Kipukas	Kona	Kohala	Maui	Molokai
R^2	0.10*	0.06*	0.09*	0.11*	0.08*	0.34*	0.23*	0.23*
Moisture	−10.4*	···	···	···	···	X	−3.9*	−5.5*
Elevation	···	−4.3*	−2.9	−5.8*	−9.1*	−5.6*	−7.7*	−2.6
(Elevation)^2	−8.1*	3.5*	···	···	···	5.0*	5.8*	2.0
Tree biomass	2.5	···	···	···	2.2	−3.5*	4.6*	3.6*
(Tree biomass)^2	···	···	−2.8	5.4*	−3.9*	3.2	−4.0*	−6.1*
Crown cover	···	···	···	···	···	···	···	2.4
Canopy height	4.0*	···	···	···	···	···	···	···
Koa	−3.4*	−2.3	X	···	···	X	···	X
Ohia	−4.8*	···	2.4	···	···	···	···	···
Naio	−3.6*	X	X	···	···	X	X	X
Mamane	−5.0*	···	2.8	···	···	X	−4.1*	X
Intro. trees	−2.3	6.4*	···	X	6.9*	···	···	···
Shrub cover	···	···	···	···	−3.5*	···	−2.7	···
Ground cover	5.7*	···	···	···	4.1*	···	2.8	···
Native shrubs	···	···	···	···	···	−2.5	···	···
Intro. shrubs	−3.6*	···	···	···	···	−2.3	···	···
Ground ferns	···	X	···	···	···	···	···	···
Matted ferns	···	···	···	···	···	···	···	···
Tree ferns	···	X	−2.7	X	···	···	−3.0	−2.4
Ieie	···	X	···	X	···	X	···	X
Passiflora	···	···	X	X	···	···	4.4*	X
Native herbs	···	X	···	···	···	···	···	···
Intro. herbs	3.9*	X	···	···	−2.3	···	···	···
Native grasses	2.8	···	···	···	···	···	···	···
Intro. grasses	···	···	···	···	···	···	3.9*	···
Ohia flowers	···	···	···	···	···	···	···	···
Olapa fruit	···	···	···	···	···	···	−2.4	···
Mamane flowers	X	X	X	···	X	X	···	X
Mamane fruit	X	X	X	X	X	X	X	X
Naio fruit	X	X	X	X	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

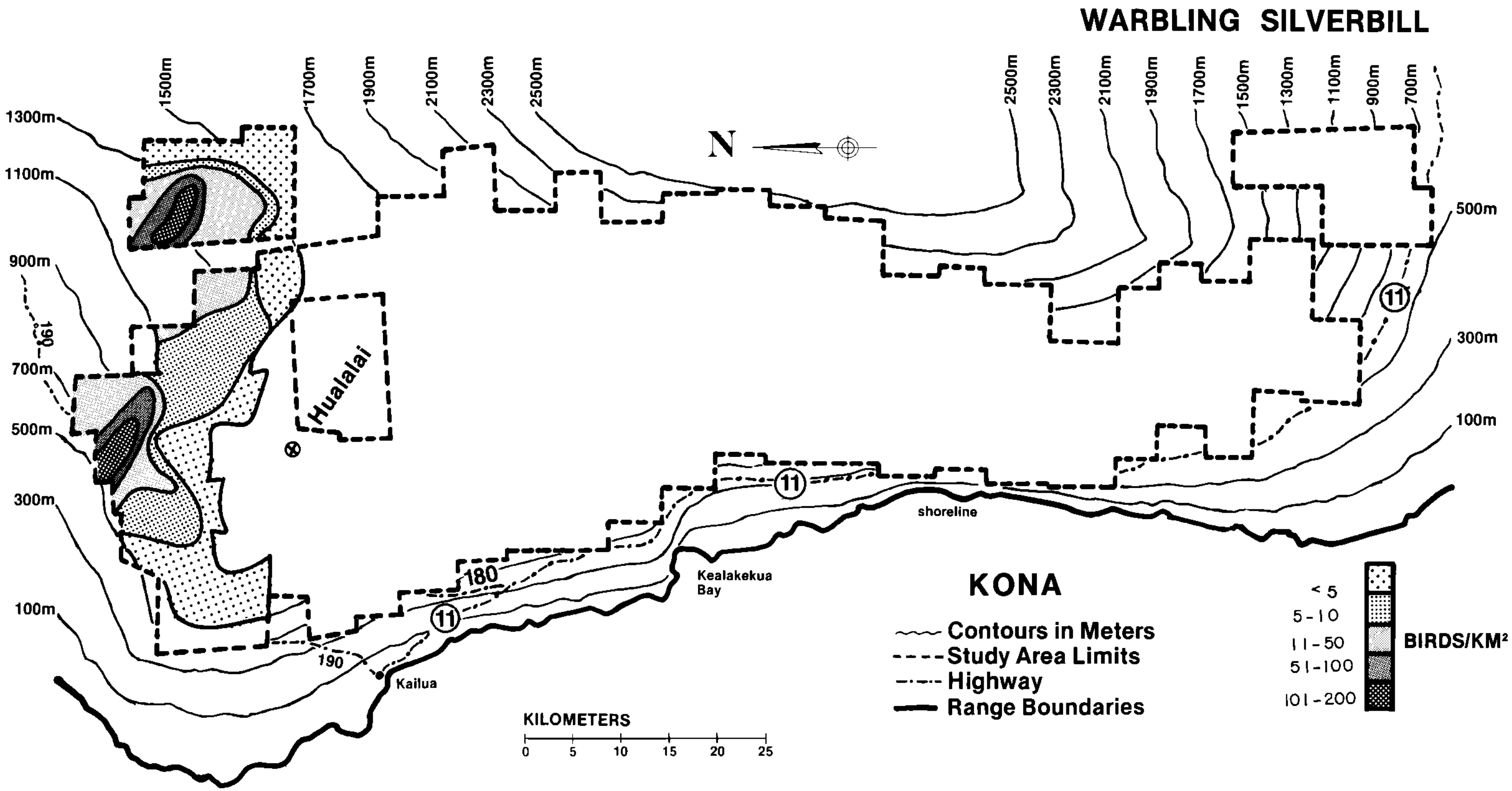


FIGURE 301. Distribution and abundance of the Warbling Silverbill in the Kona study area.

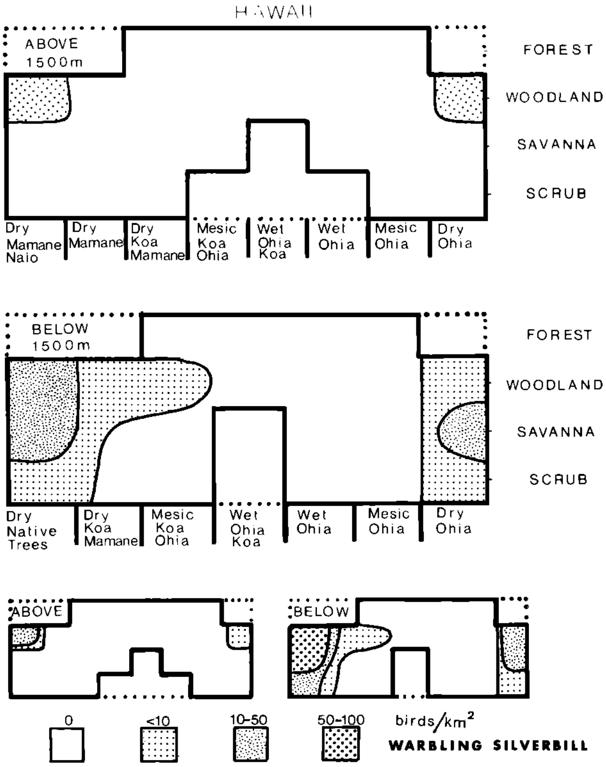


FIGURE 302. Habitat response graphs of the Warbling Silverbill. (Graphs give mean density above and below 1500 m elevation for Hawaii; half-size graphs give standard deviation.)

flocks occur on Mauna Kea and in the Mauna Kea-Mauna Loa saddle. They range to 1300 m elevation in their restricted range on Hualalai and occur to 3100 m on Mauna Kea.

Highest densities occur in our study areas in a very dry native tree association at low elevations (Fig. 302). The negative quadratic elevation term in the regression model (Table 65) reflects increasingly higher densities at lower elevations. The negative terms for all five tree species reflect association with dry open lama-ohia woodlands at Puu Waawaa.

In Africa, Warbling Silverbills occupy dry savannas, thorn-scrub, grasslands, and desert areas near water; they feed almost exclusively on seeds (Goodwin 1982). The niche and habitat of Warbling Silverbills in Hawaii appear to be quite similar to those in Africa.

NUTMEG MANNIKIN (*Lonchura punctulata*)

In the Hawaiian Islands, Nutmeg Mannikins are widely known as Ricebirds or Spotted Munias. They increased rapidly following introduction about 1865 (Caum 1933) and became pests in rice fields (Munro 1944). Berger (1981) found them well established and widely distributed on all the islands, but no longer agricultural pests. Nutmeg Mannikins are highly nomadic and occasionally appear on most sites.

We found this species in all but two study areas, usually in very open or disturbed sites or on the edge of forests (Tables 33, 34, 66, Figs. 303–309). On Hawaii an estimated 25,000 ± 5000 (95% CI) birds occur in the study areas, with most in Hamakua (42% of the total) and Kona (26%). In Hawaii Volcanoes National Park, numbers appeared to increase over the 1940–1975 interval (Conant 1975, Banko and Banko 1980). We estimated 8000 ± 3000 birds on East Maui, 3000 ± 2000 on West Maui, and 11,000 ± 4000 on Molokai. Highest densities were recorded on Molokai. We failed to find them on Lanai in early May 1979, but Hirai (1978) noted that they were abundant in the mountain forests from August to November. We also failed to find them on Kauai in May 1981, but Sincock et al. (1984) estimated populations of 2100 ± 1100 birds for our study area and 109,000 ± 38,000 birds in native forests on Kauai.

Nutmeg Mannikins occupy a wider variety of habitat types below 1500 m than above on Hawaii and Maui, although they are very infrequent

TABLE 66
DENSITY [MEAN (SE)] OF THE NUTMEG MANNIKIN BY ELEVATION, HABITAT, AND STUDY AREA[a]

	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Kauai
Elevation										
100–300 m	...	...	...	...	...	...	...	...	138 (77)	...
300–500 m	308 (120)	21 (5)	...	0	...	71 (71)	233 (177)	...	367 (155)	...
500–700 m	58 (19)	15 (9)	...	43 (12)	...	89 (47)	104 (30)	302 (107)	122 (39)	...
700–900 m	30 (10)	64 (37)	...	41 (14)	...	61 (28)	37 (10)	178 (76)	128 (42)	...
900–1100 m	22 (8)	14 (8)	...	22 (6)	...	11 (11)	56 (27)	18 (18)	61 (17)	...
1100–1300 m	17 (8)	4 (4)	40 (17)	17 (4)	...	12 (8)	63 (24)	+ (+)	47 (24)	7 (1)
1300–1500 m	9 (5)	...	62 (32)	1 (1)	...	+ (+)	104 (70)	+ (+)	0	+ (+)
1500–1700 m	3 (3)	...	0	3 (3)	...	0	38 (20)	+ (+)	...	...
1700–1900 m	+ (+)	...	0	+ (+)	...	...	55 (23)	+ (+)	...	...
1900–2100 m	+ (+)	...	11 (8)	+ (+)	+ (+)	...	+ (+)	...	...	...
2100–2300 m	0	...	0	+ (+)	+ (+)	...	6 (6)	...	...	...
2300–2500 m	...	...	...	+ (+)	+ (+)	...	+ (+)	...	...	...
2500–2700 m	...	...	...	...	82 (56)	...	+ (+)	...	...	...
2700–2900 m	...	...	...	...	27 (27)	...	0	...	...	...
2900–3100 m	...	...	...	...	+ (+)	...	...	...	...	...
Habitat										
Ohia	13 (3)	18 (4)	+ (+)	27 (7)	...	30 (9)	29 (9)	116 (35)	49 (10)	4 (4)
Koa-ohia	28 (7)	...	52 (18)	10 (2)	...	...	99 (30)	...	...	...
Koa-mamane	0	...	+ (+)	0	...	...	...	...	...	...
Mamane-naio	...	...	...	0	48 (31)	...	...	...	...	...
Mamane	...	...	...	26 (8)	6 (6)	...	0	...	...	...
Other natives	51 (51)	...	15 (10)	19 (7)	...	...	136 (38)	...	169 (43)	...
Intro. trees	89 (17)	...	...	42 (15)	...	+ (+)	52 (19)	0	251 (67)	...
Treeless	0	+ (+)	+ (+)	+ (+)	...	...	3 (3)	+ (+)	1628 (998)	+ (+)

[a] Densities are given in birds/km²; + indicates stratum was in the species range but density <0.5 birds/km²; 0 indicates stratum was outside range but was sampled; ··· indicates stratum was not sampled in study area.

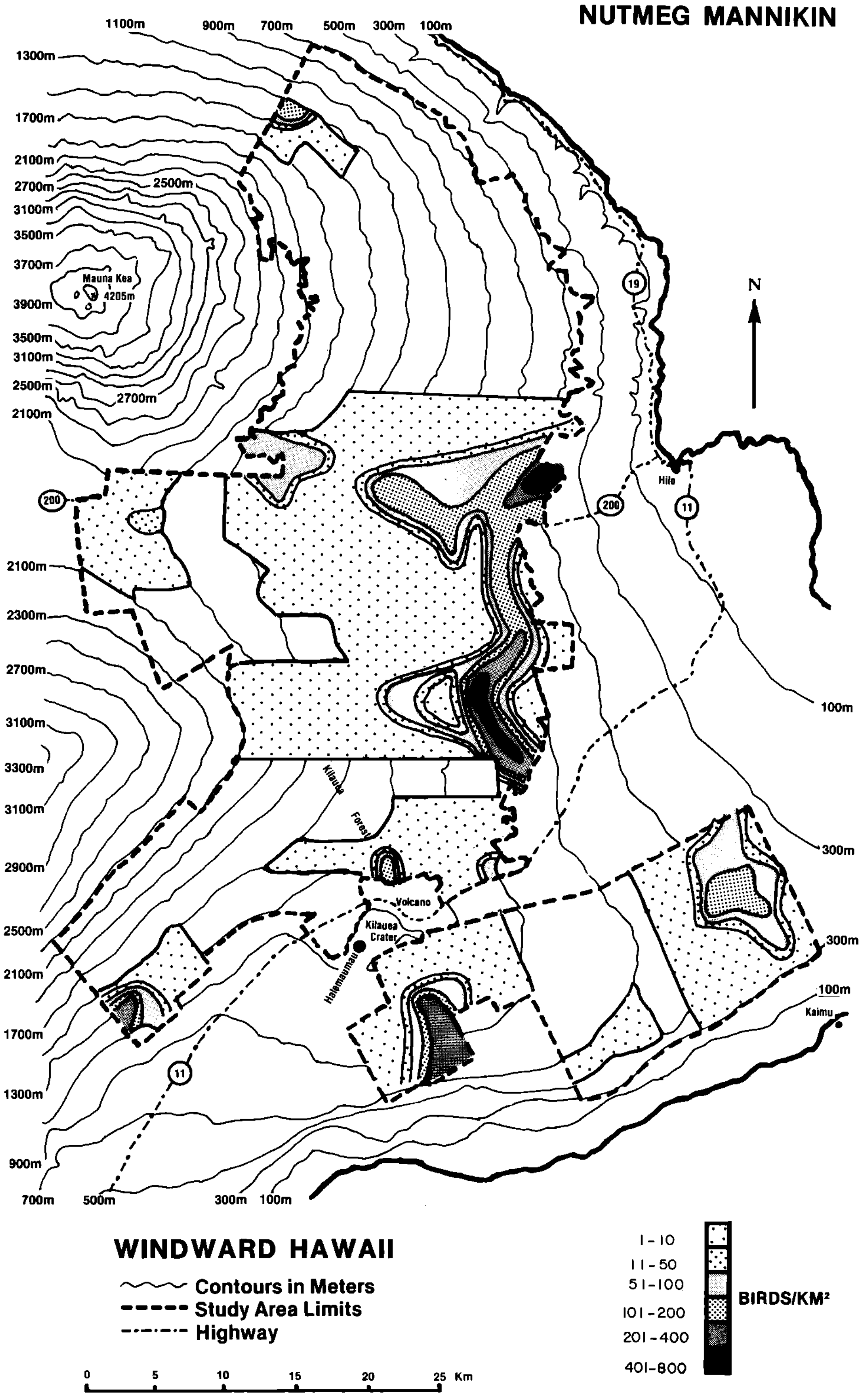


FIGURE 303. Distribution and abundance of the Nutmeg Mannikin in the windward Hawaii study areas.

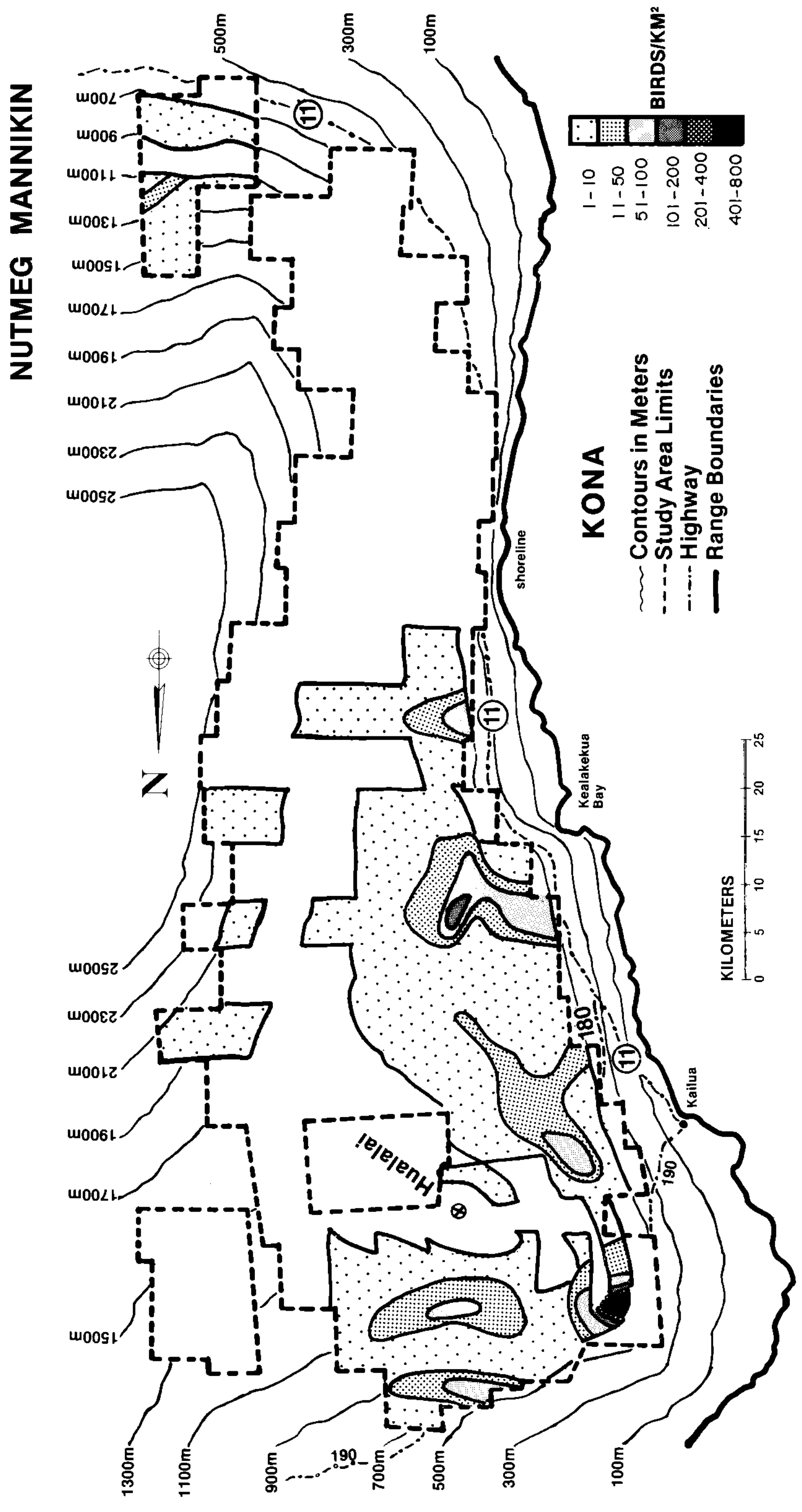


FIGURE 304. Distribution and abundance of the Nutmeg Mannikin in the Kona study area.

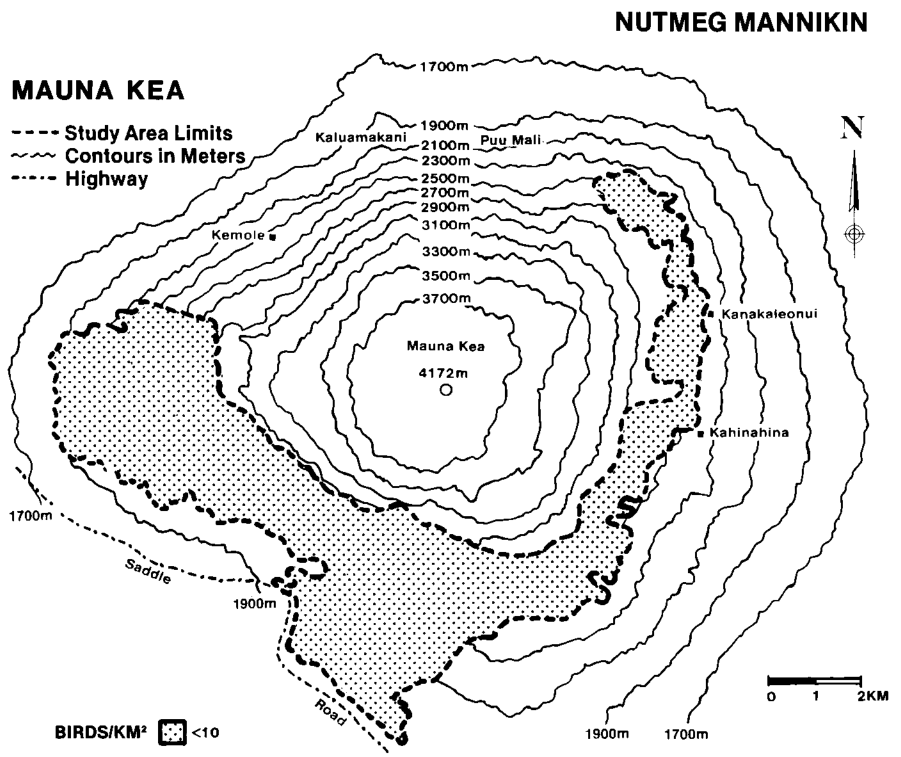


FIGURE 305. Distribution and abundance of the Nutmeg Mannikin in the Mauna Kea study area.

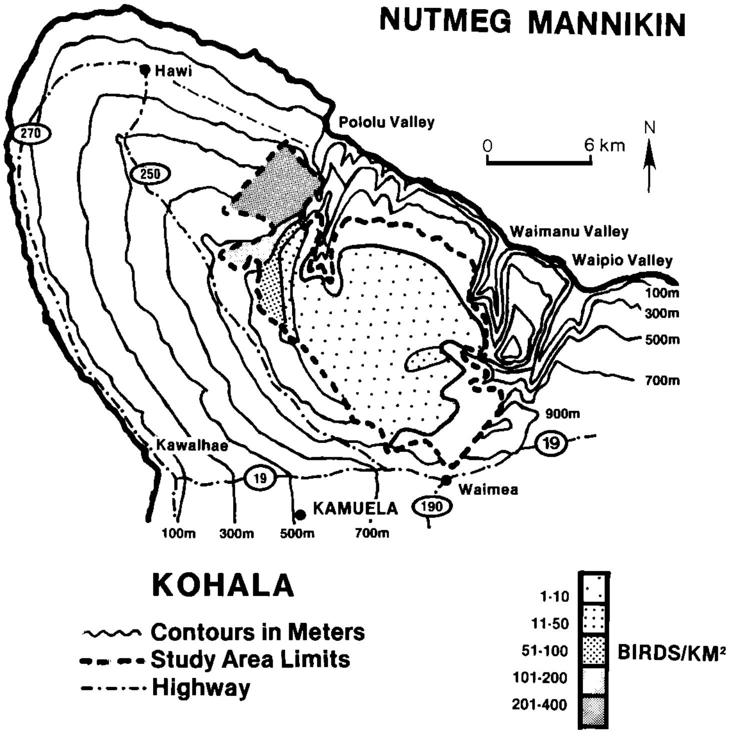


FIGURE 306. Distribution and abundance of the Nutmeg Mannikin in the Kohala study area.

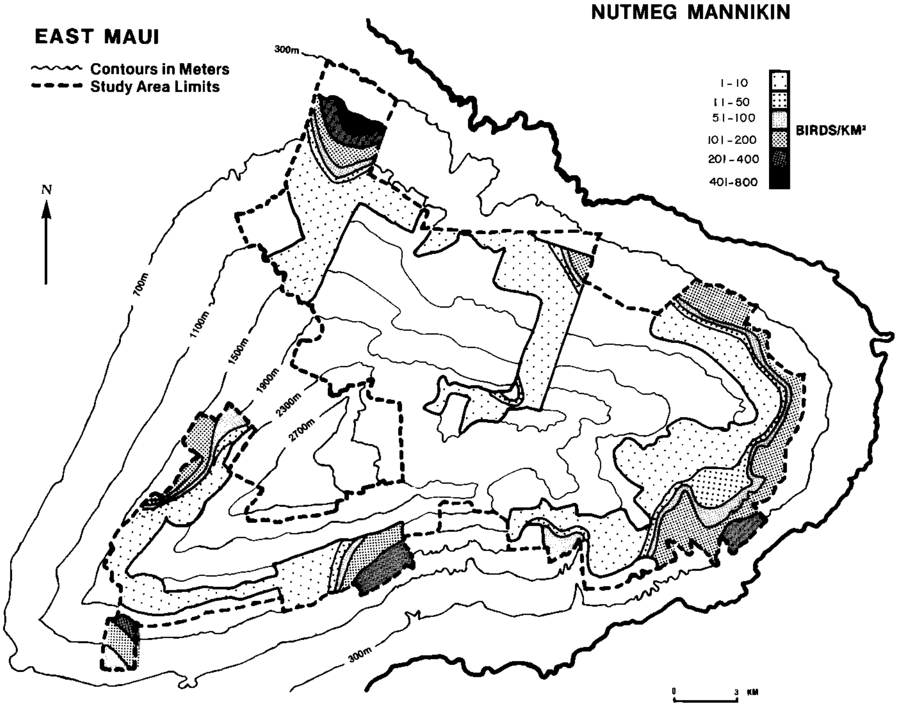


FIGURE 307. Distribution and abundance of the Nutmeg Mannikin in the East Maui study area.

in rainforest interiors (Fig. 310). The regression models (Table 65) show an association with introduced trees in low elevation areas. Other than these trends, the habitat response pattern appears to comprise a scattered, erratic series of relations to other variables. This is also seen in the high variance of the habitat response graphs, and reflects the flocking habit and highly erratic variation in seasonal and annual distribution across a broad span of habitats (see Berger 1981). Richardson and Bowles (1964) found that Nutmeg Mannikins occupy a diverse range of habitats on Kauai, from dry lowland to fairly wet montane sites.

In southeast Asia, Nutmeg Mannikins primarily occur at lower elevations in a range of open and semi-open habitats (Goodwin 1982). They feed almost entirely on seeds, and the positive response to introduced grasses in the Maui regression model may reflect attraction to grass seeds.

COMMUNITY ECOLOGY

SPECIES-AREA RELATIONSHIPS

Island area is a critical component of biogeographic theory (MacArthur and Wilson 1967; Diamond 1973, 1975; Slud 1976; Diamond and Mayr 1976). Distinctive habitats often have island-like relationships between their area and species composition, as noted for birds in deciduous forests surrounded by agricultural land (Bond 1957), in primary versus secondary tropical forest (Terborgh and Weske 1969), and in páramo habitats in the Andes (Vuilleumier 1970, Vuilleumier and Simberloff 1980). On the main Hawaiian Islands, rainforests tend to form distinctive habitat islands surrounded by agricultural land, introduced vegetation, and unforested areas. Although in a few cases boundaries are inexact (e.g., in windward and leeward Hawaii), 20 major rainforest islands may be distinguished (Fig. 311). The data from the HFBS and work on Oahu (Shallenberger and Vaughn 1978) and Kauai (Sincock et al. 1984) allowed us to examine the relationships between the area of these habitat islands, their maximum elevation, and the number of native land bird species present.

The classic species relationship, $S = cA^z$, where S = number of extant native species and A = area in km^2 (MacArthur and Wilson 1967), fits our data. The best fit ($R^2 = 0.41$, $P < 0.01$) is obtained when $z = 0.20$, a value toward the low end but within the range of typical examples for birds (MacArthur and Wilson 1967). A significantly better fit ($R^2 = 0.71$, $P < 10^{-4}$) occurs when elevation (E, in km) is included in the regression equation

$$S = -1.84 + 0.37E + 0.76 \log_e A;$$

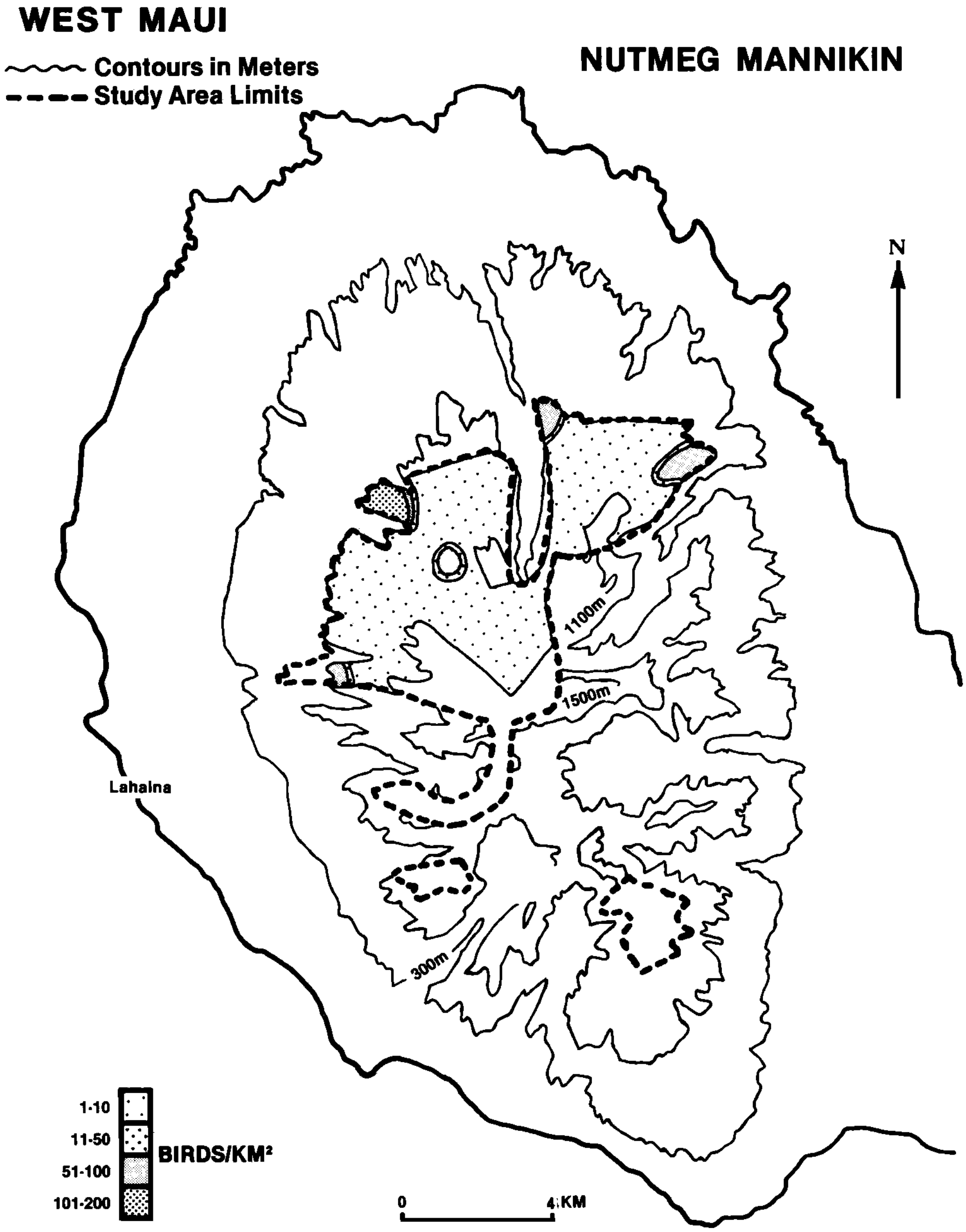


FIGURE 308. Distribution and abundance of the Nutmeg Mannikin in the West Maui study area.

the coefficients are significant at the 1% level. The relation between elevation and species number does not particularly reflect increased habitat diversity, because all species occurred in the most widespread habitat type (wet ohia forest), and the areas are rather similar in their general habitat aspect. In most habitat islands, the greatest number of species occurs near the highest elevations in the area.

The positive association between elevation and species richness reflects extensive extinctions and habitat destruction in the lowlands. Mayr and Diamond (1976) also found an association between elevation and species number in the montane avifauna of northern Melanesia, but this probably reflects the effect of isolation on geographical speciation. More typically, however, lowland areas have greater numbers of bird

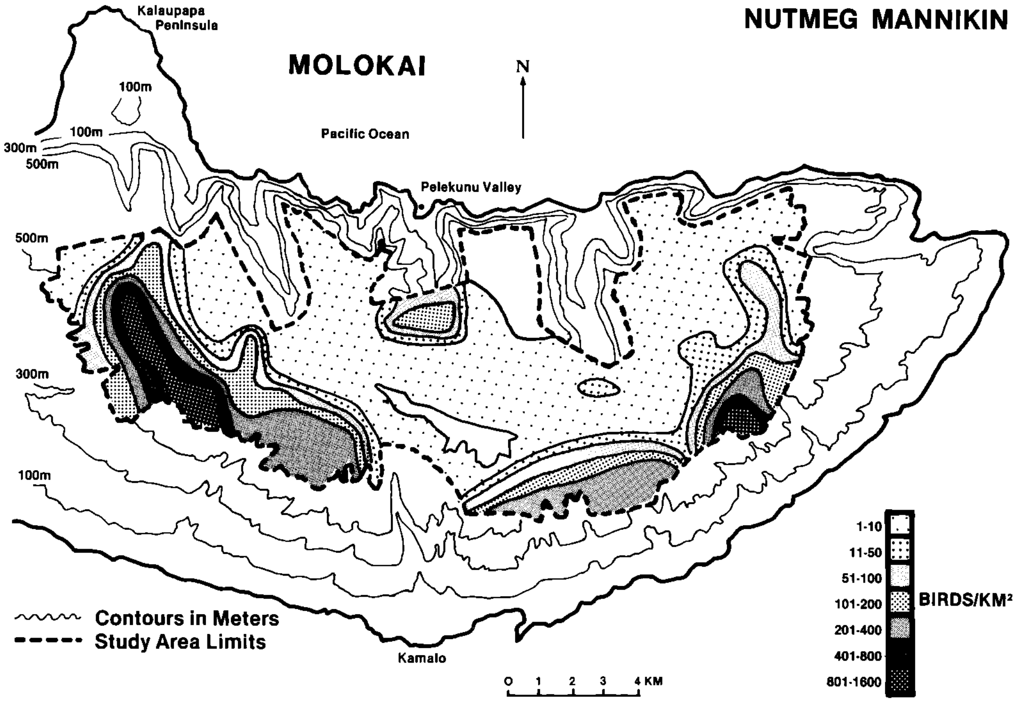


FIGURE 309. Distribution and abundance of the Nutmeg Mannikin in the Molokai study area.

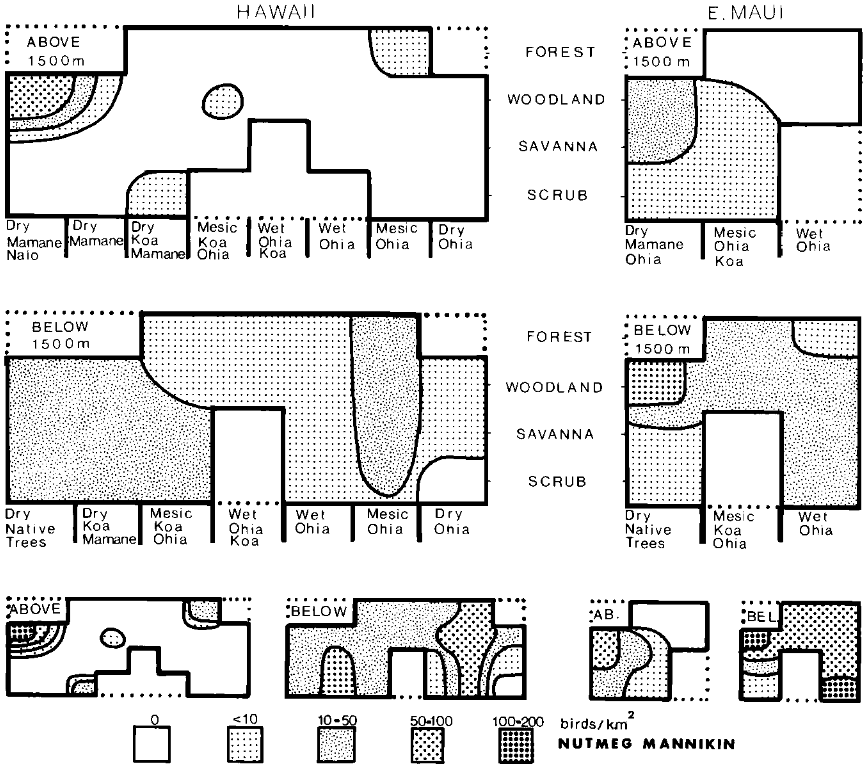


FIGURE 310. Habitat response graphs of the Nutmeg Mannikin. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

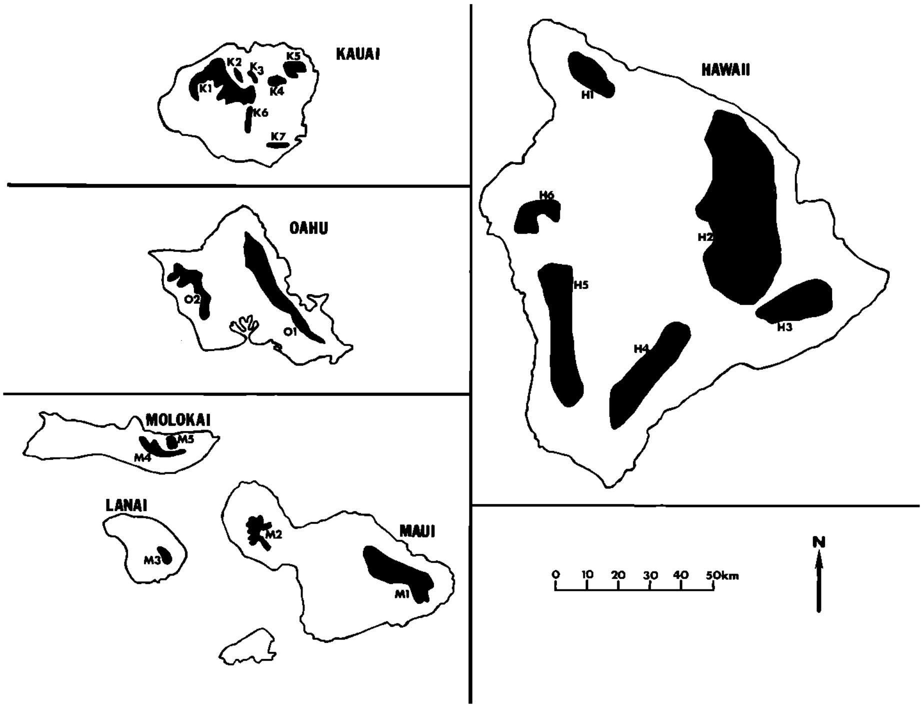


FIGURE 311. Location of "habitat islands" of montane rainforest in the Hawaiian Islands. (Codes: H1 = Kohala, H2 = Hamakua, H3 = Puna, H4 = Kau, H5 = South Kona, H6 = Hualalai; K1 = Alakai, K2 = Laau, K3 = Namolokama, K4 = Makaleha, K5 = Anahola, K6 = Kapalaoa, K7 = Hoary Head; M1 = East Maui, M2 = West Maui, M3 = Lanaihale, M4 = Kamakou, M5 = Olokui; O1 = Koolau, O2 = Waianae.)

species than montane areas, as in the West Indies (Kepler and Kepler 1970, Lack 1976), the Galápagos Islands (Harris 1973), the Solomon Islands (Greenslade 1968), New Guinea (Diamond 1972), and in temperate (Miller 1951, Able and Noon 1976, Sabo 1980, Sabo and Holmes 1983) and tropical (Moreau 1966; Terborgh 1971, 1977; Haffer 1974; Pearson and Ralph 1978) continental areas.

A scatter plot of richness, elevation, and area in the 20 rainforest habitat islands (Fig. 312) shows that several habitat islands deviate substantially from the number of species predicted by the regression. The Alakai Swamp (K1 in the figures), and to a lesser extent the other high habitat islands on Kauai, have more species than predicted. This may reflect the low incidence of mosquitoes in the Alakai, and possibly the proximity of Laau Ridge (K2), Namolokama Mountain (K3), and other peaks to the Alakai. On the other hand, our data show that the native Kauai birds have declined precipitously in the last decade. From an equilibrium standpoint, the Kauai habitat islands may be "oversaturated" with species because of the environmental changes that have occurred since Western contact, and imminent extinction of several species may reflect biogeographical "relaxation" of the fauna. The West Maui forest (M2) has the highest negative deviation (3 species instead of 7 predicted), and this in part reflects the small area at high elevations and extensive area of unforested bogs. Here it would be instructive to transplant Maui Creepers and Crested Honeycreepers to determine whether viable populations can exist.

Although species-area relationships are frequently explained as resulting from greater habitat diversity or larger population sizes (Whitehead and Jones 1969, Diamond 1975, Williamson 1981), in the Hawaiian rainforest habitat island series, the greatest numbers of species tend to occur in relatively undisturbed high-elevation areas. The relations in Figure 312 thus primarily reflect the functional association of intact communities with larger, higher, and hence more ecologically "buffered" areas.

Juvik and Austring (1979) applied biogeographic equilibrium theory to the endemic land birds of the Hawaiian Islands, using island area and all historically known species as data. Although they found a strong correspondence between island size and number of species, their results were brought into serious question by recent fossil finds of the extinct lowland avifauna

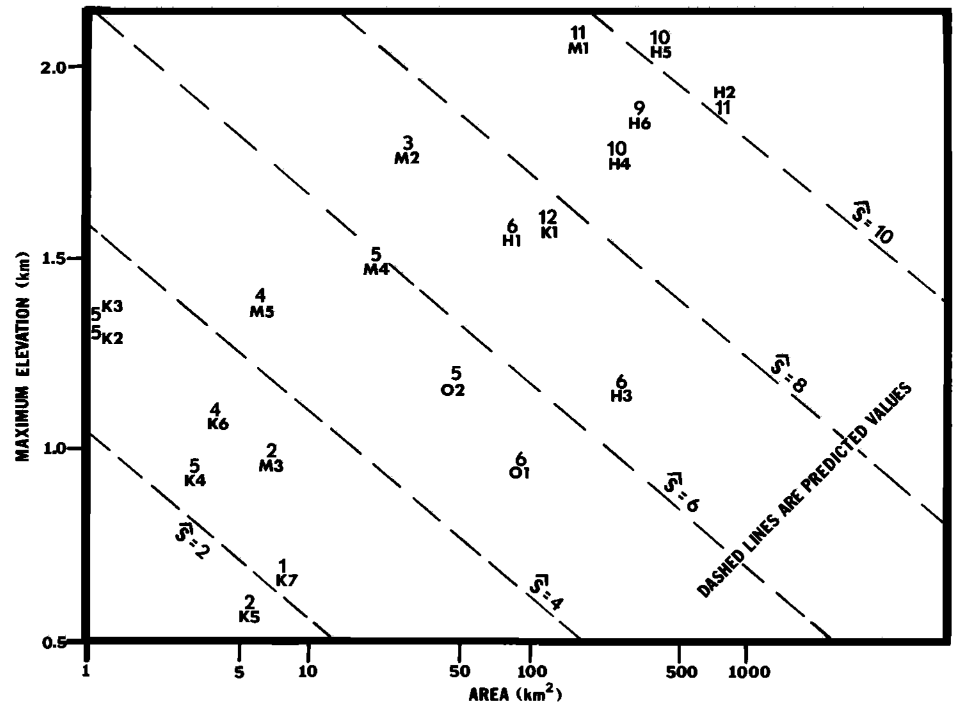


FIGURE 312. Scatterplot showing relationships between species richness, area, and elevation for 20 habitat islands of montane rainforest. (Horizontal axis is logarithmically scaled. Numbers in plot give the number of native forest bird species present in the habitat island. Code below species number identifies habitat island location as shown in Figure 311. Dashed lines give predicted species richness based on regression from elevation and area as described in the *Species-Area Relationships* section.)

(Olson and James 1982b). Even if the original avifauna did not follow the classical species-area equilibrium expectation, the analysis by Juvik and Austring may still rest on relevant ecological ground, however, because island size roughly indexes the accessibility of sites of Hawaiian cultural practices. Island size may therefore have been a good predictor in their study because it may effectively index the degree of human disturbance before Western contact.

Richness and Diversity

Native species richness

The communities with the greatest number of native species are located in relatively undisturbed forests at higher elevations. Refugia having more species than other areas are found on Hawaii (upper Kau, upper Hamakua, North Hualalai, central Kona, the Puu Laau area of Mauna Kea), East Maui, Molokai, and Kauai (Alakai Swamp).

The habitat response graphs indicate that native species richness is greatest above 1500 m elevation in mesic and wet koa-ohia forests (Fig. 313). On Maui, richness is greatest at upper elevations in mesic ohia-koa and wet ohia forests. The strongest response to native species richness in the regression models (Table 67) is to elevation, which shows a bell-shaped curve (negative quadratic coefficient) in six models. The modes of elevational response are generally above 1700 m, except for the low-elevation Puna area. Molokai has a peculiar bimodal response that appears to reflect the devastation of mid-elevation forest on the east half of the study area by feral ungulates, particularly pigs and deer. Effects of ungulates may also explain the seemingly aberrant positive response on Molokai to matted ferns, which are characteristic of lower intensity disturbance.

Moisture is associated with higher native species richness in four regression models, which reflects the generally more intact nature of wet native forest compared with dry forest. The negative term in the Molokai model corrects for sparse dry forests at low elevations; the correlation between moisture and native species richness in that study area is weakly positive ($r = 0.08$).

Native species richness is highest in forested areas, indicated by positive tree biomass terms in the Kohala and Maui regression models, by

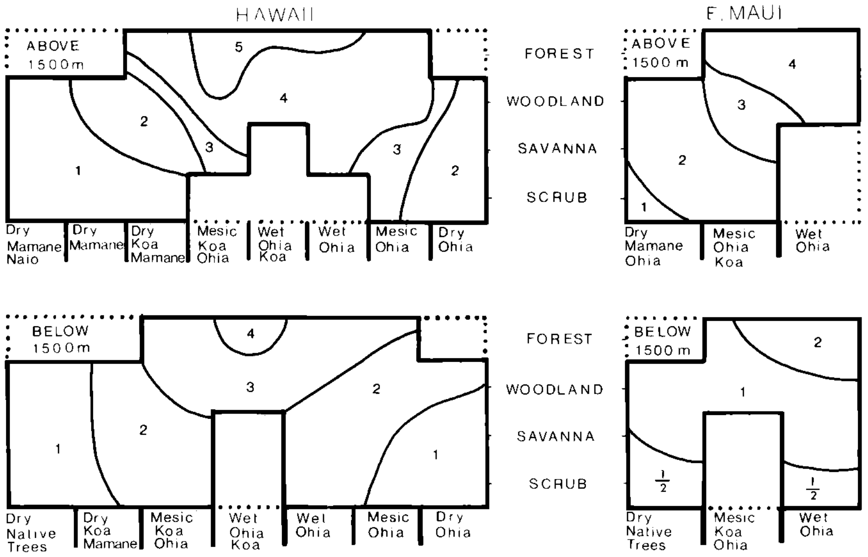


FIGURE 313. Habitat response graphs of native species richness (the number of native bird species occurring at a station).

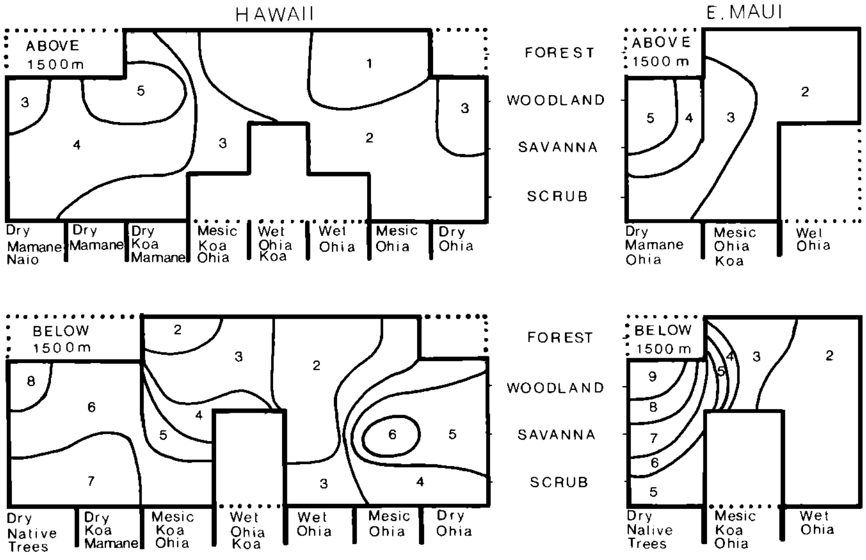


FIGURE 314. Habitat response graphs of introduced species richness (the number of introduced bird species occurring at a station).

upward-opening parabolas centered below mean tree biomass in the Kau, Hamakua, Kipukas, Kona, and Molokai models, and by positive terms for crown cover and canopy height in Puna. Crown cover has positive terms in the Kona and Puna models, but negative terms in Kau and Kipukas counterbalance tree biomass squared to yield a net effect of nearly linear response to tree biomass. Canopy height is of minor importance. Responses to individual tree species are minor, except for avoidance of introduced trees in three models.

Among understory elements, matted ferns are associated with lower native species richness. Passiflora is associated with lower species richness in Hamakua, and is a correction term for dry open forests on Maui, where it has a weak negative correlation with native species richness

TABLE 67
Regression Models for Habitat Response of Native Species Richness[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Kauai
Mean	3.44	3.03	1.97	2.56	2.32	1.19	2.04	1.82	0.82	5.96
SD	1.45	2.02	0.93	0.88	1.30	0.76	1.11	1.47	0.59	1.18
R^2	0.51*	0.67*	0.29*	0.36*	0.48*	0.27*	0.49*	0.59*	0.37*	0.04
Moisture	···	4.6*	···	2.1	12.2*	X	X	6.8*	−3.0	X
Elevation	6.5*	20.1*	6.5*	11.3*	6.7*	···	13.0*	6.2*	−5.1*	···
(Elevation)^2	−4.3*	−12.1*	−5.4*	−10.9*	−2.9	···	···	−5.1*	5.5*	···
Tree biomass	···	−4.5*	···	···	−10.8*	4.8*	2.5	8.7*	···	···
(Tree biomass)^2	7.9*	6.3*	···	4.4*	12.5*	···	···	···	6.0*	···
Crown cover	−4.3*	···	3.7*	−2.2	5.9*	···	···	···	···	···
Canopy height	···	···	2.9	−4.9*	2.5	2.1	···	···	···	···
Koa	5.4*	···	X	···	5.2*	X	X	···	X	X
Ohia	···	5.5*	···	···	···	X	···	4.3*	···	X
Naio	X	X	X	···	2.7	···	X	X	X	X
Mamane	X	···	···	4.8*	···	···	X	−4.3*	X	X
Intro. trees	X	−4.2*	···	X	−2.0	X	···	−2.1	···	X
Shrub cover	···	8.4*	···	···	···	−5.9*	···	···	···	···
Ground cover	···	−4.8*	···	···	···	···	···	2.4	···	···
Native shrubs	···	···	···	···	2.6	X	···	···	···	···
Intro. shrubs	X	8.4*	···	···	−2.3	X	···	···	···	···
Ground ferns	X	X	···	···	10.2*	X	···	···	3.9*	···
Matted ferns	···	−7.1*	−5.5*	···	···	X	−2.8	···	3.5*	···
Tree ferns	···	X	···	X	···	X	···	−4.3*	···	2.4
Ieie	X	X	···	X	−6.6*	X	X	2.3	X	···
Passiflora	X	−8.7*	X	X	···	X	···	2.5	X	X
Native herbs	X	X	···	···	−4.5*	X	···	···	···	···
Intro. herbs	X	X	−2.5	···	···	···	···	···	···	···
Native grasses	···	···	···	···	···	···	···	3.2	···	···
Intro. grasses	···	5.1*	−6.5*	···	···	−3.4	···	···	−3.4	···
Ohia flowers	···	4.9*	···	···	5.0*	X	2.7	···	4.8*	···
Olapa fruit	···	−3.5*	···	···	···	X	···	3.1	···	···
Mamane flowers	X	X	X	···	X	···	X	···	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model. No model was fit for Lanai; mean value 0.35, SD 0.51.

TABLE 68
Regression Models for Habitat Response of Introduced Species Richness[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Lanai	Kauai
Mean	1.29	2.16	2.63	2.81	4.23	2.88	2.28	2.61	2.65	3.18	2.40
SD	0.83	1.12	1.32	2.09	2.31	1.63	1.15	1.95	1.37	1.28	1.22
R^2	0.26*	0.35*	0.58*	0.72*	0.46*	0.53*	0.20*	0.40*	0.41*	0.17*	0.39*
Moisture	···	···	−7.8*	−7.7*	−6.3*	X	X	−13.4*	−19.1*	···	X
Elevation	2.9	3.4*	−5.0*	2.9	7.2*	5.1*	···	7.3*	−2.6	···	−3.8*
(Elevation)^2	−4.7*	−4.4*	−11.5*	2.9	−9.8*	−5.5*	···	−8.0*	3.2	···	3.5*
Tree biomass	···	5.3*	6.6*	···	6.8*	−11.8*	···	8.6*	···	···	−2.5
(Tree biomass)^2	···	−4.0*	···	···	−6.3*	11.8*	···	···	···	···	···
Crown cover	−5.3*	···	−5.7*	···	−6.1*	···	−2.0	···	···	···	···
Canopy height	···	2.8	−4.7*	6.5*	···	12.5*	···	···	···	···	···
Koa	3.1	4.5*	X	···	···	X	X	···	X	X	X
Ohia	···	−13.8*	···	−7.7*	−4.4*	X	···	−5.0*	···	···	X
Naio	X	X	X	···	···	···	X	X	X	X	X
Mamane	X	···	3.9*	···	11.2*	···	X	2.3	X	X	X
Intro. trees	X	−3.0	···	X	6.1*	X	2.9	···	···	···	X
Shrub cover	−4.3*	−10.2*	4.2*	···	−2.1	−8.1*	···	···	···	···	···
Ground cover	···	3.6*	−2.9	···	2.1	···	···	···	···	···	···
Native shrubs	···	9.3*	···	···	···	X	···	···	···	···	···
Intro. shrubs	X	10.3*	···	···	···	X	···	2.1	···	···	···
Ground ferns	X	X	···	···	−3.6*	X	···	···	···	X	···
Matted ferns	···	−5.1*	···	···	−5.5*	X	···	···	···	−3.7*	···
Tree ferns	···	X	−6.9*	X	···	X	···	···	···	X	···
Ieie	X	X	···	X	···	X	X	···	X	X	···
Passiflora	X	6.2*	X	X	5.9*	X	···	8.0*	X	X	X
Native herbs	X	X	···	···	−3.4*	X	···	···	···	X	···
Intro. herbs	X	X	···	5.0*	5.0*	···	···	···	···	X	···
Native grasses	···	−6.2*	−4.4*	−5.4*	−5.4*	···	···	···	2.6	X	···
Intro. grasses	···	···	3.6*	···	2.8	−6.0*	4.8*	4.2*	···	···	···
Ohia flowers	3.0	6.8*	···	···	···	X	···	···	3.0	···	···
Olapa fruit	···	3.2	···	···	···	X	···	···	···	···	−2.5
Mamane flowers	X	X	X	···	X	···	X	−3.2	X	X	X
Mamane fruit	X	X	X	X	X	···	X	X	X	X	X
Naio fruit	X	X	X	X	X	···	X	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are *t* statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model.

TABLE 69
REGRESSION MODELS FOR HABITAT RESPONSE OF BIRD SPECIES DIVERSITY (SIMPSON'S INDEX)[a]

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	Maui	Molokai	Lanai
Mean	2.92	2.92	2.26	2.72	2.79	2.06	2.66	2.54	1.80	1.41
SD	1.04	1.46	0.72	0.86	1.03	0.69	1.05	1.29	0.59	0.37
R^2	0.23*	0.61*	0.39*	0.43*	0.30*	0.20*	0.32*	0.36*	0.33*	0.23*
Moisture	· · ·	8.3*	-7.8*	· · ·	2.4	X	X	· · ·	-3.4*	· · ·
Elevation	11.0*	16.6*	5.3*	9.3*	7.1*	· · ·	9.7*	8.9*	-4.9*	· · ·
(Elevation)^2	-10.1*	-9.1*	-4.8*	-9.6*	-7.5*	· · ·	· · ·	-7.6*	6.3*	· · ·
Tree biomass	· · ·	-2.0	· · ·	· · ·	-7.4*	· · ·	-2.1	11.7*	7.5*	· · ·
(Tree biomass)^2	4.7*	3.7*	3.5*	3.7*	8.6*	· · ·	2.4	· · ·	· · ·	· · ·
Crown cover	-3.2	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·
Canopy height	· · ·	· · ·	· · ·	· · ·	5.2*	8.6*	· · ·	· · ·	· · ·	3.0
Koa	· · ·	· · ·	X	· · ·	6.0*	X	X	· · ·	X	X
Ohia	· · ·	· · ·	· · ·	-3.5*	-5.3*	X	· · ·	· · ·	· · ·	· · ·
Naio	X	X	X	-2.9	· · ·	· · ·	X	X	X	X
Mamane	X	-2.8	· · ·	· · ·	6.9*	-3.8*	X	-2.0	X	X
Intro. trees	X	-4.1*	· · ·	X	2.3	X	· · ·	· · ·	· · ·	· · ·
Shrub cover	· · ·	-3.0	· · ·	· · ·	-5.0*	3.4*	· · ·	· · ·	· · ·	-3.7*
Ground cover	· · ·	4.2*	· · ·	· · ·	2.6	3.1	· · ·	3.4*	· · ·	· · ·
Native shrubs	· · ·	5.2*	· · ·	· · ·	3.0	X	· · ·	· · ·	· · ·	· · ·
Intro. shrubs	X	10.5*	· · ·	· · ·	· · ·	X	· · ·	· · ·	· · ·	· · ·
Ground ferns	X	X	· · ·	· · ·	4.1*	X	· · ·	· · ·	3.6*	X
Matted ferns	· · ·	-7.9*	-9.6*	· · ·	-5.8*	X	· · ·	· · ·	4.0*	· · ·
Tree ferns	· · ·	X	· · ·	X	3.6*	X	· · ·	-2.7	-2.3	X
Ieie	X	X	· · ·	X	-7.4*	X	X	3.1	X	X
Passiflora	X	-2.7	X	X	2.0	X	· · ·	3.8*	X	X
Native herbs	X	X	· · ·	· · ·	-2.1	X	· · ·	· · ·	· · ·	X
Intro. herbs	X	X	-4.0*	2.6	· · ·	· · ·	· · ·	· · ·	· · ·	X
Native grasses	· · ·	-6.9*	· · ·	-8.0*	· · ·	· · ·	· · ·	· · ·	2.7	X
Intro. grasses	· · ·	· · ·	-3.9*	2.4	· · ·	· · ·	· · ·	· · ·	· · ·	· · ·
Ohia flowers	-2.6	· · ·	· · ·	· · ·	2.5	X	· · ·	· · ·	· · ·	· · ·
Olapa fruit	2.3	-4.8*	· · ·	· · ·	3.0	X	· · ·	3.1*	· · ·	· · ·
Mamane flowers	X	X	X	· · ·	X	· · ·	X	· · ·	X	X
Mamane fruit	X	X	X	X	X	· · ·	X	X	X	X
Naio fruit	X	X	X	X	X	· · ·	X	X	X	X

[a] R^2 is the variance accounted for by the model. Entries are t statistics and all are significant at $P < 0.05$; * indicates $P < 0.001$; · · · indicates variable not significant ($P > 0.05$); X indicates variable not available for inclusion in model. No model was fit for Kauai; mean value 3.65, SD 0.72.

($r = -0.05$). Introduced grasses often indicate extensive disturbance and have a negative relation to native species richness in Puna, Mauna Kea, and Molokai. In Hamakua, introduced grasses have high cover in montane pastures with scattered koa trees where several native birds occur. Ohia flowers are important in four models and reflect the response of nectarivorous birds.

Introduced species richness

The number of introduced species reaches highest levels in our study areas on north Hualalai and on the dry south side of East Maui. The high number of introduced species in the Puu Waawaa area of Kona reflects the history of that area as a release site for introduced gamebirds (Lewin 1971) and passerines (van Riper 1978b). Introduced species richness peaks below 1500 m in dry woodlands, with unbroken forest and wet habitat supporting fewer introduced species (Fig. 314).

The regression models (Table 68) indicate that introduced species richness is greatest at lower elevations in dry partly open woodlands with an understory dominated by introduced plants. Five models show more introduced bird species in dry areas. In the Molokai model, the moisture relation overwhelms the other variables. Lower elevations are associated with a greater number of species in nine models. This reflects location of introduction sites and probably poor adaptation by many introduced species to the cold montane environment.

The responses to forest development are mixed, but frequently indicate a bell-shaped response to tree biomass. Crown cover is negative in four models and indicates that few gamebirds penetrate closed forests. This is further seen in the negative terms for ohia in four models and in the positive terms for mamane (characteristic of dry open woodlands) in three models. Introduced trees are associated with introduced birds in two models, but the negative term in Hamakua is a correction term ($r = 0.12$ between introduced species richness and introduced trees).

Introduced understory elements are associated with greater introduced species richness. Introduced bird species respond positively to introduced shrubs in two models, to passiflora in three, to introduced herbs in two, and to introduced grasses in four. Disturbed areas thus harbor greater numbers of introduced bird species than native communities and are potential avenues of dispersal. Response to native understory components is weak, except for four negative responses to native grasses (the positive response in Molokai was a correction term), and three negative responses to matted ferns.

Use of ohia flowers, and to a lesser extent olapa fruit, by the Red-billed Leiothrix, Japanese White-eye, and House Finch is seen in the positive terms for these variables.

Bird species diversity

The reciprocal of Simpson's index of diversity, $1/\Sigma\ p^2$, gives the number of equally common species that would produce the same heterogeneity as observed at a station (Peet 1974). This diversity index tends to be highest in well-developed forests at mid-elevations (Table 69). Although Kauai (Alakai Swamp) has the highest diversity of any study area, no model is fitted, indicating a homogeneous cluster. Bird species diversity peaks in well-developed forests with partly open shrub and closed ground cover, but is low in areas dominated by matted ferns.

Diversity increases in wetter habitat in the Hamakua and Kona models, but in Puna and Molokai the dominance of introduced birds, especially gamebirds, generates higher diversity in drier habitat.

Bell-shaped responses to elevation appear in six models. The modes occur between 1300 and 1700 m in most models, and at 800 m for the low-elevation Puna area. Hamakua has a mode of 2150 m, reflecting high diversity in disturbed montane koa-ohia pastures. Molokai has a bimodal response, reflecting two areas of high diversity, one of gamebirds in the lowlands, the other of passerines in montane forests.

Diversity responds positively to tree biomass in almost every forest, but crown cover and canopy height have little effect on diversity. Positive responses in Kona to mamane and koa reflect the extensive dry open forests. On Mauna Kea, the negative mamane term reflects the greater number of species associated with mixed mamane-naio areas, probably a result of the greater diversity of plant resources. Generally the responses to individual tree species are weak.

Bird diversity tends to increase with ground cover in four models. The negative relations to shrub cover in the Hamakua and Kona models are balanced by positive terms for native and introduced shrubs, suggesting higher diversity in partly open shrub cover. Matted ferns tend to lower diversity, as expected from their low cover and food value. In Hamakua and the Kipukas, the negative responses to native grasses reflect low diversity in high elevation scrublands. On Molokai the positive responses to native grasses, ground ferns, and matted ferns indicate higher densities in less disturbed areas. Other understory variables such as tree ferns, ieie, passiflora, introduced herbs, and introduced grasses have conflicting, usually weak, responses across the models; this pattern resists explanation and seems to reflect peculiarities within the individual species pools. Terborgh (1977) found a similar problem in analyzing bird diversity indices for study sites in the Peruvian Andes; fundamental differences in the natural history of the species in different guilds led to distinct patterns of response to elevation, making compound indices difficult to interpret.

Comparisons of habitat responses among community variables

The strong contrasts in habitat response between native and introduced species richness accent the retreat of native species to montane refugia, the lowland introduction sites of introduced passerines, and the abundance of gamebirds in dry open brush. Native species richness usually responds positively to elevation, whereas introduced species richness has negative responses. Diversity reflects the occurrence of native and introduced birds, and has a markedly bell-shaped response to elevation. Forests support a greater number and diversity of birds than deforested areas. This relationship is frequently noted among bird communities compared across landscapes (Johnston and Odum 1956, MacArthur and MacArthur 1961, Recher 1969, Karr and Roth 1971, Willson 1974, Sabo 1980, May 1982). Matted fern understories have few food resources and are often associated with reduced species richness. Increased food levels probably explain positive responses of introduced birds to introduced herbs (e.g., for gallinaceous birds) and passiflora, and of both native and introduced birds to ohia flowers.

General Patterns of Habitat Response

The Hawaiian Islands offer an ideal situation for studying avian habitat response. Striking variations in vegetation occur within distances of 10–30 km, encompassing montane rainforests, mixed mesophytic forests, fragments of rich dryland forest, dry subalpine woodlands, desert and subalpine scrublands, alpine grasslands, cinder deserts, grazed rangelands, and lush lowland rainforests composed entirely of introduced plant species. The land birds are generally rather conspicuous and offer an interesting contrast between coevolved endemic spepcies on the one hand and haphazardly introduced species on the other. Although local movements do occur, the land birds are year-round residents so that long-distance migration does not complicate the interpretation of habitat response.

An important approach in ecology is the search for repeated patterns to compare and contrast species responses to a spectrum of habitat features in order to gain insight into the factors determining habitat response (see MacArthur 1972:1). The 164 fitted models of species habitat response may be viewed as samples from the total population of habitat responses of Hawaiian forest birds. In this section we identify common patterns running through this set of case histories and relate these patterns of community structure to the patterns occurring in other bird communities. The major gradients structuring habitat response patterns among the Hawaiian forest birds in this study are (1) the "abiotic" landscape factors of elevation and moisture; (2) gross vegetation structure, especially the density and height distribution of foliage; (3) detailed physiognomic structure, floristic composition, and temporal phenological variation (essentially fine vegetation structure and correlated food resources); and (4) other factors inferred to be limiting, notably absence of water in arid areas, habitat heterogeneity, minimum forest size, and bioenergetic requirements. Before embarking on this discussion, however, let us first evaluate the relative importance of the habitat variables included in our analysis.

Relative importance of habitat variables

For a rough measure of the importance of each habitat variable in determining species response, we computed the percent of regression models into which a particular variable entered, out of all those models it could have entered. These percentages were tallied from the models analyzed earlier, according to three groups: introduced nonpasserines (gamebirds), introduced passerines, and native passerines (Table 70). In order to reduce the variation from minor variables and poorly-fit models, we based our calculations on those variables and regression models that had a significance level of 0.1% or lower; 155 fitted models met this criterion for analysis. Obviously this analysis provides an overview of the roles of different habitat variables; for a particular species, certain variables may be far more important than in the general pattern.

Elevation, moisture, and tree biomass (as an index of forest development) are important variables in all three groups of birds. Individual tree species and certain understory components, especially passiflora, are also major variables. Most understory components have little influence (<20% of the models) on any group.

Elevation has a dominant influence on habitat response and appears in 74% of all regression models. In 43% of all models the response to elevation is significantly curved (i.e., quadratic term present). In 28 models (18%) the response is truly bell-shaped (i.e., an inverted parabola with a symmetry axis located within one standard deviation of the mean elevation), indicating the importance of nonlinear effects. A similar role for nonlinear terms was found in a study of avian habitat response by Meents et al. (1983), where 41% of the models had polynomial terms.

Moisture is most important in gamebird regression models where it reflects numerous successful introductions in dry habitats. Although moisture enters fewer native passerine models, it is still important. The low percentage of native passerine models that incorporate moisture is a result of the tendency of those birds to inhabit wetter forests. Since wet habitats dominate most study areas, moisture would not enter a model if highest densities occur in moderately wet forests. Birds preferring either dry habitat or very wet rainforest, however, produce a moisture term in most models that indicates significant departure from the average moisture regime.

Forest development enters 52% of the regression models as tree biomass. Curved responses for this factor are less frequent than for elevation, with quadratic terms present in only 24% of all models. True bell-shaped responses are rare, occurring in only 2% of all models. Since tree biomass is entered into the regression models before crown cover and canopy height, these latter two variables index specific foliage configurations rather than general forest development (unlike in most other studies). Their occurrence in only 14% of all models indicates that, for many birds, the volume occupied by foliage is a sufficiently precise measure of the vegetation configuration. As identified in the species accounts, crown cover and canopy height tend to change the interpretation of models when tree biomass is also entered. When several of these related variables are included in a model, surrogate relations occur that sometimes indicate bell-shaped response, e.g., preference for partly open woodland. This phenomenon probably explains the low incidence of true bell-shaped curves for tree biomass. For a better indication of the frequency of bell-shaped response to forest development per se, canopy height, crown cover, and probably individual tree species should be deleted from the models. An alternative would be to remove the effect of tree biomass from these variables by a prior analysis of covariance, but this correction would differ for each study area, and the resulting models would be difficult to compare.

Individual tree species vary in their ability to shape habitat response patterns. Koa is important for native passerines, entering 51% of the regression models. Introduced passerines respond less strongly to koa, and in gamebird models, koa is a minor variable. Gamebirds have stronger responses than passerines to ohia and mamane, but usually these trees act as indicators of rainforest and dry open woodland, respectively. Mamane and naio sometimes indicate dry woodland in passerine models. Although the less frequent response of native birds to ohia (and ohia flowers) seems unexpected at first glance, most study areas have fairly high mean values for ohia, and no term is needed to indicate that response coincides with the mean value. The situation parallels that of moisture, and gamebirds have more frequent, but usually negative, responses to ohia. Introduced trees are relatively unimportant except to introduced passerines.

Most understory components generate feeble habitat response, with 13–29% of the models incorporating total shrub or ground cover. Taking 20% as a benchmark, we find that native shrubs, ground ferns, matted ferns, ieie, native herbs, introduced herbs, and introduced grasses generally fall below it, implying that, in general, birds

TABLE 70

RELATIVE IMPORTANCE OF HABITAT VARIABLES: PERCENTAGE OF MODELS IN WHICH VARIABLES ARE INCLUDED AT $P < 0.001$

Variable	Gamebirds	Introduced passerines	Native passerines
Number of species	12	13	14
Number of models	38	65	52
Moisture	62	56	43
Elevation[a]	79	71	73
Tree biomass[a]	63	42	56
Crown cover	16	18	12
Canopy height	16	23	10
Koa	15	33	51
Ohia	35	29	22
Naio	6	33	31
Mamane	35	30	32
Intro. trees	21	29	13
Shrub cover	21	25	15
Ground cover	29	26	13
Native shrubs	14	10	14
Intro. shrubs	12	20	20
Ground ferns	25	11	18
Matted ferns	6	13	18
Tree ferns	20	7	31
Ieie	5	15	32
Passiflora	45	19	50
Native herbs	4	11	18
Intro. herbs	16	23	19
Native grasses	32	21	31
Intro. grasses	13	18	23
Ohia flowers	...	14	29
Olapa fruit	...	12	10
Mamane flowers	...	12	7

[a] Percentage of models with linear term, quadratic term, or both.

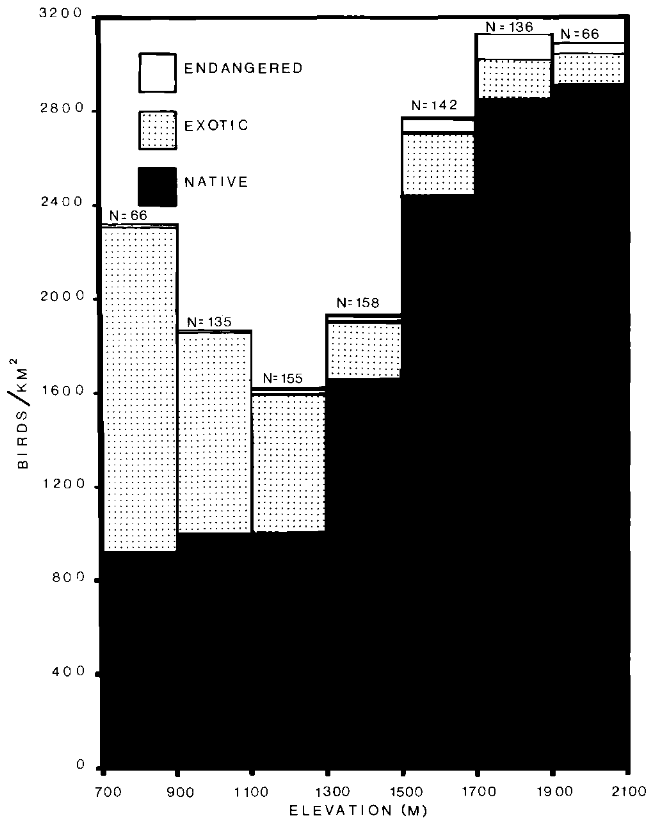


FIGURE 315. Relation of total native, introduced, and endangered bird density to elevation in the Kau study area. (N = number of stations sampled)

discriminate weakly among these habitat components. Birds tend to respond negatively to some of these elements, notably matted ferns and introduced grasses, because these plants lower habitat quality by displacing food source plants (e.g., fruiting shrubs). These minor understory variables often appear to act as indicators of disturbance. Introduced shrubs, native grasses, and tree ferns enter about 20% of the models. Native grasses often enter models as indicators of alpine grassland.

The understory variable with the greatest effect on habitat response is passiflora. Unlike other understory components, passiflora (in particular banana poka) offers abundant nectar and fruit and dominates sizable areas. It thus has mostly positive terms in the models, but some species (Omao, Elepaio, Akiapolaau) have lower densities in infested areas. Passiflora enters models with about the same frequency (37%) as individual tree species. Native passerines have the highest proportion of entries for this variable (51%). Its role in structuring habitat response is thus greater than would be predicted from its contribution to the configuration of the foliage column.

Abiotic factors

Elevation and moisture are geological and meteorological variables that are exogenous to the system. they interact with one another, affect many other habitat variables, and underlie landscape-wide patterning. Elevation enters three quarters of the fitted models and is closely related to temperature, introduction sites for introduced biota, the distribution of disease vectors, and disturbance from human activities. Moisture enters 53% of the models and is related to plant species richness in our study areas (Table 2), although dry lowland areas originally had more species than wet areas before Polynesian contact (Rock 1913).

The following are the main patterns of habitat response to these variables. Introduced passerine birds tend to be more common at lower elevations, reflecting the lowland introduction sites

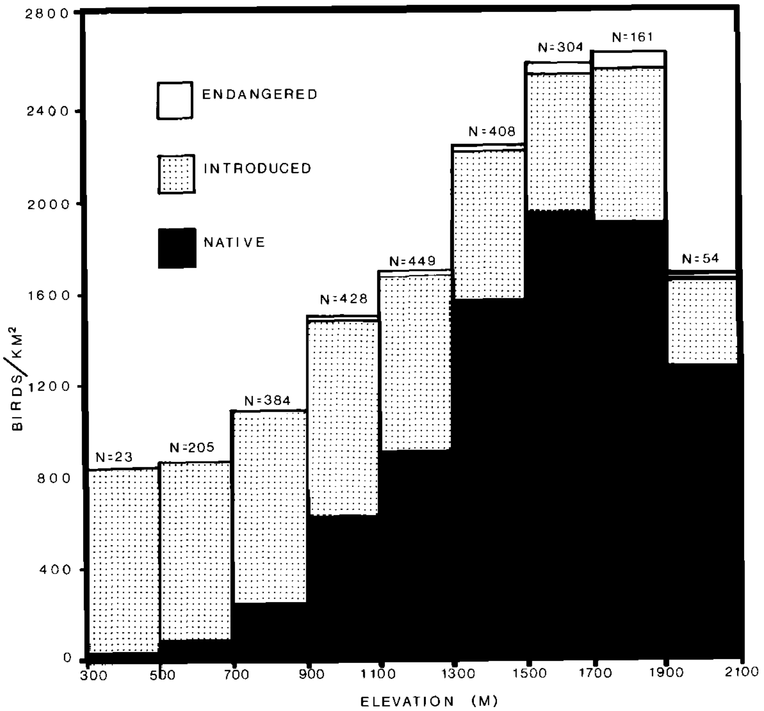


FIGURE 316. Relation of total native, introduced, and endangered bird density to elevation in the Hamakua study area. (N = number of stations sampled)

and probably lack of thermoregulatory adaptation of some species to the cold environments above 1500–2000 m. Introduced gamebirds tend to be more common in dry areas, probably because most species selected for introduction are natives of dry habitats. Native passerines tend to be more common at higher elevations below timberline in less disturbed native forests, probably because the habitat is relatively intact and the area relatively disease free. The responses of native, introduced, and endangered bird densities to elevation show similar patterns in the Kau (Fig. 315), Hamakua (Fig. 316), Kona (Fig. 317), and East Maui (Fig. 318) study areas. Endangered bird densities generally follow native bird densities, except for the sharp drop-off below 1300–1500 m. Native species tend to be more abundant in wet habitats than dry because of the greater number of woody plant species and the probable greater diversity of food resources. Bell-shaped responses to elevation are fairly frequent (18% of the species models), with the models for the Omao, Ring-necked Pheasant, Red-billed Leiothrix, House Finch, native species richness, and bird species diversity serving as typical examples. The habitat responses for many introduced birds seem very similar to their responses in their native lands, suggesting that habitat responses are closely related to innate physiological, morphological, and behavioral traits.

Terborgh (1977) found that the chronic environmental hardships associated with cool environments at high elevations generally result in depauperate avifaunas in the Peruvian Andes. This is most clearly reflected in the Hawaiian forest by the few introduced bird species that enter the montane rainforest. A similar reduction in the number of species at higher elevations also occurs in the subalpine zone of New England mountains (Able and Noon 1976, Sabo 1980, Sabo and Holmes 1983). Moisture has been less emphasized than elevation as a determinant of habitat response in most studies. Orians (1969) found that wet tropical sites have greater between-habitat species diversity than dry sites; wet tropical areas generally have greater productivity than dry areas (Lieth 1973). This pattern reappears in temperate grasslands, where low rainfall sites have fewer bird species and lower plant biomass than more mesic sites (Wiens 1973). Moisture is a primary gradient effecting bird species distribution in temperate deciduous forests (Bond 1957, Smith 1977, Kendeigh and Fawver 1981) and tropical lowlands (Karr and Freemark 1983),

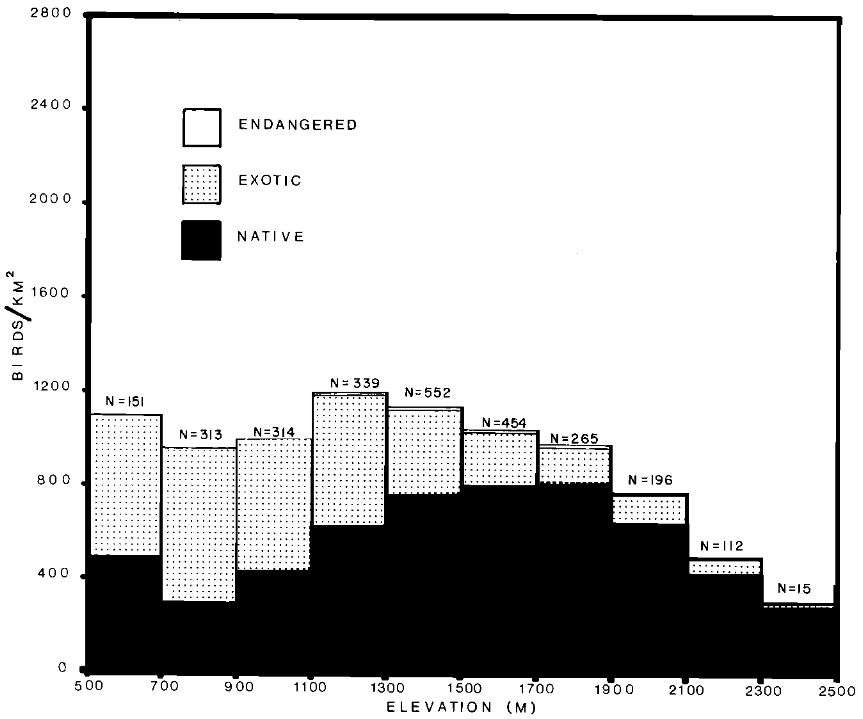


FIGURE 317. Relation of total native, introduced, and endangered bird density to elevation in the Kona study area. (N = number of stations sampled)

and guild structure in coniferous forests (Wiens and Nussbaum 1975).

Gross vegetation structure

Gross vegetation structure, the vertical layering of foliage, follows a gradient from grasslands to forests in structural development and overlies secondary patterns of ground and shrub cover. Although response to ohia dieback reflects response to gross structure, we defer our discussion of that topic to a separate section. The subtle habitat qualities of fine vegetation structure, discussed in a later section, were considered by several workers (MacArthur and MacArthur 1961, Recher 1969, DesGranges 1980) as unnecessary or irrelevant in explaining community patterns.

The most important variable describing gross vegetation structure in our study is tree biomass, which roughly indexes foliage volume, indicates position on the grassland-forest gradient, and integrates the effects of substrate, logging, grazing, and succession. Tree biomass enters 52% of all models. Less important, partly because of overlap with tree biomass and variables of floristic composition and detailed physiognomy, are canopy height, crown cover, shrub cover, and ground cover. As expected, the models show that forest birds need forests and gamebirds occur in open habitats. Native species richness and diversity are associated with more developed forests, but introduced species richness is strongly influenced by gamebirds and is highest in broken woodland. Several species are associated with specific shrub and ground cover configurations. The Ring-necked Pheasant, Common Peafowl, Wild Turkey, House Finch, and introduced species richness are associated with open shrubs and dense ground cover; Northern Cardinal, House Finch, and Iiwi with dense shrubs.

Willson (1974) showed the disproportionate influence on avian habitat response of the presence of trees, probably through adding new resources (Holmes, Bonney, and Pacala 1979). Owing to the great importance of trees, many multivariate studies of avian habitat response have shown that the most important variables are related to general habitat aspect, such as crown cover, canopy height, or shrub cover (James 1971; Anderson and Shugart 1974; Whitmore 1975, 1977; Sabo 1980; Rice et al. 1983). Studies on the effect of logging and thinning on bird response also indicate the importance of tree density and diameter (Hagar 1960, Kilgore 1971, Franzreb and Ohmart 1978, Szaro and Balda 1979), as have studies on bird distribution along plant succession gradients (Adams 1908; Odum

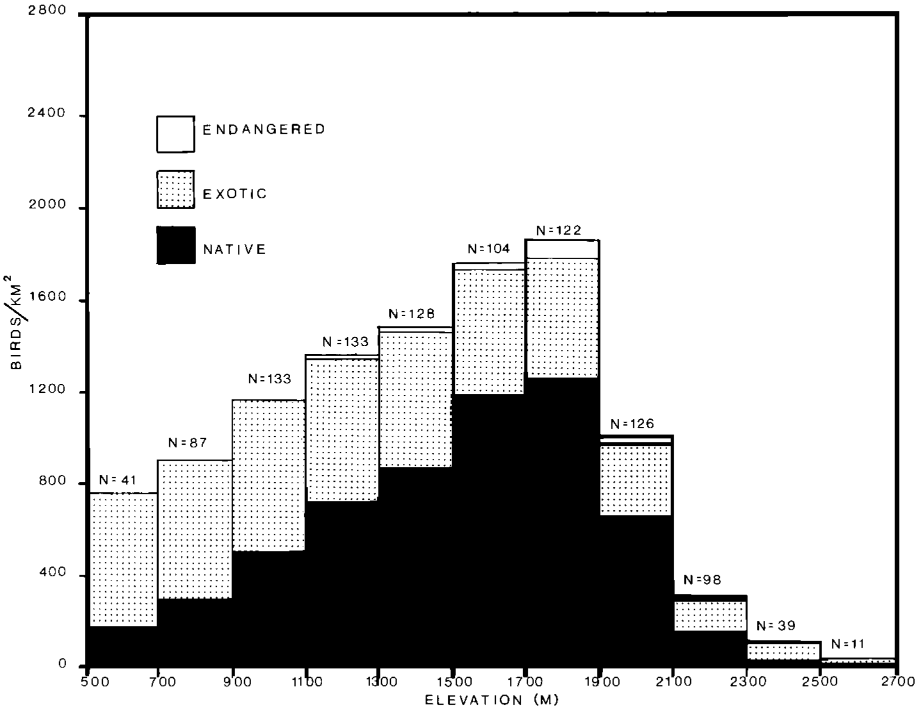


FIGURE 318. Relation of total native, introduced, and endangered bird density to elevation in the East Maui study area. (N = number of stations sampled)

1950; Johnston and Odum 1956; Salt 1957; Haapanen 1965, 1966; Shugart and James 1973; Głowacinski and Weiner 1977; Smith and MacMahon 1981; May 1982). The importance of the individual canopy, shrub, and ground layers was first studied in relation to information indices of bird species diversity and foliage height diversity (MacArthur and MacArthur 1961, MacArthur 1964, MacArthur et al. 1966, Recher 1969, Karr and Roth 1971). Gradually it was recognized that variation within individual layers is also important (Willson 1974, Folse 1982), and eventually many examples were reported where individual dominant plant species predict habitat responses better than height profiles (see references in *Fine vegetation structure* section, beyond).

Response to ohia dieback

Life history strategy of the dominant plant species also modifies bird distribution. Death and defoliation of canopy ohia trees occur in a few years over large areas of native montane rainforest in the dieback phenomenon (Mueller-Dombois and Krajina 1968, Petteys et al. 1975, Jacobi 1983, Mueller-Dombois 1983a). These areas are widespread at 600–1800 m elevation in the Kau, Hamakua, and East Maui study areas, and appear to be successional phenomena related to ohia's role as a pioneering species (Jacobi 1983, Mueller-Dombois 1983b). Often matted ferns dominate the understory after foliage loss of the canopy dominants. Obviously such changes in vegetation structure can have a major impact on avian communities. Comparing ohia dieback areas with adjacent tall closed ohia forests in Hamakua, dieback sites have 70% lower Apapane, 77% lower Iiwi, 47% lower Omao, and 93% lower Elepaio densities, but 30% higher Red-billed Leiothrix and 34% higher Japanese White-eye densities ($P < 0.05$ for all differences). The dieback areas are thus associated with much lower densities of native species and higher densities of some introduced species.

Fine vegetation structure

Variables describing detailed physiognomy, floristic composition, and phenological status form a loose group of fine habitat attributes. Often these attributes are directly related to food resources—specific flower or fruit resources, insect faunas associated with certain plant species, and understory components particularly low in food resources ("sterile"). Other times these variables act as indicators of specific configurations of environment and vegetation.

Ohia flowers are a key food resource. Ohia exhibits profuse flowering; most populations are obligate outcrossers and have a mutualistic relation with nectarivorous birds (Carpenter 1976). Ohia flowers are positively associated in our analysis with the Common Amakihi, Iiwi, Crested Honeycreeper, Apapane, Red-billed Leiothrix, Japanese White-eye, native species richness, and introduced species richness. Localized interference competition for nectar organizes native species into a dominance hierarchy (Baldwin 1953, Pimm and Pimm 1982), but does not modify large-scale habitat response (Mountainspring and Scott 1985). On Molokai and probably on Maui, a five-member dominance hierarchy based on ohia flowers originally occurred, with Bishop's Oo as the alpha member of the series, followed by Black Mamo, Crested Honeycreeper, Iiwi, and Apapane. These birds were primarily nectarivorous and usually drove away Common Amakihi and *Paroreomyza* creepers when they occasionally attempted to feed at flowers (Perkins 1903).

Olapa fruit, another important food resource in wet forests, generates positive response among several frugivores, notably the Omao, Puaiohi, Red-billed Leiothrix, and Japanese White-eye. Two nectarivores, Crested Honeycreeper and Apapane, also feed on olapa fruit when ohia flowers are scarce. Passiflora, particularly banana poka, attracts numerous species to its flowers and fruit. Common Amakihi and Iiwi feed on the nectar, and many introduced species feed on the fruit (Erckel's Francolin, Gray Francolin, Kalij Pheasant, Common Peafowl, Wild Turkey, Red-billed Leiothrix, Northern Mockingbird, Northern Cardinal, Yellow-fronted Canary) or on both (Japanese White-eye) (Warshauer et al. 1983). Not unexpectedly, passiflora is positively associated with introduced species richness. Mamane nectar is a dietary staple for Common Amakihi (van Riper 1984) and also attracts Iiwi and Apapane. Mamane flowers were quantified in only three study areas, however, so that their *prima facie* effect on habitat response is limited. Two variables, mamane fruit (pods) and naio fruit, were quantified only on Mauna Kea. Mamane pods attract the Palila, the honeycreeper adapted to feed on them, and the Northern Cardinal. Naio fruit sustains a number of frugivorous passerines and gamebirds, especially the Wild Turkey, Melodious Laughing-thrush, and Red-billed Leiothrix. The phenology of *Broussaisia, Clermontia, Coprosma, Freycinetia, Ilex, Myrsine,* and introduced *Eucalyptus* may also affect bird distribution, but we did not gather quantitative data for these species.

Many native passerines preferentially exploit certain plants. The habitat response pattern of Palila is closely correlated with the primary food source, mamane pods (van Riper 1980, Scott et al. 1984). Other native species are or were specialized to feed on particular plants and have habitat response patterns that probably reflect the distribution of food resources: Bishop's Oo, Hawaiian Akialoa, Iiwi, Black Mamo, and Hawaii Mamo on lobeliad flowers (Perkins 1903, Rock 1919, Spieth 1966); Kona Grosbeaks on naio seeds (Perkins 1893); Lesser and Greater Koa-Finches on koa seeds (Perkins 1893); Ou on ieie bracts (Perkins 1903); Hawaiian Crows on fleshy fruit (Giffin 1983); and Hawaiian Geese on succulent ground covers (Banko and Manuwal 1982). In this regard, the large number of potential food species in remnant mature dry forests (Table 2) offers a tantalizing suggestion of the complex ecological relationships that probably occurred between the recently discovered extinct honeycreepers (Olson and James 1982a, b) and the dryland flora.

The attraction of birds to flower and fruit resources is well-known. Lovejoy (1974) found that the more common bird species in the Amazon basin tend to use conspicuous flower, fruit, and army ant resources. In our study a similar pattern appears for species feeding on ohia flowers. Snow and Snow (1971) reported that the number of frugivorous and nectarivorous bird species increases with floristic diversity on Trinidad. Similar associations between the numbers of bird species and plant species have been found on subantarctic islands (Abbott 1974), the Galápagos Islands (Bowman 1961, Hamilton and Rubinoff 1964, Lack 1969, Harris 1973, Power 1975, Abbott et al. 1977), the California Channel Islands (Power 1972), and in South America (Terborgh 1977, Pearson and Ralph 1978). The role of food levels in determining distribution is illustrated by the dramatic response to conifer seeds in many continental species including Red Crossbill (*Loxia curvirostra*) (Griscom 1937), Pinyon Jay (*Gymnorhinus cyanocephalus*) (Ligon 1978), and Clark's Nutcracker (*Nucifraga columbiana*) (Vander Wall and Balda 1977), that may migrate hundreds of kilometers to areas with good seed crops. On a more subtle level, Sage Sparrows (*Amphispiza belli*) prefer to winter in mesquite habitat with abundant inkweed (*Suaeda torreyana*), because the seeds are a food resource (Meents et al. 1982).

Differential response to dominant plants by insectivorous bird species is related in some cases to insect resource levels. Swezey (1954) and Gagné (1979) found that many Hawaiian insect taxa are specific to certain plant hosts (usually at the generic level), and Gressitt and Samuelson (1981) noted substantial variation between host species in the abundance of wood-boring larvae. Resource levels seem to explain the extensive use of koa by Akiapolaau (C. J. Ralph, pers. comm.), of *Coprosma* and *Pelea* by Maui Parrotbill (S. Mountainspring, pers. observ.), and possibly of koa by Elepaio, Common Amakihi, and Hawaii Creeper (Conant 1981). The lower densities of Red-billed Leiothrix and Japanese White-eye in pure ohia forests may reflect the lower insect levels and lack of fleshy fruit compared with mixed stands. Several understory components bear neither fruit nor flowers and usually support low insect populations. For this reason matted ferns and tree ferns may be avoided by the Common Amakihi, Hawaii Creeper, Maui Creeper, Iiwi, Crested Honeycreeper, Kalij Pheasant, Elepaio, Red-billed Leiothrix, and Northern Cardinal. Matted ferns generate negative responses to the variables indexing community structure. Melodious Laughing-thrush, however, skulk in the underbrush and seem to find matted ferns with a few trees quite acceptable habitat. Although passiflora attracts many nectarivorous native species, the negative responses by the non-nectarivorous Omao and Elepaio suggest that passiflora lowers the resource base for these species.

Resource-based explanations were proposed to explain differential use of tree species by woodpeckers (Kilham 1964, 1970), of juniper and oak by foilage insectivores (Balda 1969), and of tree species by insectivorous passerines (Holmes, Bonney, and Pacala 1979, Sabo and Whittaker 1979, Holmes and Robinson 1981). The relative efficiency of foraging in different foliage configurations appears to influence avian use of tree species in these studies. Morse (1976) noted that some spruce (*Picea*) species are easier for warblers to forage in than others because of needle morphology and arrangement. Root (1967) emphasized the interaction between morphology and vegetation characters in determining foraging patterns. Some species are adapted to feed on a single taxon, such as the Point-tailed Palmcreeper (*Berlepschia rikeri*) on *Mauritia* palms (Vaurie 1980). Edington and Edington (1972) and Eckhardt (1979) emphasized the correlation of behavioral and morphological specializations with the preferred habitat. Innate and imprinted preferences for specific foliage types also affect habitat response (Klopfer 1963, Emlen 1981).

No functional coupling via food resources occurs when a floristic component acts as a surrogate or indicator species in the regression model to characterize a certain regime of temperature, moisture, forest development, etc. Mamane commonly acts as an indicator of dry, partly to very open woodland in models for the Elepaio, Chukar, California Quail, Eurasian Skylark, Northern Mockingbird, House Finch, Yellow-fronted Canary, and introduced species richness. The negative responses to ohia in Common Peafowl, California Quail, Zebra Dove, Eurasian Skylark, and Common Myna regression models reflect low numbers of these birds in wet closed ohia forests. Grazing activity is typically reflected in high cover values of introduced herbs, introduced grasses, and low covers of native grasses and ground ferns. By inference, grazing generates positive responses with the Common Amakihi, California Quail, Ring-necked Pheasant, and Japanese White-eye, and negative responses with Omao and Maui Creeper. Native grasses are typical of alpine grasslands and undisturbed forests, and indicate the restriction to forests of the Maui Creeper, Crested Honeycreeper, and Japanese Bush-Warbler, and low numbers of Elepaio, Wild Turkey, Spotted Dove, Common Myna, Japanese White-eye, Northern Cardinal, and House Finch in either or both habitats.

Other habitat features

A number of factors are indirectly inferred to determine the observed habitat responses. In semi-desert areas, drinking water is important for gamebirds, especially Chukar, California Quail, Spotted Dove, and Zebra Dove, and, to a lesser degree, Ring-necked Pheasant (Schwartz and Schwartz 1949). Introduced passerines (e.g., Saffron Finch, House Finch, Warbling Silverbill) are also attracted to drinking water in arid areas.

Habitat heterogeneity, or patchiness, may be a requirement of some species and permit more species to co-occupy an area (Levin 1974, Whittaker and Levin 1977). Obligate nectarivores and frugivores need a variety of flower and fruit species to provide year-round resources (Snow and Snow 1971, Pimm and Pimm 1982). Higher densities of Iiwi and Apapane tend to occur in areas where both mamane and ohia are in bloom, and areas with a greater density of understory components are preferred by Iiwi and Melodious Laughing-thrush. In intensive studies elsewhere in the tropics, tree falls increase local patchiness and are correlated with higher bird diversity (Willson and Moriarity 1976, Schemske and Brokaw 1981). Roth (1976) demonstrated a correlation between patchiness and bird diversity in subtropical scrub. On a larger scale, birds may use separate roosting and feeding areas, as demonstrated for Iiwi, Apapane (MacMillen and Carpenter 1980; C. B. Kepler and J. M. Scott, pers. observ.), and Spotted Dove (Schwartz and Schwartz 1949, 1951a).

The area of a general habitat-type needs to provide sufficient food resources and room for behavioral activities to support an adequate population size. Mosquito-free areas that may exist on West Maui or on the Olokui Plateau of Molokai are probably too small to support viable populations of many disease-susceptible species. The koa-ohia forests on north Hualalai have an area of only 16 km^2 and lack Akiapolaau. Assuming a density of 5 birds/km^2, the north Hualalai area would support 80 Akiapolaau; the small size of the area combined with the proximity of mosquito-infested areas at lower elevations might be insufficient to sustain a population indefinitely.

The interaction of thermoregulation and environmental adversity may underlie some habitat response patterns, particularly in determining upper and lower range boundaries. For example, Palila are heat-stressed at 31° C (Weathers and van Riper 1982); birds from the Mauna Kea population would not survive in many lowland areas. MacMillen (1974) found that Common Amakihi perish at 40° C, but both this species and Anianiau have thermoregulatory adaptations that result in energetic savings at the low ambient temperatures typical of montane forests at night. The relation of standard metabolic rate to body mass for Common Amakihi and Apapane deviates from the passerine allometric pattern; this adaptation conserves energy in cold, wet environments and is probably related to nectar exploitation (MacMillen 1981). Thermoregulatory adaptations to cold climates may slow dispersal into warmer lowland areas. On the other hand, roosting flights taken by Iiwi and Apapane appear to be energetically profitable because overnight energy savings result from thermal protection in mature forest and escape from nocturnal fog (MacMillen and Carpenter 1980). Our analysis suggests that Red-billed Leiothrix cannot sustain lowland populations, possibly because of thermal stress. Melodious Laughing-thrush and other introduced species may be absent from high montane rainforests because of poor adaptation to cold, wet environments. The critically high costs of overnight thermoregulation were first noted by Holmes, Black, and Sherry (1979) for passerines in a temperate montane forest. The preference of Spotted Owls (*Strix occidentalis*) for old growth coniferous forests reflects low tolerance to high diurnal temperatures (Barrows 1981). The temperature and moisture regimes of preferred breeding habitat are related to the thermoregulatory and metabolic differences among congeneric thrushes (Holmes and Sawyer 1975), finches (Salt 1952), and warblers (Sabo 1980). Variation of thermoregulatory parameters beyond normal allometric patterns is adaptive to warm environments for pigeons (Dawson and Bennett 1973), larks (Trost 1972), and the House Sparrow (Blem 1973). Kendeigh and Blem (1974) and Weathers (1979) more fully review the subject. Many native Hawaiian rainforest birds nest in cavities or protected sites (Scott et al. 1980, Kepler and Kepler 1983); this may be adaptive to frequent cold wet weather.

Conclusions on habitat response

The habitat response pattern of each species is unique. The many factors that are involved in determining habitat response recur and interplay in different patterns and at different levels of scale for each species. Although ecologists may have once attributed observed patterns to one "causal agent" (Cody 1974), studies of bird communities in tropical forests (Karr 1976a, 1980), shrubsteppes and grasslands (Rotenberry and Wiens 1980a), temperate montane forests (Sabo and Holmes 1983), and riparian vegetation (Rice et al. 1983) have shown that many underlying factors operate and interact over a wide range of spatial and temporal scales. The habitat responses we studied appear to reflect underlying factors of food, water, cover, and thermoregulatory adaptation to environmental adversity. In our study these factors appear as a tapestry pattern woven from the common threads that run through the habitat responses of individual species.

A critical objective of habitat response analysis is to characterize the major environmental gradients (or directions of variation) and to place the observed response patterns into this perspective. Adequate data are obviously necessary. Titus and Mosher (1981), for example, noted that variances for habitat variables in random samples stabilize after 50–60 sites, and several studies (James 1971, Whitmore 1975, Sabo 1980, Rice et al. 1983) utilized hundreds of sites to characterize landscape patterning in avian habitat response. It may be inappropriate to base broad-scale (continental) comparisons on as few as 20–30 point sites, as some workers have done. The regression models in our study are based on 77 to 2847 randomly sampled points (each with a minimum of two count periods). Those models based on low numbers of points (Lanai with 77, Kauai with 140, Kohala with 215) show few and weak relations, with probable major effects not always identifiable. In models based on 400–900 points (Kau, Kipukas, Molokai, and Puna), the major effects are usually identifiable, and many minor relations are also apparent. In the largest models (Hamakua with 2478 points, Kona with 2847), major relations achieve astronomical significance levels, minor relations are numerous, and in some cases variables with no presumed biological significance attain low statistical significance.

As the next higher level of abstraction from the individual community, the landscape is a useful construct for understanding variation within and between species (Whittaker 1967,

TABLE 71
ELEVATIONAL AND LATERAL DISTRIBUTIONAL ANOMALIES[a]

	Elevational anomalies[b]								Lateral anomalies[c]				
	H1	H2	H3	H4	H5	M1	M2	K1	H6	H7	M3	M4	K2
Insectivores													
Elepaio	+	+	+	0	+	···	···	+	0	+	···	···	0
Kauai Oo	···	···	···	···	···	···	···	+	···	···	···	···	*
Maui Parrotbill	···	···	···	···	···	+	···	···	···	···	+	+	···
Common Amakihi	+	+	!	0	+	+	!	+	0	+	0	+	0
Anianiau	···	···	···	···	···	···	···	+	···	···	···	···	+
Nukupuu	···	···	···	···	···	r	···	r	···	···	r	r	*
Akiapolaau	+	+	x	+	x	···	···	···	+	+	···	···	···
Kauai Creeper	···	···	···	···	···	···	···	+	···	···	···	···	+
Hawaii Creeper	+	+	x	+	x	···	···	···	+	+	···	···	···
Maui Creeper	···	···	···	···	···	+	···	···	···	···	+	+	···
Akepa	+	+	x	+	x	+	···	+	+	+	r	+	+
Poo-uli	···	···	···	···	···	+	···	···	···	···	r	+	···
Nectarivores													
Iiwi	+	+	r	0	+	+	+	+	+	+	+	+	0
Crested Honeycreeper	···	···	···	···	···	+	···	···	···	···	+	+	···
Apapane	0	0	0	0	+	+	0	+	0	0	0	0	0
Frugivores													
Hawaiian Crow	x	x	x	+	···	···	···	···	···	x	···	···	···
Kamao	···	···	···	···	···	···	···	+	···	···	···	···	+
Olomao	···	···	···	···	···	x	+	···	···	···	x	x	···
Omao	0	+	+	r	x	···	···	···	0	0	···	···	···
Puaiohi	···	···	···	···	···	···	···	+	···	···	···	···	*
Ou	x	+	r	x	x	x	x	+	x	x	x	x	*

[a] Symbols indicate distributional patterns associated with the anomalies described in text: + = range truncated or species less common in anomaly area; 0 = no response to anomaly observed; ! = species more common in anomaly area; * = species confined to Alakai Swamp (non-anomaly area); r = species appears to respond to anomaly but too rare to quantify; x = species extinct in study area; ··· = species not present on island.

[b] Elevational anomalies by study areas: H1, Kau; H2, Hamakua; H3, Puna; H4, Kona; H5, Kohala; M1, East Maui; M2, Molokai; K1, Kauai, based on 1968–1973 data in Sincock et al. (1984).

[c] Lateral anomalies: H6, north Hamakua, Hawaii; H7, Kahuku tract (south Kona and Kau), Hawaii; M3, Waikamoi, Maui; M4, transect 11, Maui; K2, gradient into Alakai Swamp, Kauai.

Whittaker et al. 1973). The landscape is the set of permutations of habitat elements, although individual permutations are not equally common in nature. We found contour graphs of species response in habitat space to be effective for summarizing and displaying the major directions of variation, and regression models were found to be useful for examining the roles played by many different variables. When the landscape perspective is complemented by more detailed niche (within-community role) data, the underlying factors patterning species response could often be inferred and quantitatively modeled. The species accounts stress the importance of a knowledge of the ecological requirements and behavior of the species in understanding the factors determining habitat response. Although communities are sometimes conceptualized as n-dimensional hyperspaces (Hutchinson 1958, Whittaker 1977), species responses in these hyperspaces are individualistic. Each species uses community resources in a unique manner, so that underlying habitat factors are weighted differently by each species. The habitat response of a species is thus an idiosyncratic transformation, projection, or collapse, of the n-dimensional hyperspace. Essentially, then, the analysis must focus on many individual species in order to gain the "big picture," because no single species responds to all the factors determining habitat response and no superficial community approach can identify the actual factors determining the response patterns for the species present. Examining the variation between habitat responses thus offers a promising approach to identifying the factors that underlie community structure.

DISTRUBUTIONAL ANOMALIES

In a number of areas, densities of one or more bird species appear to be unexpectedly low. These "distributional anomalies" affected many native birds, and the geographic patterns could be characterized as related to (1) habitat structure, (2) elevation, (3) lateral anomalies that tend to lie perpendicular to the slope and not correspond with vegetation boundaries, (4) the Kona study area south of Hualalai, and (5) localized effects. We identified the distributional anomalies in the major HFBS study areas and classified each species as to the principal means of foraging (Table 71).

Distributional anomalies that correspond with major vegetation boundaries such as forest/nonforest and koa forest/ohia forest are fairly frequent and probably due to gross differences in habitat structure and food resources. This probably explains the absence or low densities of birds in places where non-forested areas adjoin forests: on Hawaii, in the Kapapala area between the Hamakua and Kau forests, in the Puu Lehua area between the Hualalai and central Kona forests, and in the Waimea Plains area between Kohala and Hamakua forests; on Maui, in the Kahikinui area and in the Haleakala Ranch area west of Waikamoi Preserve; on Molokai, in the eastern part of the study area that was devastated by feral ungulates; and on Lanai, in the areas surrounding the remnant forest. Distributional anomalies that are probably explained by less drastic vegetation boundaries include (1) the reduced densities of Elepaio and absence of Akiapolaau in the south half of the Kau study area, corresponding to the dropout of koa; (2) the great reduction or range termination of virtually all species at the boundary between mature forest and ohia dieback in Hamakua, with a less marked response occurring on East Maui where the dieback zone is smaller; and (3) the reduced densities of Common Amakihi, Akiapolaau, and Akepa along, and the range truncation of Ou at, the Saddle Road, probably reflecting the presence of several large lava flows and younger forests on more recent substrates.

Reduced densities and range truncations at lower elevations are very frequent, occurring in 81% of the cases tallied in Table 71. The three general foraging guilds show fairly consistent responses (88% of insectivore, 63% of nectarivore, and 89% of frugivore cases), suggesting that the phenomenon is not necessarily related to food resources. Elevational anomalies appear for every endangered passerine examined, and only the Apapane on Hawaii consistently shows no response, except in Kohala. In Puna and Molokai, the Common Amakihi shows the only reverse responses, greater densities at lower elevations, but this probably reflects their association with the drier habitats at lower elevations. The most striking elevational anomalies occur in the south corner of the Kau study area and in the Hamakua and East Maui areas, where virtually identical habitat at lower elevations is nearly devoid of birds that occur at higher elevations. The 1968–1973 survey of Kauai forest birds (Sincock et al. 1984) also showed virtual absence of most native species from low-elevation native forests.

A number of distributional anomalies occur along elevational contours. These distributional anomalies often occur within several kilometers of forest-edges. Examples of this include the Kahuku Tract between the Kona and Kau study areas, near Kukaiau Tract in north Hamakua, and on Waikamoi Preserve on East Maui, and equal 64% of the possible occurrences tallied in these three areas (Table 71). This does not appear to be an "edge effect" per se, however, because numerous species at other similar forest edge boundaries display no such effect. This pattern appears for every endangered passerine species in these three areas, with the possible exception of those too rare to sample. The pattern appears among 77% of the insectivores and 57% of the nectarivores. The Apapane and the only frugivore, the Omao, showed no response.

If mosquito-borne avian disease is indeed a major limiting factor of many species, as evidence presented in a later section suggests, then these lateral anomalies could be explained as areas of higher mosquito density due to prevailing wind regimes. Wind appears to be a dispersal agent for mosquitoes (Hopkins 1941, Russell et al. 1944, Wolfenbarger 1946), and trade wind patterns would be particularly effective in dispersing mosquitoes into unbroken forest from surrounding infested areas where the trade flow crosses over and around mountain shoulders. Strong winds during winter "Kona" storms may also contribute to the dispersal of mosquitoes into montane forests. Four such instances appear on Hawaii and East Maui: the northern ends of Mauna Kea and Haleakala, the southern end of Mauna Loa, and the southeastern end of Haleakala. The first three of these areas correspond sharply to the Kukaiau, Waikamoi, and Kahuku anomalies. We would expect a fourth anomaly to occur near the top of transect 11 on East Maui, west of Hana, and here, eight of the nine native passerines show a range truncation or a sharp reduction in densities. The disease factor may also explain many of the elevational anomalies discussed above, and an anomaly found in the Alakai Swamp. Several endangered species have declining densities along the gradient from the most remote part of the Alakai to the Kokee area, the natural access point with lower elevations. In addition several other species are confined altogether to the Alakai (Table 71). Mosquitoes occur in the Kokee area, but are either very rare or absent from the Alakai (J. L. Sincock, unpub. data), again presenting a striking coincidence.

In the Kona study area south of Hualalai, many species have strikingly lower densities than elsewhere on Hawaii (Akiapolaau, Hawaii Creeper, Akepa) or have become extirpated or extinct (Omao, Hawaii Oo, Ou, Palila, Lesser Koa-Finch, Greater Koa-Finch, Kona Grosbeak, Hawaiian Akialoa, Ula-ai-hawane, Hawaii Mamo). These

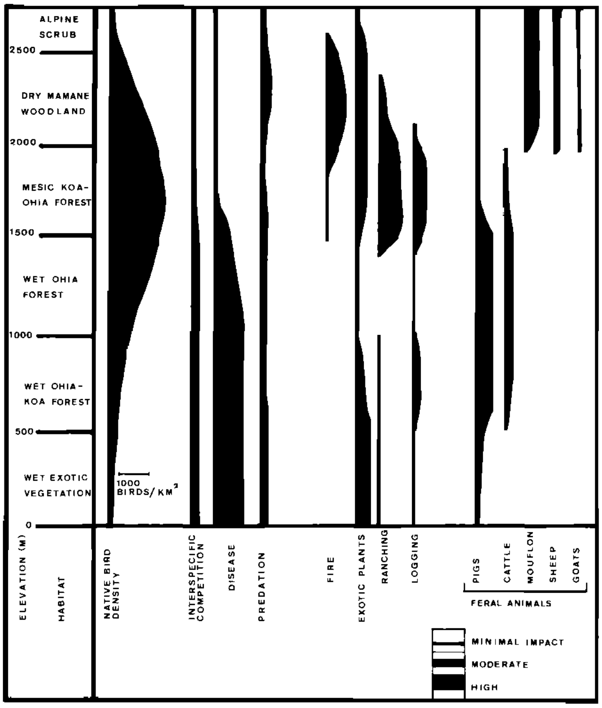


FIGURE 319. Generalized diagram of major limiting stresses on native bird populations, typical for area shown in Figure 320.

populations were apparently declining in the 1890s (Perkins 1903). The causes for the declines are unknown, but may include extensive habitat fragmentation due to coffee farming, logging, and grazing, as well as avian disease (discussed below).

Three localized anomalies were identified in our analysis. In the Mauna Kea study area, Elepaio, Palila, and Akiapolaau are nearly absent from the Pohakuloa Flats area, where the habitat is quite similar to that occupied elsewhere. Possible factors, including thermal stress, avian disease, site tenacity, past habitat disturbance, and military activity, were discussed by Scott et al. (1984). A second local anomaly occurs on the north slope of Hualalai, where Akiapolaau are absent from the koa-ohia forest that harbors Hawaiian Crow, Hawaii Creeper, Akepa, and other common native birds. Possibly the area and quality of that "habitat island" is inadequate to sustain indefinitely the Akiapolaau population. A third anomaly is the high density of Akepa near timberline in the middle of the Kau study area, contrasted with the almost complete absence of this species in the south part of that area.

Multidisciplinary approaches may be valuable in unraveling the factors causing some of these distributional patterns. Additional surveys to document seasonal and annual variation in the geographic distribution of the anomalies may also provide useful insight into their significance and on the role of sampling error in identifying their boundaries. Translocating radio-tagged birds into these areas and following them should provide valuable insight into why a species does not occur there naturally.

LIMITING FACTORS

Numerous factors stress endemic Hawaiian bird populations and propel many species towards extinction. A key principle in wildlife management is the identification and control of those factors that are particularly important in reducing the unimpeded rate of population increase inherent in a species (Leopold 1933, Giles 1978). The limiting factors of Hawaiian forest birds fall into these general categories: habitat modification, predation, disease, interspecific competition, and major environmental perturbations. Aside from these, pesticide contamination from agricultural practices is a potential problem for Hawaiian Hawks, Short-eared Owls, and possibly Hawaiian Crows and waterbirds.

The relative impact of different stresses varies among areas and species, and is conceptually de-

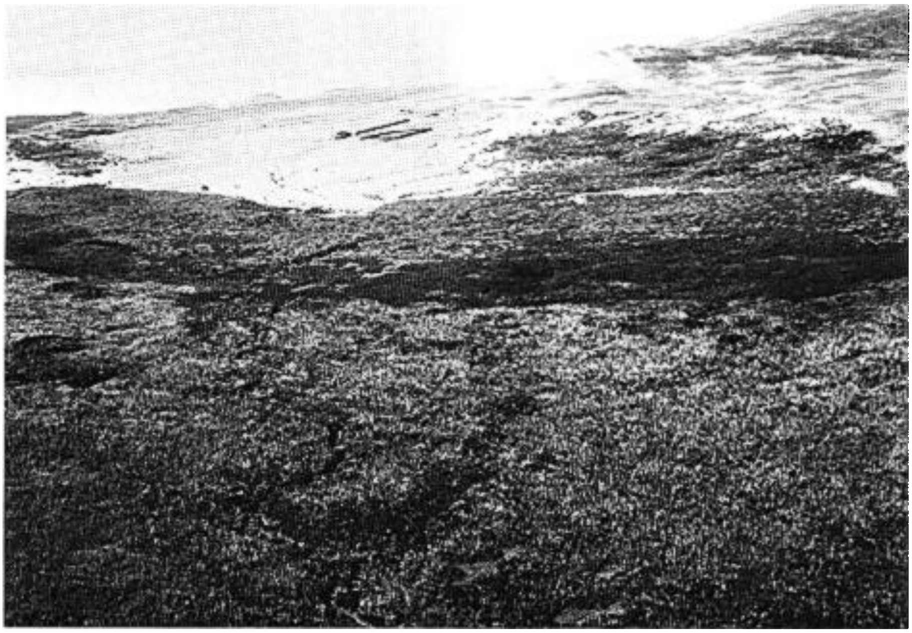


FIGURE 320. Elevational zonation of vegetation on windward Mauna Kea. Lowest zone dominated by dieback of wet ohia forest; next zone (darkest band), by ohia rainforest; top forested zone, by mesic ohia-koa forest. Above this lies open pasture, and still higher lies an indistinctly visible band of mamane woodland (see Figures 49 and 323). Dark triangle in middle of grassland is planted eucalyptus. (Photograph by J. D. Jacobi)

picted in Figure 319 for typical passerines on windward Hawaii (Fig. 320). Where native habitat still remains, disease is believed by many to be the strongest single force below 1500 m elevation (Warner 1968, van Riper et al. 1982). Habitat disturbance is severe in many areas, and large tracts have been converted to introduced vegetation. Pigs, other ungulates, and introduced plants pose a long-term threat to rainforest interiors, especially on steep slopes and in areas already suffering some disturbance. For some ground-dwelling and understory birds, predation may have (or have had) a major effect (Atkinson 1977). Interspecific competition is usually weak but may eventually cause the displacement of some native birds by ecologically similar introduced species. Finally, single cataclysmic events or poor weather conditions attain prominence for perilously low populations.

HABITAT MODIFICATION

Browsers, grazers, and rooters

Goats (*Capra hircus*).—Where domestic goats have been introduced, they almost always create problems for the native flora and fauna—on the Galápagos Islands, the Channel Islands off California, the Hawaiian Islands, New Zealand, and elsewhere throughout the Pacific basin (Baker and Reeser 1972). Goats were abundant by 1850 in the Hawaiian Islands (Marques 1905), but there was little official concern before 1910 (Tomich 1969). Goats cause great damage to drier and more open Hawaiian ecosystems, and usually browse on native plants instead of introduced species. On Haleakala, goats increase erosion by overgrazing, compacting soil, removing cover, and initiating rock slides (Yocom 1967).

Goats were a severe problem in the dry forests of Hawaii Volcanoes National Park (Spatz and Mueller-Dombois 1973), and still are a major problem in Haleakala National Park and adjacent areas where they devastate alpine grassland (Fig. 321) and subalpine scrubland, and also enter high-elevation wet forest below the Kalapawili Ridge, in Kipahulu Valley, and between Kuiki Peak and Manawainui Gulch. Overbrowsing is particularly severe in Kahikinui, the dry south slope of East Maui, where formerly extensive koa, ohia, and mamane forests have been reduced to relictual patches in gulches surrounded by barren eroded slopes. On Molokai, goats degrade dry lowland forest, areas along cliff faces, and local areas in the northern valleys. On Kauai, goat damage is evident along the drier perimeter of the Alakai Swamp, and goats invade the wetter, more pristine habitats during drier periods (J. L. Sincock, pers. comm.). On Kahoolawe, where goats have resided for 200 years, almost

FIGURE 321. Severe erosion following overgrazing by goats and rooting by pigs at 2500 m elevation on windward slope of Haleakala, East Maui. (Photograph by C. B. Kepler)

FIGURE 322. Extreme overgrazing and overbrowsing by goats and axis deer have reduced former open to closed canopy native forest to sparse barren grassland on many areas of Lanai. (Photograph by C. B. Kepler)

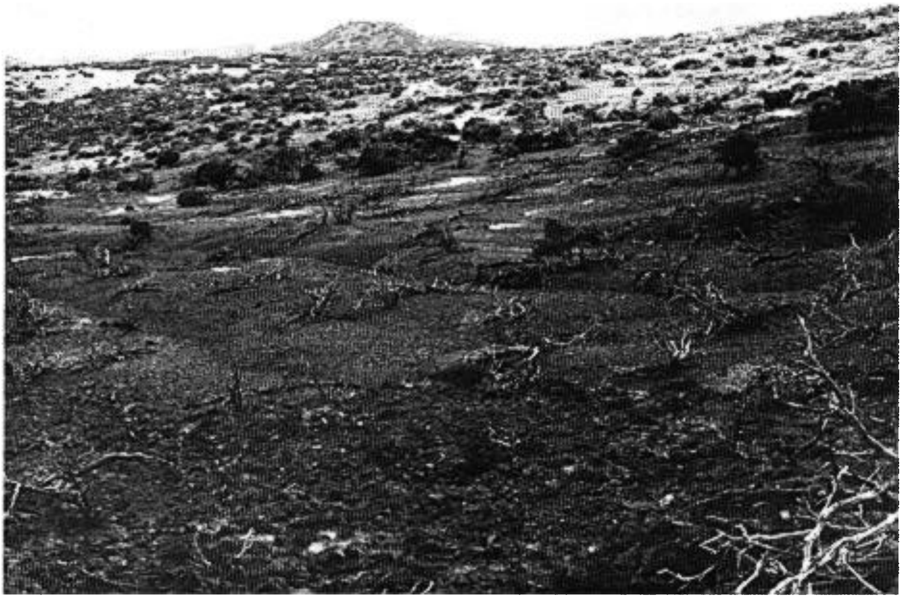


FIGURE 323. Mamane woodland on west slope of Mauna Kea looking down from timberline at 2800 m elevation. Dead trees in foreground, erosion, heavy browse line, and 200 m elevational retreat of treeline are caused by feral sheep. (Photograph by P. W. Scowcroft)

FIGURE 324. Sheep and mouflon exclosure in mamane woodland at 2700 m elevation on Mauna Kea. Regeneration of mamane in exclosure after two years stands in marked contrast to denuded areas outside. (Photograph by P. W. Scowcroft)

FIGURE 325. Aerial view of wet ohia forest in Kohala study area with Maui in background. Heavily grazed grassland on left formerly covered with mesic and dry native forest. Water supply of Lapakahi and other coastal villages failed shortly after forest was cleared. Deep amphitheatre-headed valley barely visible on right. (Photograph by J. D. Jacobi)

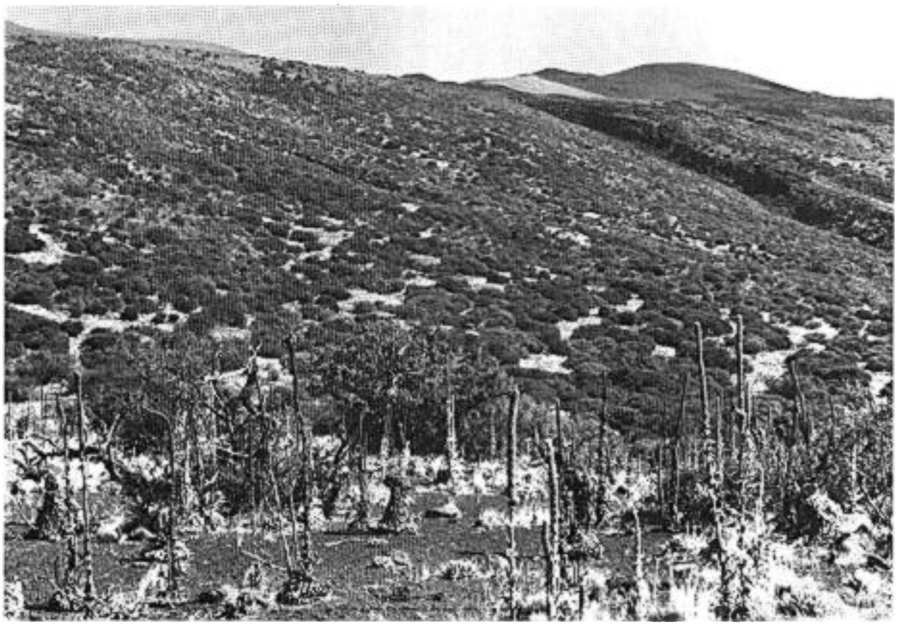


FIGURE 326. Open mamane woodland (dark band) on southeast slopes of Mauna Kea lies between barren alpine desert above and heavily grazed pasture below. Narrowness of this woodland (3 km) appears to strongly limit Palila numbers in this area. (Photograph by J. D. Jacobi)

FIGURE 327. Replacement of native understory by introduced grasses and opening of canopy in koa-ohia forest as a result of grazing by cattle at 1300 m elevation near Puu Waawaa on Hawaii. Hawaiian Crow, Akepa, and Hawaii Creeper are the species most threatened by this type of habitat modification in the north Hualalai area. (Photograph by C. B. Kepler)

FIGURE 328. Extreme overbrowsing and overgrazing by cattle, pigs, and axis deer have reduced a once lush closed canopy ohia forest to a sedge mire punctuated by skeletal tree fern remnants on East Molokai. (Photograph by J. D. Jacobi)

FIGURE 329. Undisturbed ohia rainforest with lush native understory and ground cover at 1150 m elevation on Olokui Plateau, Molokai. Feral ungulates are absent from this inaccessible area because of sheer cliffs. (Photograph by C. B. Kepler)

none of the native flora remains, and the island has largely become a desolate, wind-swept dome of hardpan clay.

Because goats have such a negative impact on dry and mesic habitats, they indirectly place a severe stress on the birds present. On Hawaii, Palila and Akiapolaau have been the most affected endangered bird species. Feral goats have now been virtually eliminated on Mauna Kea by the Hawaii Division of Forestry and Wildlife (R. L. Walker, pers. comm.). On Maui, goats are preventing regrowth in Kahikinui and Manawainui that would regenerate dry koa-mamane-ohia woodland suitable for Maui Parrotbill, Nukupuu, and Akepa. The advance of goats into upper wet forest edges on Maui threatens these birds and other species such as Crested Honeycreeper and Poo-uli. On Lanai, the habitat for Apapane and Common Amakihi (if not yet extirpated) consists of only a small remnant of wet forest heavily disturbed by goats and deer in the past (Fig. 322). Attempts to eliminate the Lanai goat herd by hunting in the past five years appear to have succeeded. As wet and mesic native forests regenerate, populations of bird species that formerly occurred could be reintroduced to Lanai. On Kauai the incursion of goats into wet forests on the perimeter of the Alakai Swamp results in forest degradation that promotes avenues of invasion for other introduced animals and plants that further degrade the habitat and stress native birds (Sincock et al. 1984).

Several techniques can be used to control goats (Baker and Reeser 1972). The most practical control is a combination of fencing and systematic hunting. Hunting is most effective when continual and supported by trained dogs and helicopters. Because of the high breeding potential of goats, complete eradication is necessary for effective control. The novel "Judas goat" tech-

FIGURE 330. Severe damage to understory from pig rooting in a wet ohia forest at 1500 m elevation, Koolau Forest Reserve, East Maui. Note lack of ground cover and sparse understory; compare with Figure 329. (Photograph by C. B. Kepler)

nique has proven effective at Hawaii Volcanoes National Park for locating the last few head in a large area (D. D. Taylor and L. Katahira, pers. comm.). A captured goat is radio-tagged, color-marked, and released into the control area. This goat eventually joins one of the remaining herds, which can then be radio-located and exterminated. The color-marked Judas goat is spared to find another herd.

Sheep (*Ovis aries*).—When Captain Vancouver brought three sheep to Kealakekua Bay, Hawaii, in 1793, he introduced an animal that, because of its fecundity and utility to man, ultimately would be found by the thousands on Hawaii, Molokai, Lanai, Kahoolawe, and Niihau (Kramer 1971). Fortunately Maui and Kauai were spared the stresses imposed by these mammals. Feral sheep have now been eliminated from all islands except Hawaii, where they are well established above 1000 m elevation in many dry areas, particularly the western slopes of Mauna Loa, where herds of several hundred are frequent. On Mauna Kea they have ranged to the summit region from 1822 to the present; the population was about 40,000 in the 1930s (Bryan 1937).

Sheep are particularly destructive to mamane woodlands (Fig. 323, Giffin 1976, Scowcroft 1983, Scowcroft and Giffin 1983, Scowcroft and Sakai 1983). On Mauna Kea their activities have displaced timberline downward about 200 m (Berger 1981), and with cattle have created a broad gap on the windward slopes between the mamane woodland and the koa forests below. The tendency of sheep to flock and repeatedly use the same trails intensifies their impact on native ecosystems (Giffin 1976).

Four taxa of native birds found in the mamane woodlands on Mauna Kea (Palila, Akiapolaau, the Mauna Kea subspecies of Elepaio, and Common Amakihi) have been severely threatened by sheep. These four birds reach greatest densities near Puu Laau, an area of large old mamane trees with moderately heavy past browsing pressure. Sheep damage is severe at high elevations in south Kona, and, along with damage caused by other feral and domestic ungulates, may contribute to very low Akiapolaau densities and absence of Palila in the koa and mamane woodlands there. Sheep were nearly eliminated from Mauna Kea in 1982 pursuant to a legal ruling under the Endangered Species Act, but they are still common in south Kona.

Sheep are effectively controlled by fencing and hunting. Fewer than 100 remained on Mauna Kea in 1983 and these will eventually be exterminated (R. L. Walker, pers. comm.). A dramatic increase in new growth of native plants followed sheep control in 1983 (Fig. 324). As the habitat returns to a healthier state, the numbers of birds, including the endangered species, should increase. Although there is at present little interest in removing sheep from Mauna Loa, the dry upper-elevation woodlands of south Kona would regenerate ideal habitat for Palila and Akiapolaau.

Mouflon (*Ovis musimon*).—Mouflon occur on Hawaii at upper elevations on the east slopes of Mauna Kea and in the open subalpine woodland of the Kau study area, and on Lanai. Mouflon were first introduced in 1954 and hybridize freely with feral sheep (Tomich 1969). Like sheep, they prefer dry open habitat and are a great threat to mamane woodland (Fig. 324, Scowcroft and Giffin 1983, Scowcroft and Sakai 1983). On Mauna Kea, mouflon extensively overbrowse mamane, especially at timberline, and have a damaging effect on native vegetation similar to that of feral sheep (Giffin 1982). Palila, Akiapolaau, Elepaio, and Common Amakihi populations on Mauna Kea are thus threatened with an uncertain future until mouflon are controlled, or preferably removed.

In Kau the damage caused to native vegetation near timberline by a growing population of mouflon and other feral ungulates threatens the survival of the Akepa, which reaches its greatest densities in the ecotone between subalpine ohia woodland and alpine scrub. The Hawaiian Goose and Hawaii Creeper may also be adversely affected in this area.

On Lanai, mouflon do not presently penetrate remnant patches of native forest. Mouflon can be controlled by hunting and fencing; there is no systematic control program currently in effect.

Cattle (*Bos taurus*).—Feral cattle are now restricted to forested areas on Hawaii in south Kona, upper Hamakua, and Puna; on Maui in very low numbers west of Waikamoi Stream and in Waihoi Valley; and on Kauai around Puu Ka Pele (R. L. Walker, pers. comm.). They were formerly very numerous and territorial forester C. S. Judd (1927) labelled 1815–1921 as the "cattle period in Hawaiian forestry." Overall, cattle have been the single most destructive agent to native Hawaiian ecosystems, particularly to mesic forests. They usually prefer native plants to introduced species. Koa reproduction is completely suppressed by grazing (Baldwin and Fagerlund 1943), and cattle are mostly responsible for converting large tracts of forest to open pasture through suppressing regeneration on south and northwest Haleakala, lower elevations of west Maui and Lanai, much of Molokai, the dry side of Kohala Mountain (Fig. 325), the Waimea plains, the north and east side of Mauna Kea below 2200 m elevation (Fig. 326), the mesic and wet slopes of Hualalai, most of south Kona, and the slopes between Mauna Loa and Kilauea. A consistent pattern of cattle invading wet forests from adjacent mesic areas recurs at ecotones on Maui and Hawaii, and formerly occurred on Kauai before control in the 1920s to 1930s (Sincock et al. 1984).

Domestic stock are a major threat to the 25-km² relictual forest on the north slope of Hualalai that harbors one of the two remaining Hawaiian Crow populations, 74% of the Hawaii Creeper, and 99% of the Akepa on leeward Hawaii (Fig. 327). Initial steps by the Hawaii Board of Land and Natural Resources to create a wildlife sanctuary in the area should lead to recovery of that ecosystem. Fragmentation and modification of mesic koa-ohia forests in Kona is one of several factors responsible for the present grim status of the Hawaiian Crow (Burr et al. 1982, Giffin 1983). Many bird species on Hawaii have gaps in their distribution because of conversion of mesic and dry forests to rangelands and scrublands on the Kapapala Tract, the southern shoulder of Mauna Loa (Kahuku Tract), the south slopes of Hualalai (Puu Lehua area), and between the Mauna Kea mamane woodland and the koa-ohia forests of upper Hamakua. These fragmented populations are more vulnerable to extirpation than would be a single continuous population. This is particularly true on the high eastern slopes of Mauna Kea, where cattle, sheep, and goat activity has reduced the mamane woodland to a 1-km band separated from the lower koa forests by 8–10 km of open pasture. This has resulted in a drastic restriction of the range of Palila, Akiapolaau, Hawaii Creeper, and Akepa in this area, and reforestation of these pasturelands to reconnect the mamane woodland and koa forests is a critical management need on Hawaii for these bird species (Scott et al. 1983).

On Maui a century of ranching has severely reduced the range of all forest birds, particularly Maui Parrotbill, Nukupuu, Akepa, and Crested Honeycreeper. Large numbers of domestic cattle range freely into the Kahikinui Forest Reserve, where they further degrade the remnant mesic forests.

Feral cattle are no longer the problem they were a century ago, thanks to extensive efforts early in this century by the Hawaii Division of Forestry to fence forest reserves and eliminate feral animals. Unfortunately many of these fences are in disrepair and need maintenance if feral cattle are to be eliminated from forest reserves. In 1983 the Hawaii Department of Forestry and Wildlife began fencing the lower boundary of Kahikinui and removing cattle during extensive drives; legal notice by the State under Hawaii Revised Statutes 183-19 of impending action to remove, without compensation, domestic stock from public conservation lands generated prompt cooperation by ranchers.

Domestic cattle pose a serious threat to the long-term survival of the Hawaiian Crow, Akepa, Hawaii Creeper, Akiapolaau, and Palila on Hawaii, and have restricted the distribution of forest birds on Maui. Rangelands that contain forests essential to the preservation of these species have been identified in the recovery plans (Berger et al. 1977, Burr et al. 1982, Scott et al. 1983, Kepler et al. 1984), and rehabilitation of key segments of these forests is essential to preserve forest birds on Hawaii. Mesic and wet forests important to many species have recently been secured for conservation management by the Nature Conservancy on Hawaii, Maui, and Molokai (Little 1984), but key parcels of mesic koa forest above 1500 m elevation remain unprotected on Hawaii on north Hualalai (for Hawaiian Crow, Akepa, Hawaii Creeper), in central Kona (for Hawaiian Crow, Akiapolaau, Hawaii Creeper), north of Kilauea (for Akiapolaau, Hawaii Creeper, Akepa), and between the Mauna Kea mamane woodland and upper-elevation Hamakua forests (for Akiapolaau, Hawaii Creeper, Akepa). On Maui, the Kahikinui Forest Reserve fences need to be extended and maintained, and all feral ungulates within the reserve removed.

Axis deer (*Axis axis*).—Axis deer were introduced in 1868 on Molokai, in 1920 on Lanai, and in 1960 on Maui (Tomich 1969). Browsing and soil compaction by feral deer, in conjunction with pigs, has converted the vegetation on East Molokai from rainforest to open mire and created a biological disaster (Fig. 328) that extends to the coral reef ecosystem off the south coast of Molokai, now largely smothered in silt and invaded by introduced mangroves. On Lanai, vegetation destruction by deer is believed partly responsible for the probable extirpation of Common Amakihi and decline of Apapane, and axis deer have replaced goats as the most serious threat to the remnant forests there. Although the numbers of axis deer on Maui are small and confined to disturbed ranchlands, they constitute a major threat to the mesic and wet native forests on Haleakala. Their removal should constitute a high-priority management action (Kepler et al. 1984).

Black-tailed deer (*Odocoileus hemionus*).—This species occurs only on Kauai, where it is a potential threat to essential habitat in the Alakai Swamp. It was released in 1961 (Tomich 1969) and is spreading to many lowland areas. It should be hunted year-round to prevent invasion of the Alakai Swamp.

Pig (*Sus scrofa*).—Feral pigs, first introduced by the Polynesians (Tomich 1969), occur on all the main islands except Lanai and Kahoolawe. Pigs apparently did not establish substantial populations in native forests until after European pigs were introduced (Tomich 1969, Warshauer 1980). The majority of feral pigs live in wet forests, mesic forests, and dry high elevation areas. They feed on tree ferns, grasses, roots, earthworms, and other animal matter (Kramer 1971). The rooting activity of pigs is very destructive to vegetation and soil substrates (Fig. 329 and 330; Ralph and Maxwell 1984), particularly on steep slopes where erosion becomes severe (J. D. Jacobi and F. R. Warshauer, pers. comm.).

Although pig densities may reach 125 animals/km^2 in some Hawaiian rainforests, these concentrations are exceptional, and the maximum carrying capacity for most areas is probably 50 pigs/km^2 (Giffin 1978). Densities at this level, however, still cause extensive and severe damage to the ecosystem, and Giffin (1978) recommended a maximum allowable density of 8–10 pigs/km^2 in Hawaiian rainforests to minimize disturbance to the vegetation and soil. In many forests inhabited by endangered bird or plant species, pigs should be eliminated completely because they radically alter understory composition, hinder forest regeneration, and facilitate the invasion of introduced plants (Mueller-Dombois 1981). Almost all Hawaiian forests have moderate to severe pig damage (J. D. Jacobi and F. R. Warshauer, pers. comm.). Rare exceptions include the outstanding pristine forest on the inaccessible Olokui Plateau on Molokai (Fig. 329) and several isolated peaks of the West Maui Mountains. Control measures for pigs are being developed at Hawaii Volcanoes National Park, and at present it seems possible to eliminate pigs from fenced areas as large as 800 ha (D. D. Taylor and C. P. Stone, pers. comm.).

On Hawaii general habitat degradation by pigs has a negative effect, especially on Elepaio and

Omao, but Akiapolaau, Ou, and Hawaii Creeper are also affected. On Maui, where the threat to the habitat of endangered forest birds by pigs is increased greatly by steep slopes, Poo-uli are strikingly limited to areas of lighter pig disturbance (S. Mountainspring, pers. observ.), and Maui Parrotbill also appear to be sensitive to understory disturbance by pigs (S. Mountainspring, pers. observ.). On Molokai, pigs stress the habitat of Olomao in Kamakou Preserve (Kepler et al. 1984). On Kauai, Kamao, Puaiohi, and Kauai, Oo are probably negatively affected by pig activity (Sincock et al. 1984). The eggs and nestlings of Townsend's (Newell's) Shearwater are occasionally taken by pigs (Telfer 1983); in addition shearwater burrows are trampled and adults eaten (J. L. Sincock, pers. comm.).

Introduced plants

With few exceptions, introduced plant species have become weeds and serious pests on every island that man has visited (Smith 1985). Less than 2% of the 4600 plant species introduced to the Hawaiian Islands have become serious pests in native ecosystems, with lowland areas suffering the greatest disruption by introduced species (Smith 1985). The aboriginal Hawaiians introduced some two dozen species that became naturalized (St. John 1973), but none of these has become a serious pest, except perhaps *Ipomoea congesta,* the status of which as a member of the native flora is uncertain. The present introduced pest flora has thus arrived after Western contact from (1) immigrating peoples from diverse areas who brought plants important in their cultures; (2) agricultural importations of pasture grass and forb seed stock contaminated with weed seeds; (3) foresters who brought trees for reforestation and establishment of a forestry industry; and (4) horticulturists who imported plants of potential interest (Smith 1985). The main impacts of introduced pest plant species on native ecosystems include (1) physical displacement of native species by formation of dense monotypic stands; (2) change of the fire characteristics of communities; (3) alteration of the soil-water regime; (4) modification of the nutrient cycling of ecosystems; and (5) development of synergistic relationships with introduced animals, exemplified by the relation between strawberry guava and pigs in seed bed preparation (Smith 1985).

For prime forest bird habitat, the worst threat is probably posed by banana poka, a weedy passiflora that infests significant areas of koa-ohia forest on Hawaii and Kauai (La Rosa 1984). Continuous populations of banana poka occur on Hawaii on northeast Mauna Kea, the Olaa Tract near Kilauea Crater, the north and west slopes of Hualalai, and on Kauai in Kokee State Park (Warshauer et al. 1983). In most areas banana poka infestations become dense enough to smother large tracts of native forest. The regression models indicate that Omao, Elepaio, and Hawaii Creeper have significantly lower densities in infested areas. Biological control (e.g., by heliconiine butterflies) may be feasible (Warshauer et al. 1983) and efforts to this end are currently underway.

Strawberry guava, lemon guava, and several gingers are abundant below 1200 m elevation and crowd out native tree seedlings; these species extend above 1500 m. Numerous species of *Rubus* likewise penetrate forest interiors, and are better defended against browsers than native plants. Fire tree is a weedy pest on windward Hawaii that alters soil nitrogen levels. Fountain grass destabilizes dry forests in the Puna, Kona, and Mauna Kea study areas, including Hawaiian Crow breeding habitat, by promoting wild fire through buildup of dead biomass above ground. In other dry forests, kikuyu grass, broomsedge, and molasses grass smother native tree seedlings; the first two grasses also release allelopathic substances (Rice 1972, Smith 1985). In the koa-ohia forest near Kokee State Park, Kauai, lantana crowds out native herbaceous vegetation (J. L. Sincock, pers. comm.).

Several strategies may mitigate the impact of introduced plants. Perhaps the most cost-effective is to prevent further noxious introductions by a combination of public education (including tourists) on the need for importation control, and greater government effort to enforce existing regulations and prohibit importation of all potential problem species. At present, government efforts focus solely on illegal plants and agricultural pests, and virtually ignore species that pose threats to native ecosystems. Following needed research on the autecology of pest species, development of integrated pest management systems offers considerable hope through use of biological controls, despite many problems associated with this strategy (Smith 1985). Introduced plants can be controlled, or more accurately, prevented from establishing populations, by closely controlling human access to relatively pristine areas, removing feral ungulates that disperse propagules and create seed beds, and quickly eliminating species before they become established. Richardson and Bowles (1964) describe a control plan for the Alakai Swamp, and The Nature Conservancy has a management plan for their Kamakou Preserve on Molokai that has guided the eradication of several species of introduced plants.

Physical habitat disturbance provides the major avenue for introduced plants to invade intact native ecosystems; in Hawaii Volcanoes National Park invasions of introduced plants are directly

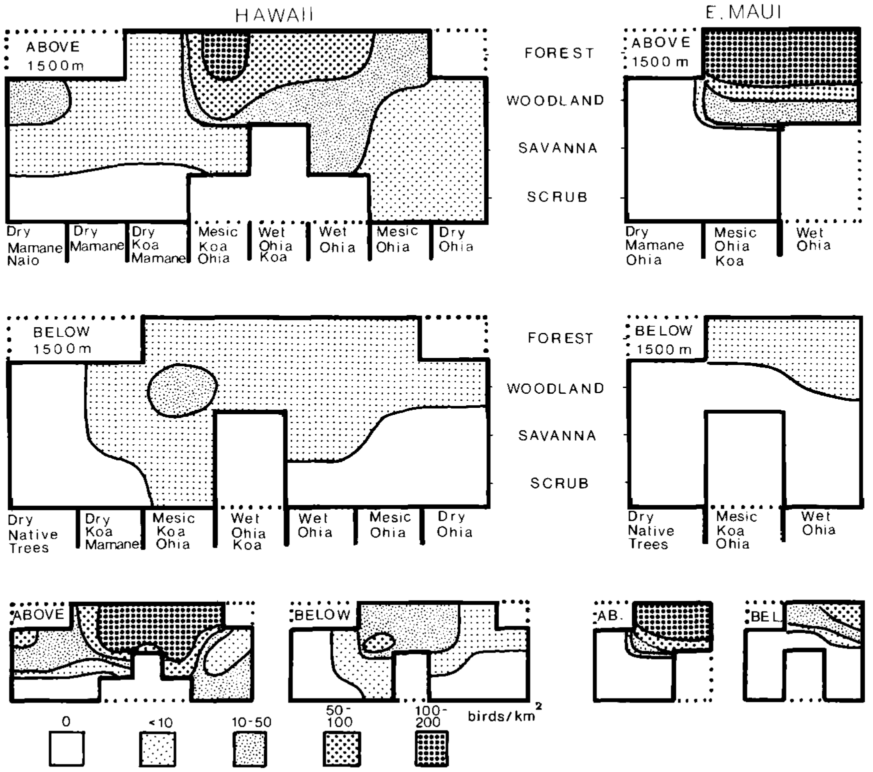


FIGURE 331. Habitat response graphs of endangered passerine species density. (Graphs give mean density above and below 1500 m elevation for Hawaii and East Maui; half-size graphs give standard deviation.)

related to habitat disturbance, particularly by feral pigs (Mueller-Dombois 1981). The Japanese White-eye also facilitates invasion of introduced plants by dispersing their fruit (Guest 1973), as probably do the Red-billed Leiothrix, Melodious Laughing-thrush, Northern Mockingbird, Common Myna, House Finch, and several gallinaceous gamebirds. The most encouraging note, sounded by Egler (1942), Hatheway (1952), and Mueller-Dombois (1981), is that the native biota will frequently hold its own and succeed in the competitive struggle with many introduced plant species, provided disturbance from ungulates and humans is excluded from the system. This point underscores the importance of habitat management as an integral part of conservation strategy for the islands.

Anthropogenic habitat degradation

Logging and clearing.—Early in the 19th century extensive sandalwood harvests probably disrupted bird populations on leeward Hawaii and Maui. Commercial timber harvest on Hawaii threatens some species associated with koa. Prime old-growth koa-ohia forests on Hawaii that should be preserved from logging lie northwest of Kilauea crater, at 1500–2000 m elevation in Hamakua, in central Kona, and on the north slopes of Hualalai. These forests harbor Hawaiian Hawk, Akiapolaau, Hawaii Creeper, Akepa, and in Kona, Hawaiian Crow, as well as many rare plants and invertebrates. The impact of reduced canopy cover on the endangered passerines is clearly shown in Figure 331. Conservation easements and fee simple acquisition are being sought for these areas, but wider public support is needed. Clearing for subdivision and agricultural development, such as occurred on Kalopa Mauka, Puu Waawaa Ranch, and the Honomalino Tract, particularly threatens Hawaiian Crow.

Ranching.—Cattle ranching is a major economic activity in the Hawaiian Islands, but significant populations of endangered birds presently occur on only a handful of ranches. The impact of cattle was discussed earlier; here, the salient point is that economic incentives are essential in persuading those ranchers who control prime forest bird habitat to manage their land for conservation objectives. Conservation easements, tax write-offs for inactive land, and improved watershed quality are potential benefits more likely than lawsuits to win the cooperation of landowners. Such procedures have been highly successful on Maui and Molokai, where over 4000 ha of prime habitat has been protected by The Nature Conservancy (Little 1984). For state-lease lands, it is appropriate to withdraw essential habitats areas from the lease and dedicate the land as a sanctuary.

Fire.—Fire is a threat mainly in the mamane-naio woodland on Mauna Kea to Palila, Akiapolaau, Common Amakihi, and the Mauna Kea subspecies of the Elepaio, and to Hawaiian Crow in the lama-ohia woodland and drier koa-ohia forest on the north slopes of Hualalai. Palila and Mauna Kea Elepaio are especially vulnerable because their entire populations lie within dry woodland. Three Townsend's (Newell's) Shearwater colonies on Kauai were recently destroyed by fire (J. L. Sincock, pers. comm.).

PREDATION

Black rat (*Rattus rattus*).—Black rats are found on all eight main islands. Atkinson (1977) argued from temporal correlations with harbor construction that black rats had a significant negative affect on native birds through nest predation. However, the development of shipping was also correlated with numerous developments other than the probable dates of black rat introduction. Such factors as agricultural expansion and increased importation of domestic fowl, cats, songbirds, etc., may confound Atkinson's argument. It is nonetheless quite possible that during their population explosions black rats were one of many factors in the decline of some native birds, particularly cavity nesters. Black rats caused the extinction of transplanted populations of the Laysan Rail and Laysan Finch on Midway Atoll (Berger 1981), and were no doubt partly responsible for the extinction of the Hawaiian Rail on Hawaii. Black Rat predation also affects the Dark-rumped Petrel (Harris 1970, Simons 1983), and rats may compete for food, especially fruit, with Hawaiian Crow, Omao, Olomao, Kamao, Puaiohi, and Ou. In the koa-ohia forest north of Kilauea Crater, black rats feed primarily on seasonally abundant fruit but occasionally raid passerine nests. Bird species that have survived to this date in large numbers are unlikely to be annihilated by rats (Tomich 1981), although the rarest forest birds could be severely impacted by rats when subjected to other stresses as well. Rats (this species and/or the next) occasionally damage koa trees by stripping the bark (Scowcroft and Sakai 1984).

Polynesian rat (*Rattus exulans*).—Polynesian rats arrived with the Polynesians and occupy all forested Hawaiian islands. Predation by Polynesian rats has been observed on adult Laysan Albatross (*Diomedea immutabilis*) and other seabirds (Kepler 1967, Tomich 1969). Like the black rat, this species is an agile climber (Atkinson 1973), but its impact on forest birds is unknown. Presumably bird populations had reached an equilibrium with predation from Polynesian rats by the time of Western contact. Above 1500 m elevation, Polynesian rats are much less common than black rats (Tomich 1981; C. P. Stone, pers. comm.). Feathers have been found in the stomachs of both black and Polynesian rats, but it is not known whether rats actually prey on live birds (Stone 1985).

House cat (*Felis catus*).—Cats have been present in the Hawaiian Islands since Western contact and were abundant by the 1860s (Twain 1872:Chap. 63). Feral populations occur on all the main islands. Cats are most common at lower elevations but are also frequent in the mamane-naio woodland on Mauna Kea and have been observed in high-elevation rainforests on Hawaii and Maui. In a single ravine on Lanai, Perkins (1903:393, 433) found 22 native birds killed by cats over a two-day period and twice witnessed them feeding on Ou. Cats appear to exert a modest but continued pressure on bird populations (George 1974) that is probably most severe for birds that forage mostly in the understory, including the Elepaio, Omao, Olomao, Kamao, Puaiohi, Maui Parrotbill, and Poo-uli. Cats probably contributed significantly to the extinction of Hawaiian Rail, and probably feed on young Hawaiian Geese. Cats may also compete with Hawaiian Hawks and Short-eared Owls for rodent prey (George 1974). On Kauai, cats caused mortality at about 75% of the nesting Newell's Shearwater burrows at one colony in 1982 (T. Telfer, pers. comm.), and are a source of predation on Dark-rumped Petrels above 3000 m elevation on Maui (Simons 1983).

Without detailed study it is difficult to quantify the effect that feral cats have upon native birds, particularly insular species that have evolved without mammalian predators. Feral cats were present for many years on Little Barrier Island, New Zealand, and were known to be serious predators of nesting procellarlids. Within two years of the eradication of cats from the island, the population of Stitchbird (*Notiomystis cincta*), a very rare nectarivorous meliphagid, increased between three- and six-fold, much to the surprise of the New Zealand Wildlife Service, as cats had not previously been suspected as predators of this species (C. R. Veitch, R. Hay, pers. comm.). Cats may exert a similarly significant but as yet unknown pressure on the Hawaiian avifauna.

Small Indian mongoose (*Herpestes auropunctatus*).—This species was introduced to the Hawaiian Islands in 1883 and occurs on Oahu, Molokai, Maui, and Hawaii from sea level to the upper limits of vegetation (Baldwin et al. 1952). No population is known from Kauai, although one lactating female was found dead on a highway in 1976 (but had no internal or external injuries, and may have been a hoax), and the general public has reported several dozen possible sightings (J. L. Sincock, pers. comm.). The mongoose is a generalized carnivore that feeds mainly on rodents and insects (Kramer 1971). Birds constitute about 4% of the diet, with Zebra Dove and other gamebirds most frequently taken (Baldwin et al. 1952).

Among native forest birds, the mongoose constitutes a persistent threat, probably of generally small magnitude, and as with cats, understory birds will be most affected. The mongoose is a predator at Hawaiian Goose nest sites and is considered an important factor in reducing nesting success (Walker 1966, Banko 1982, Banko and Manuwal 1982, Stone et al. 1983). Mongoose predation on Hawaiian Crows occurs during the first two weeks after the young leave the nest, when the fledglings cannot sustain upward flight and often perch on the ground for extended periods (Giffin 1983). Local control of mongooses around nest sites may effectively reduce crow mortality from this source. The mongoose is also implicated in seabird predation in the Hawaiian Islands, and probably was a key factor in reducing Townsend's (Newell's) Shearwater populations to near zero levels on Oahu, Molokai, Maui, and Hawaii (King and Gould 1967). Bryan (1908) found mongooses occupying Dark-rumped Petrel burrows on Molokai, and mongooses are a major source of predation at the petrel colony in Haleakala, where an active trapping program has led to increased nesting success (Simons 1983).

Common Barn-Owl (*Tyto alba*).—Common Barn-Owls were introduced to the Hawaiian Islands in 1958 and occur on all of the larger islands in most habitats (Berger 1981). Although they feed primarily on rodents, they have been observed taking numerous seabirds on Kauai (Byrd and Telfer 1980) and are known to take passerines in small numbers (Bent 1938).

Common Myna (*Acridotheres tristis*).—In the 1890s Common Mynas "increased prodigiously," occurred deep into native forests, and were observed feeding on the young and eggs of native birds (Perkins 1903:394). Our survey showed that they prefer disturbed habitat and are generally not found in association with the rarer native species. Nonetheless, during their population explosions, Common Mynas and other introduced birds may stress native bird populations directly through predation and indirectly through competition for nesting cavities and food, and may have had significant impacts on some species in the past.

Man (*Homo sapiens*).—Illegal taking, usually by shooting, primarily affects the larger native birds. Poaching of Hawaiian Geese was a problem especially in the past, although incidents still occur (Baldwin 1945a, Stone et al. 1983). Hawaiian Hawks are probably occasionally shot in some hunting areas. Indirect evidence suggests that shooting is a factor in the decline of the Hawaiian Crow on the north slopes of Hualalai (Burr et al. 1982, Giffin 1983). Public education, establishment of limited-access sanctuaries, and strict enforcement of protective statutes are measures that would reduce the impact of shooting. In earlier times, Hawaiians took Dark-rumped Petrel and Townsend's (Newell's) Shearwater nestlings for food (Munro 1944).

DISEASE

Because the endemic Hawaiian avifauna evolved in the absence of many diseases common in continental areas, a reduction in the effectiveness of immunogenetic mechanisms has probably occurred (van Riper and van Riper 1985). When native birds encounter introduced pathogens, they may thus be more strongly affected than introduced birds from continental areas. The role of disease in reducing native Hawaiian bird populations was first suspected by Perkins (1893, 1903) and Henshaw (1902), but a long time passed as evidence was amassed and techniques were developed that substantiated this hypothesis. Compelling evidence of the debilitating role that malaria appears to play was presented by Warner (1968) and van Riper et al. (1982). In New Zealand, Myers (1923) suggested that population reductions in some native species were due to high susceptibility to malaria. Declines of endemic insular birds due to introduced diseases seem to parallel the decrease of Polynesians and other island peoples due to diseases (e.g., measles, common colds) caught from Westerners in whom their effects were much less severe (Lack 1954:168–169).

Native passerines, particularly Hawaiian honeycreepers, have experimentally shown great susceptibility to and mortality from avian malaria (Warner 1968, van Riper et al. 1982). After reviewing previous studies, Laird and van Riper (1981) concluded that only one species of avian malaria occurred in Hawaii, *Plasmodium relictum capistranoae,* but found unusual morphological forms of this species at high levels of parasitemia. The ornithophilous night-biting mosquito *Culex quinquefasciatus* (=*C. pipiens fatigans*) is the primary vector (van Riper et al. 1982). Although van Riper was not successful in transmitting malaria with *Aedes albopictus,* his sample sizes were small and he also had difficulty in completing the sexual stage of malaria in the primary vector; Boyd (1949) reported that *A. albopictus* was a vector of secondary importance for malaria. Malaria was probably introduced to the Hawaiian Islands via introduced birds, with candidates including the Common Myna (first introduced in 1865), Nutmeg Mannikin (1865), House Finch (1870), and House Sparrow (1871), although van Riper et al. (1982) speculated that the date was later.

Malaria has been identified in blood smears from wild Townsend's (Newell's) Shearwater, Hawaiian Crow, Elepaio, Omao, Common Amakihi, Iiwi, and Apapane, as well as in wild Rock Dove, Red-billed Leiothrix, Japanese White-eye, Northern Cardinal, House Finch, House Sparrow, and Nutmeg Mannikin (for primary references see review by van Riper and van Riper 1985). In inoculation experiments, introduced species have far higher survival rates than native species (100% vs. 42%); native species whose range does not include mosquito-infected areas (Laysan Finch, Palila) have 0% survival after malarial inoculation (van Riper et al. 1982). In North America, isodiagnosis (the inoculation of blood from wild birds into susceptible captive hosts) revealed prevalences of over 60% for malaria in wild bird populations, apparently representing a high degree of immunity to fatal disease in populations that evolved in the presence of malaria (Herman 1968). Similarly in North America, native birds are less susceptible to the native eastern equine encephalitis than introduced birds that evolved in its absence (Karstad 1971).

The role of avian pox in regulating native bird populations is not fully understood at present. Avian pox is caused by several strains of the virus *Poxvirus avium,* and recovery usually confers immunity, at least to the infecting strain. Avian pox has two manifestations, wet pox leading to lesions in the mouth and upper respiratory tract, and dry pox leading to integumentary lesions (Cavill 1982). It is transmitted directly by contact with an infected individual, by secondary contact with infected objects, or mechanically by vectors (Cavill 1982). Mosquitoes of all species are ideal vectors, because the virus needs a small break in the integument for infection (van Riper and van Riper 1985). In the Hawaiian Islands pox virus was first isolated from a Red-tailed Tropicbird (*Phaethon rubricauda*) (Locke et al. 1965), and not until 1984 was the virus isolated from a main island passerine (C. B. Kepler, pers. observ.).

Perkins (1893) noted the occurrence at lower elevations in Kona of apparent pox lesions on Elepaio, Greater Koa-Finch, Palila, and Apapane, and noted that a similar phenomenon occurred on Oahu. Pox-like lesions have also been found on Hawaiian Goose (Banko and Manuwal 1982), Hawaiian Hawk (Perkins 1903), Hawaiian Crow (Perkins 1903, Giffin 1983), races of Elepaio on Hawaii (van Riper et al. 1982) and Kauai (J. L. Sincock, pers. comm.), Omao (van Riper and van Riper 1985), Kamao (S. Mountainspring, pers. observ.), Kauai Akialoa, Molokai Creeper (Perkins 1903), Nukupuu (S. Mountainspring, pers. observ.), Akiapolaau (J. M. Scott, pers. observ.), Common Amakihi, Iiwi, and Apapane (van Riper et al. 1982), as well as on the introduced Ring-necked Pheasant, California Quail, Japanese White-eye, Northern Cardinal, House Finch, House Sparrow (van Riper and van Riper 1985), and Red Junglefowl (J. L. Sincock, pers. comm.). Birds with pox-like lesions are more likely to have malaria than unblemished birds (van Riper et al. 1982), and mortality apparently from pox has been observed on several occasions for wild native birds (Perkins 1903; C. van Riper III, pers. comm.; C. B. Kepler, pers. observ.).

Although numerous records of integumentary pox-like lesions have been reported, infections by *Aspergillus, Trichomonas,* or bacteria may also cause such lesions (Karstad 1971). *Aspergillus* and *Trichomonas* are apparently quite rare in wild Hawaiian passerine populations, and although integumentary lesions of bacterial origin have not yet been diagnosed from wild populations of Hawaiian birds, the record is too fragmentary to be definitive (van Riper and van Riper 1985). Recently W. R. Hansen and C. van Riper III (in van Riper and van Riper 1985) have isolated and clinically diagnosed pox virus from pox-like lesions on five native and four introduced Hawaiian passerine species, suggesting that the large number of pox-like lesions reported may be a true reflection of the prevalence of pox infection in the Hawaiian Islands. A high prevalence of pox in the islands is also suggested by the necessity of vaccinating poultry against pox in commercial operations (Bice 1933; J. L. Sincock, pers. comm.).

Because of the important role that mosquitoes play in transmitting avian disease, it is instructive to examine the relations between the distributions of mosquitoes and native birds. Mosquitoes were first released in the Hawaiian Islands in 1826 by sailors who dumped water casks containing larvae into a stream on Maui (Hardy 1960). The species with the widest elevational range, *Culex quinquefasciatus,* occurs year-round as high as 1500 m in many areas, while *Aedes albopictus* occurs as high as 1200 m seasonally (Goff and van Riper 1980). Mosquitoes need to occur only seasonally or during irregular intervals to inoculate native bird populations in an area; pathogen reservoirs in these areas would

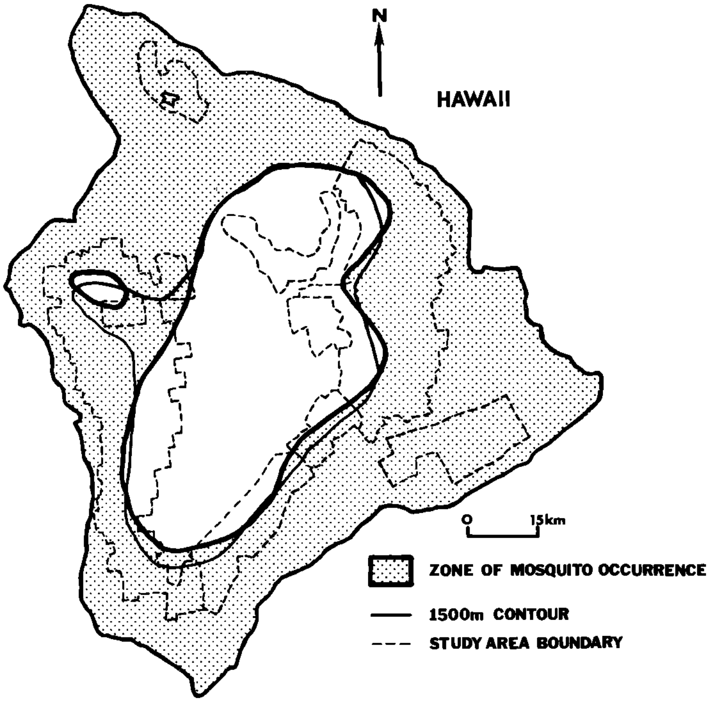


FIGURE 332. Approximate distributional limits of mosquitoes (chiefly *Culex quinquefasciatus*) on Hawaii.

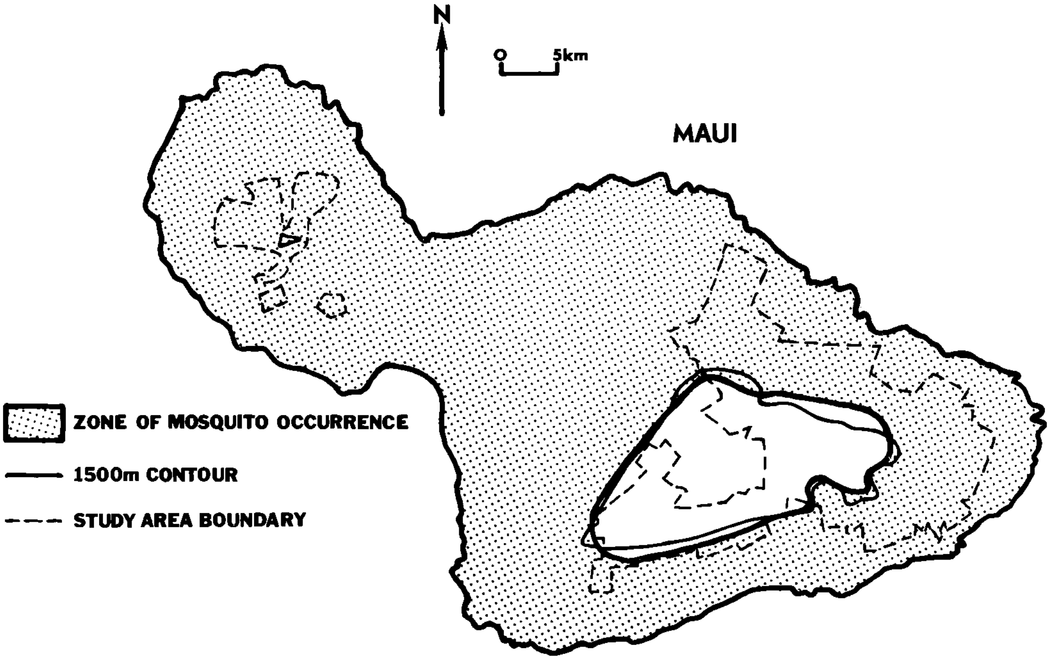


FIGURE 333. Approximate distributional limits of mosquitoes (chiefly *Culex quinquefasciatus*) on Maui.

TABLE 72
RESPONSE OF NATIVE BIRDS TO MOSQUITO PRESENCE[a]

Species	Study area				
	Kau	Hamakua	Kipukas	Kona	Maui
Hawaiian Crow	X	X	X	−6.1*	X
Elepaio	−4.5*	−3.0	···	−9.6*	X
Omao	···	···	−2.1	X	X
Ou	X	−5.8*	X	X	X
Maui Parrotbill	X	X	X	X	−8.2*
Akiapolaau	···	−2.4	X	−2.9	X
Common Amakihi	−2.8	···	2.8	···	−5.9*
Hawaii Creeper	···	···	X	−5.6*	X
Maui Creeper	X	X	X	X	−21.0*
Akepa	···	−8.1*	X	−9.2*	X
Iiwi	−2.4	−2.1	···	−4.4*	−7.2*
Crested Honeycreeper	X	X	X	X	−20.3*
Apapane	···	···	···	−6.8*	−4.1*

[a] Entries are t statistics for including the variable of mosquito presence in the regression models in Tables 14–32; all t statistics are significant at $P < 0.05$; * indicates $P < 0.001$; ··· indicates no significant response; X indicates no model for that entry.

probably be introduced species, or less susceptible native species (e.g., Apapane) that migrate daily to lower elevation areas where vectors are common.

To quantify the potential role of mosquitoes on native bird distribution, we constructed maps of mosquito distribution for Hawaii and Maui (Figs. 332 and 333) from over 200 campsite records and literature records, taking into account human activities, local variation in wind patterns, water sources, and forest edge. These maps reflect the occurrence of *Culex quinquefasciatus* and *Aedes albopictus,* both of which are proven vectors of malaria and strongly suspected vectors of pox. Although these maps are admittedly less accurate than our bird distribution maps, we include them for their heuristic value. The zones of mosquito presence on these maps indicate regions where we predict that mosquitoes are present for at least several weeks each year at densities sufficiently high to infect native bird populations and be detectable by human observers. In some montane areas, mosquitoes occur only seasonally during certain prevailing wind regimes (e.g., weak trades, Kona storms) (Goff and van Riper 1980).

Each census station was scored as 0 if it fell outside the zone of mosquito occurrence, and 1 if it fell within. We then took the final equations (regression models) for the habitat response of native species in those study areas where both mosquito presence and absence zones occur, and offered the new variable "mosquito presence" to these models. This procedure partials out the potentially confounding effect of the habitat variables.

In 42% of the native passerine models, a negative response to mosquito presence is registered at the 0.1% significance level (Table 72); no positive responses appear at this level, but a weak positive term occurs in a Common Amakihi model, a species with populations that are more resistant to avian malaria than are many other native species (van Riper et al. 1982). Virtually all the rare passerines—Ou, Maui Parrotbill, Akiapolaau, Hawaii Creeper, and Akepa—are much rarer in mosquito-infested areas, as are some populations of more common species such as Elepaio, Omao, Common Amakihi, and Apapane. Staggering drop-offs of densities in mosquito-infested areas occur for Maui Creeper (94% fewer than in identical mosquito-free habitat), Crested Honeycreeper (82% fewer), and Iiwi (75% fewer). The distributional patterns on Maui for Nukupuu, Akepa, and Poo-uli, and on Kauai for Kamao, Puaiohi, Kauai Oo, Ou, Kauai Akialoa, Nukupuu, Kauai Creeper, and Akepa strongly suggest that mosquito-borne diseases currently restrict the ranges of these species too, although we are unable to analyze quantitatively the effect of mosquito presence on density.

The assumed mosquito-free refugia harbor the best remnants of the original avifauna and are relatively few and small: the dry Mauna Kea woodland and the upper wet and mesic forests of Hamakua, Kau, central Kona, north Hualalai, East Maui, and the Alakai Swamp on Kauai. Range truncation is strongly suggested for species that have their highest densities at the lowest elevations of mosquito-free areas; Hawaiian Crow, Ou, and possibly Nukupuu fall into this category. These are the species that may be the most vulnerable to extinction due to avian disease, because nearby mosquito-infested habitat is similar in physiognomy and resources to mosquito-free habitat, and may be more attractive because of fewer conspecifics. The species restricted to the Alakai Swamp may be particularly vulnerable because the absence of high elevations on Kauai might preclude a permanent refugium from mosquitoes.

Resistance to malaria and pox has developed or may have originally been present in some native bird populations, and would seem to explain high densities of some species in mosquito-infested areas. Resistance can vary among the populations of a species; Common Amakihi from mosquito-free areas on Hawaii are quite susceptible to malaria, but those from mosquito-infested areas are resistant (van Riper et al. 1982). The peculiar present-day distribution of Omao may reflect early extinction of susceptible populations in Kohala and Kona due to mosquito-borne disease as well as development of resistance and subsequent dispersal of populations in Hamakua and Puna. Some of the uncommon native birds (Iiwi, Hawaii Creeper) have distributions suggesting that they are slowly developing resistance, but densities are still quite low in mosquito-infested areas.

Although we have interpreted the existing, largely circumstantial evidence as indicating a major role for avian disease in limiting present native bird populations, restricting their ranges to high elevations, and causing the extinction of several forms, further study is needed on the seasonal and annual variation in mosquito distribution and abundance, the identity of pox vectors, the biology of disease transmission, the prevalence of disease in wild populations, and the physiological effects of avian disease, before conclusive statements can be made regarding the exact role of disease in limiting native birds.

Maintaining unbroken forest where possible may slow mosquito advances into prime forest bird habitat. Habitat fragmentation and forest edges are important modifiers of the flight and dispersal pattern of mosquitoes (Kennedy 1975). Wide-ranging flights over poorly defined areas are typical of mosquitoes in savannas and cultivated areas; restricted flights over sharply defined areas are typical in forests and unbroken woodlands (Gillies 1972). In Kona the extinction of many native bird species at the end of the 19th century, and the near absence of endangered passerines now over most of the area, may reflect early habitat fragmentation below 1000 m elevation due to coffee farming (Munro 1944), and to strong sea breezes that blow mosquitoes to higher elevations during the day. Significantly the north Hualalai refugium, where most endangered birds in Kona occur, lies in a relatively windless area protected from trade winds, winter Kona storms, and sea breezes (J. C. Giffin, pers. comm.). In the distributional anomalies section, we tentatively attribute a number of species responses on windward Hawaii and Maui to trade wind patterns that blow mosquitoes into unbroken forests.

Options for controlling mosquitoes over large wilderness areas seem few, although genetically engineered strains of mosquitoes may have management potential, and biological controls and sterile male releases offer a distant hope. In intensively managed areas, elimination of mosquito breeding sites would be helpful in reducing vector densities. Mosquitoes often breed in wallows and tree fern sites created by feral pig activity, and mosquito densities appear significantly lower in pig-free kipukas (forest habitat-islands) than in nearby pig-damaged ones (L. Katahira, pers. comm.). Control of pigs in endangered species habitat may reduce disease transmission rates. Adding larvicides innocuous to vertebrates to high-elevation ponds and water tanks would also reduce breeding sites. It may be possible to develop pox and malaria vaccinations that confer lifetime immunity, a technique that would have use for intensively managed species. For species in captive propagation, it may be possible to develop genetic resistance to disease by selective breeding. Further introductions of birds that are liable to host pathogens and that enter montane rainforests (e.g., Kalij Pheasant to Maui and Kauai) should be banned. Strengthening quarantine and importation controls to monitor and clear parasites on introduced birds and to prevent establishment of other mosquito species would prevent introduction of disease problems not yet present; papers in Laird (1984) discuss control measures for curbing the spread of disease vectors by commercial activity. Introductions of native species bred elsewhere must also be carefully examined; for example several potentially serious parasites that are not yet present in the Hawaiian Islands have been found on captive Hawaiian Geese in Slimbridge, England (van Riper and van Riper 1985).

INTERSPECIFIC COMPETITION

The role of interspecific competition in modifying avian habitat response has been widely studied (Svärdson 1949, Cody 1974). Abbott et al. (1977) suggested that interspecific competition interacted with floristic diversity in determining the occurrence, morphology, and foraging behavior of Galápagos finch species. Noon (1981) identified competition as a major factor in differentiating the ecological patterns of sympatric forest thrushes in eastern North America. Williams and Batzli (1979) showed that competition affected woodpecker behavior by experimental removal of the dominant species. Pearson (1975) suggested that competition with monkeys affected bird community structure in the Amazon basin. Diamond (1973, 1975, 1978), Terborgh (1971), and Terborgh and Weske (1975) inferred that competition was responsible for many patterns of elevational distribution among congeneric species. Others have suggested a minor role for competition. Rotenberry and Wiens (1980b) found very little evidence of close biological coupling between bird species in their shrubsteppe sites, partly because of unpredictable climate. Landres and MacMahon (1983) also found only weak evidence of competition among fly-catching birds in oak woodlands.

To evaluate the role of interspecific competition from other bird species in modifying the habitat response of Hawaiian forest birds, we conducted an analysis of the correlation between various pairs of species after all the habitat variables had been partialed out (Mountainspring and Scott 1985). A total of 170 partial correlations were examined among 14 species in seven study areas (Table 73). Only 6% of the partial correlations are significantly negative, but 67% of them are significantly positive. The correlations between very similar species, where competition is most likely to operate, are mostly positive (e.g., omnivorous introduced species such as Melodious Laughing-thrush, Red-billed Leiothrix, and Japanese White-eye; insectivorous natives such as Elepaio, Common Amakihi, Kauai Creeper, and Akepa; nectarivorous natives such as Iiwi and Apapane). The pattern of positive association rather than avoidance dominates every data set.

Wiens (1977) suggested that competition is a rare phenomenon in a varying environment because populations are seldom at the carrying capacity, and resources are often superabundant. We might thus expect to see few negative correlations within our data set.

The average negative correlation is low (r = 0.06), which indicates that the small-scale geographic displacement (or depression of population density) between native and introduced species is rather minor (the area involved would be on the order of 1% of the species' range for total displacement but larger if low densities coexisted). This is a measure of the displacement occurring at a given instant, however, and if the negative association is sustained over time, the net effect would be competitive displacement of the less successful species over a region as displacements accumulate over time.

Two species-pairs show a consistent pattern of negative partial correlations over several adjacent study areas—Japanese White-eye/Elepaio in windward Hawaii (Hamakua, Puna, Kohala, and Kau study areas; $P = 0.06$), and Japanese White-eye/Iiwi in montane Hawaii (Hamakua, Kau, and Kona study areas; $P < 10^{-7}$). The Japanese White-eye/Elepaio relation probably reflects a response to interspecific competition because both species depend on insects in the understory and the subcanopy; moreover, Elepaio frequently defend their territory from Japanese White-eye, particularly on Hawaii (Conant 1977).

TABLE 73
Distribution of Negative and Positive Partial Correlations Across Study Areas by Native or Introduced Status of the Members of Each Species Pair

Study area	Intro./ intro. − +	Native/ native − +	Native/ intro. − +	P^a
Kau	0−1	0−10	6−4	.003
Hamakua	0−3	0−10	4−11	.075
Puna	0−3	0−6	6−6	.034
Kona	0−3	0−6	5−7	.063
Kohala	0−3	0−3	3−6	.250
East Maui	0−3	0−10	2−13	.230
Kauai	0−1	5−16	6−8	.234
Overall	0−17	5−61	32−55	≪.001

[a] Probabilities are for the two-tailed test that native/introduced species pairs have a greater proportion of negative correlations than do native/native pairs.

The Japanese White-eye/Iiwi relation probably reflects interspecific competition for limited nectar resources, because both species frequently take nectar from understory trees and shrubs. Iiwi are specialized to exploit high-quality resources and probably have difficulty exploiting poor resources (Pimm and Pimm 1982). When ohia or mamane flowers are locally unavailable, Iiwi rely heavily on alternate nectar sources that may be in short supply, unlike Apapane or Common Amakihi, which switch to insects and fruit. This specialization may thus make Iiwi particularly vulnerable to the negative impact of the omnivorous foraging behavior of Japanese White-eyes.

King (1977) and Berger (1981) suggested that introduced birds may compete for food resources with native birds. To examine this hypothesis, we divided the species-pairs into three groups according to the native or introduced status of the two species in the pair. We then tallied the positive and negative partial correlations for native/native, native/introduced, and introduced/introduced species pairs.

Interactions of native/native and introduced/introduced species-pairs have virtually no negative associations (Table 73). The five negative native/native post-habitat correlations from Kauai are negligible, with $r = -0.08$ for the greatest magnitude among the five. More important is the substantial proportion of negative correlations among native/introduced species-pairs.

TABLE 74
PERCENTAGES OF NEGATIVE PARTIAL CORRELATIONS AMONG PRIMARY AND SECONDARY POTENTIAL COMPETITORS IN NATIVE/INTRODUCED SPECIES PAIRS

Study area	Primary potential competitors	Secondary potential competitors
Kau	67	50
Hamakua	33	20
Puna	67	33
Kona	60	29
Kohala	33	33
East Maui	40	0
Kauai	50	33
Overall	47	25

Native/introduced pairs have significantly higher proportions of negative correlations than either native/native (Chi-square test, $P < 10^{-4}$) or introduced/introduced pairs (Chi-square test, $P < 0.003$). In each area native/introduced pairs have a higher proportion of negative correlations than native/native pairs. Among the native/introduced species-pairs in each study area (Table 74), the interactions between primary potential competitors (those species that feed on similar foods) account for more negative associations than do interactions between secondary potential competitors (species that have little overlap in diet) (Chi-square test, $P < 0.04$). This suggests that competitive interactions between species for food are one cause of negative interspecific correlations. Our results show that a broad and diffuse "front" of competition occurs between the native and introduced avifaunas, affecting about one-half (47% in Table 74) of the primary potential competitors among native/introduced species pairs in a forest. Competition with introduced species may be one of several factors causing the decline of the native Hawaiian avifauna in this century.

Japanese White-eyes are the most abundant, widespread, and omnivorous forest passerines, and their negative correlations with Elepaio, Iiwi, Common Amakihi, and Kauai Creepers indicate that Japanese White-eyes are a focus of the native/introduced encounter. If we restrict the scope to primary competitors, native/introduced pairs involving Japanese White-eyes have a significantly greater proportion (62% vs. 32%) of negative correlations (8+, 13−) than all other native/introduced pairs (17+, 8−; $Z = 2.03$, $P = 0.04$). To see whether it is reasonable to conclude that Japanese White-eyes were partly responsible for the decline of Hawaii Creepers in the 1940s as Dunmire (1961) suggested, we calculated the partial correlation between the two species for the Hamakua study area, where over 70% of the Hawaii Creeper population occurs. Despite the rarity of Hawaii Creepers, the post-habitat correlation is significantly negative ($r = -0.064$, $P < 0.003$), thus supporting the hypothesis. Because Japanese White-eyes were introduced relatively recently (1929–1937) and may have arrived in some remote areas only in the past 15 years or so, it is very likely that in many areas native bird populations have not yet adjusted to their presence. Japanese White-eyes are the most abundant bird in many areas, and their high densities, coupled with their facultative omnivory, suggest that the effect of this species on native birds is much greater than the effect of native species on it, further indicating the potent role that Japanese White-eyes play in depressing native bird populations.

Another phenomenon relevant to the native/introduced species pairs competition is the explosive expansion of range and numbers that introduced species sometimes undergo soon after introduction, only to decline in later years as other factors come into play. This is documented for the Red-billed Leiothrix on Oahu by annual Christmas bird counts (Anonymous 1974). Common Mynas experienced a population explosion into heavily forested areas in the 1890s, possibly adversely affecting the survival of some now-extinct species (Perkins 1903). Since then, Common Mynas have declined and are not found in dense forests. Interspecific competition for resources was possibly more severe during these population explosions. As most introduced birds occur in disturbed areas and forest edges, native birds may be buffered from violent fluctuations in introduced bird populations by dwelling in refugia of undisturbed native forests. Diamond and Veitch (1981) also noted the propensity of introduced birds to associate with disturbed vegetation in New Zealand. In view of this, management of rare insectivorous species such as the Hawaii Creeper, Nukupuu, or Poo-uli, should include a policy to preserve unbroken blocks of forest and reduce forest edges where feasible.

The prospects are poor for controlling introduced species. A more realistic strategy is to restrict importation of bird species not yet present in the islands and to restore the integrity of native ecosystems, because disturbed areas provide the chief avenues of introduced bird dispersal.

Interspecific competition doubtless occurs from introduced species other than birds (Banko and Banko 1976). Numerous predatory insects have been introduced, such as the notorious yellowjacket wasp (*Vespula pensylvanica*). The introduced carnivorous snail *Euglandina rosea* decimates native land snail populations (see Clarke et al. 1984). Another introduced snail

(*Oxychilus alliarius*) suspected of preying on native snails, is abundant within the range of the Poo-uli, and may contribute to the declining numbers of that species. Data are presently too meager to assess fully the impacts of introduced invertebrates on the native biota, but effects include reduction not only of native invertebrate populations by predators and parasites (thereby seriously depleting the food resources of native birds), but also of native plant populations by herbivores, pathogens, and pathogen vectors (Howarth 1985). Although biomass trends of canopy arthropods along an elevational transect in Hawaii Volcanoes National Park (Gagné 1979) show little resemblance to elevational trends in native bird density (particularly in the drop-off below 1300 m elevation), more extensive studies are needed on the diets of native birds and the impact of introduced species on resource levels. The most cost-effective strategy to reduce problems caused by introduced invertebrates is (1) prevention of further introductions by strengthening quarantine procedures, (2) fumigation of imported biological material (e.g., Christmas trees, cut flowers), and (3) improvement of the surveillance of importations (Howarth 1985). Minimizing disturbances of native ecosystems (e.g., land clearing, grazing, pig rooting, invading weeds) that favor introduced invertebrates will also lessen their impact.

DISASTERS

Usually enough individuals survive hurricanes and heavy storms to perpetuate the population, but unfavorable events are potentially important when populations are extremely low. Laysan Island, 1500 km northwest of Honolulu, originally supported an endemic subspecies of Apapane, the Laysan Honeycreeper (*Himatione sanguinea freethii*). Laysan Honeycreepers frequented tall grass and low bushes (Fisher 1906). Unfortunately, rabbits were introduced in 1903 and by 1911 had destroyed most of the vegetation (Dill and Bryan 1912). By 1923 the rabbits had removed the last vestiges of vegetation, and members of the 1923 Tanager Expedition found only three Laysan Honeycreepers. These birds "perished during a three-day gale that enveloped everything in a cloud of swirling sand" (Wetmore 1925).

A severe tropical storm is thought to have been responsible for eliminating the Puerto Rican Bullfinch (*Loxigilla portoricensis grandis*) from the island of St. Kitts (Raffaele 1977). Cataclysmic storms could adversely affect other precariously low populations. Particularly vulnerable are those species having very small ranges. Broadside hits on the Alakai Swamp or the northeast slope of Haleakala could eliminate several species.

The island of Hawaii is the site of frequent volcanic eruptions and massive lava flows moving from volcano summits to the ocean. These flows are as wide as 1 km, destroy large tracts of native forest, and fragment the range of forest birds (see Fig. 48). Presently the greatest threat may be to nesting areas of the Hawaiian Crow; the 1984 Mauna Loa lava flow covered part of the area where Ou were most numerous in the 1977 survey. It has been 200 years since an eruption on Maui, but renewed eruptions are possible; the small range of Poo-uli could be demolished by a major eruption along the east rift zone of Haleakala, but this is quite unlikely. Fires resulting from volcanic activity are an additional threat in dry and mesic habitats.

CONSERVATION

HISTORY OF HUMAN DISTURBANCE

The recent history of the Hawaiian biota may be divided into three cultural periods: the pristine period before Polynesian contact (ca. 400 A.D.); the Polynesian period before Western contact (1778); and the modern period to the present. The series of changes that Polynesians initiated drastically altered pristine ecosystems that had evolved in isolation for millions of years and were in fact older than the main islands themselves. The main Hawaiian islands are geologically young (0–6 million years) and transient, formed in succession as the Pacific Plate slowly slides northwest over a hot spot in the earth's mantle. In 8 to 10 million years, each island in turn moves over and past the hot spot to erode away, while the native birds colonize new islands emerging to the southeast. From Kure Atoll in the Northwestern Hawaiian Islands, a line of seamounts continues north until subducted near the Aleutians, with the northernmost over 70 million years old. Based on DNA hybridization studies, Sibley and Ahlquist (1982) inferred that the ancestral Hawaiian honeycreeper may have colonized the archipelago 15–20 million years ago on forested high islands that have since become low islands or seamounts. Thus the fauna and flora that Polynesians found on the young main islands may have had their origins back millions of years on now submerged islands. Existing in isolation for eons, free of many stresses faced by their continental ancestors, many species lost their defensive biochemistry, morphology, and behavior. Plants lost their alkaloids and thorns (Carlquist 1970), birds lost some of the immunity they had to disease, some birds became flightless (James and Olson 1983), and many insects lost their wings altogether (Zimmerman

1948). These species, successful in isolation, became increasingly vulnerable to alien influences poised around them on the Pacific rim and on islands to the south.

The Polynesian colonists brought with them a collection of plants and animals. Most of the plants, such as bananas, coconuts, taro, and yams, were food crops for their own consumption, but inadvertent introductions include weedy species such as *Ludwigia octivalvis, Oxalis corniculata, Urena lobata, Thelypteris interrupta, Waltheria americana, Merremia aegyptia* (Kirch 1982), and perhaps *Ipomoea congesta.* They also brought domestic animals such as dogs, pigs, and junglefowl, and such anthropophilic stowaways as the Polynesian rat, a gecko, a skink, and several snails. Most importantly, they transported with them a concept of landscape that would radically transform the pristine ecosystems into facsimiles of those of their home islands (Rappaport 1963, Kirch 1982). One of their tools was fire (Barrau 1961), and soon "the process of conversion of a natural ecosystem into an actively manipulated cultural landscape" began (Kirch 1982).

Archaeological evidence from dated village sites shows that the Hawaiian populations grew slowly for the first 600 years, then rose rapidly to a peak of over 200,000 people by about 1650 A.D. (Kirch 1982). This translates to an average density of about 22 people/km^2 in the habitable parts of the islands, and about 250 people/km^2 in heavily settled areas such as Halawa Valley on Molokai. All the islands except Oahu were more densely and uniformly settled than they are now! By the time of Western contact, populations were lower, and Kirch (1982) suggests the decline resulted from habitat destruction and a "consequent reduction in carrying capacity." The evidence for habitat destruction is compelling. Early explorers clearly described the lack of forest cover on the dry sides of all the islands, and descriptions such as "destitute," applied to Kahoolawe by missionary William Ellis (1827), were appropriate to much of Maui, Oahu, and Kauai as well. Extensive lowland grasslands in many areas were obviously anthropogenic; ash-laden soil underlying them has revealed fossil snails and birds that inhabited a pre-existing xeric forest (Kirch 1982, Olson and James 1982b). Interred with these materials are the bones of geckos and skinks that suddenly appeared on the islands with the Polynesian settlers. In many cases erosion was severe; Kirch (1982) reports finding buried irrigation systems and large alluvial basins of sediment interbedded with ash.

The dryland forests that succumbed to Polynesian fires may have been the richest terrestrial ecosystem in the islands. Rock (1913) estimates that 60% of all Hawaiian plants occurred there. More than 45 fossil bird species found by James and Olson (1983) were dryland species. These birds included at least 15 drepanidines, 35% of the known species in the subfamily. At least 11 additional species described in historic times also occurred in dry forests. Five of these are now extinct, suggesting that birds such as the Palila, Greater Koa-Finch, Lesser Koa-Finch, and Kona Grosbeak may have been represented by relictual populations, possibly in marginal habitat, in mid- and upper-elevation dry-forest refugia when discovered by Westerners.

Damage to the mesic and wet Hawaiian forests was far less severe and restricted to their lower elevations, particularly the broader, more habitable valleys. The limited distribution of the Greater Amakihi above the upper level of Hawaiian cultivation on windward Hawaii may have resulted from habitat destruction in this area.

Walls around yam and taro patches on leeward Hawaii indicate that pigs occurred up to 1000 m elevation, and perhaps had penetrated even higher forests, although it is thought that Polynesian pigs had little effect upon pristine forest (Warshauer 1980; P. H. McEldowney, unpub. data).

In addition to eliminating most Hawaiian dry forests, Polynesians apparently hunted at least seven species of flightless geese (*Geochen rhuax, Thambetochen* spp.) and two species of flightless ibis (*Apteribis* spp.) to extinction (Olson and James 1982a). Discovery and interpretation of recent fossil findings are only partially complete at this time (S. L. Olson, pers. comm.), emphasizing our incomplete knowledge of the pre-Western periods.

Although Zimmerman (1963) stated that "fires of the early Polynesians swept vast areas of woodland away," such statements had been largely ignored until recently. It was assumed that the ancient Hawaiians were ardent conservationists, and that "extreme increases in instability did not occur until the advent of Western man and his advanced technology and civilization" (Murdock 1963). Carlquist (1970) reinforced these ideas by stating that "during the human occupation of the islands, especially by peoples other than the Polynesians, much dry forest was removed." Although these ideas are common in anthropological and ornithological works on Hawaii (Amadon 1950, Berger 1981), they are strangely at odds with descriptions of the islands by the first explorers. It is through the efforts of Olson and James (1982a, 1982b) and Kirch (1982) that we now know why many areas of the islands were barren when the first Europeans arrived.

When Captain Cook first sighted Kauai on 18 January 1778 he inaugurated the third or Western period in the ecological history of the Hawaiian Islands. After trading for provisions and collecting the type specimen of the Iiwi (Medway 1981), he sailed to Niihau and on 2 February released three goats on the island (Tomich 1969). Although his motives were humanitarian (to provide a new source of protein for the natives) and utilitarian (to ensure meat when ships returned), his understanding of the ecological consequences of his actions was poor indeed. During the Western period an inordinate number of introductions, coupled with commercial exploitation, led to progressively massive retreat and extinction among the native biota. Following introduction, feral ugulates such as cattle, sheep, goats, and pigs multiplied rapidly, and inexorably destroyed huge tracts of native forest by grazing, browsing, trampling or rooting up ground cover, and feeding on tree seedlings and understory plants (Tomich 1969, Kramer 1971, Baker 1979). Cattle in particular grazed what remained of the low-elevation dry forests and penetrated the wet forests; on Mauna Kea and Haleakala large numbers moved into subalpine woodlands and scrublands. The mesic koa forests provided ideal pastureland and were soon drastically reduced on Maui and heavily stressed on Hawaii. Goats rapidly penetrated dry and mesic forests throughout the islands, and European pigs invaded the pristine wet forest except where obstructed by impassable topography.

The forests also suffered from the direct impacts of man. The commercial harvesting of sandalwood began in 1790, and by 1820 the vast preponderance of sandalwood in the islands had been removed (Rock 1913, Judd 1927, A. Kepler 1984). Koa, the co-dominant tree in mesic forests, was rapidly removed to make way for cattle, and a koa timber industry developed on Hawaii that continues to this day. By the end of the 19th century, many of the forests extant when Cook arrived had been destroyed or severely degraded.

Animals were not the only group that became feral. An incredible diversity of foreign plants—now numbering over 4600 species, three times the number of native species (St. John 1973)—were brought to the islands for food, ornamentation, reforestation, or as weeds. About 10% of these introduced plant species have naturalized (St. John 1973), and 2% have become serious pests in native ecosystems, notably strawberry guava, banana poka, lantana, various blackberries and gingers, the melastome *Clidemia hirta*, and numerous grasses (Smith 1985).

The natural predators of native forest birds in pristine conditions included an extinct accipiter, the Hawaiian Hawk, and probably at least three extinct long-legged owls (Olson and James 1982b). The introduction of potential predators of native forest birds began with the Polynesian rat, a known bird predator (Kepler 1967; Atkinson 1973, 1977; Atkinson and Bell 1973). The list of new predators has since grown to include the black rat, Norway rat, mongoose, domestic cat, Common Barn-Owl, and Common Myna.

The Hawaiian Islands have had more bird introductions (162 species) and more exotic species established (45 definitely established, 25 probable) than any other area on earth (Long 1981). It has been suggested that competition for food between native birds and established introduced species has resulted in a decline of native species (Berger 1981, Mountainspring and Scott 1985). Far more importantly, introduced birds brought with them diseases that have probably had a severe impact upon native Hawaiian passerines (Warner 1968, van Riper et al. 1982).

The general trend from the pristine period to the present has thus been a steady retreat of the native biota into the least disturbed upland habitats. Montane rainforest and dry subalpine woodland provide the greatest "biological buffering" for the Hawaiian land birds. In effect, the initial patterns of species occurrence and response in a large hyperspace are destabilized, fragmented, and eroded away by an interminable procession of disturbance elements, much as ocean breakers wear down a headland, leaving the most resistant core community mainly intact. The relatively short history of human occupancy on the Hawaiian Islands has had a devastating impact far more severe than that of long-term human influence in continental tropical areas (Karr 1976b, Pearson 1977). Many endangered species that survive undoubtedly do so as relict populations in areas at the environmental extremes of their original range.

CONSERVATION STRATEGIES

Conservation strategies for individual species have been described in detail in U.S. Fish and Wildlife Service recovery plans for the Hawaiian Goose (Kosaka et al. 1983), Hawaiian Hawk (Griffin 1984), Hawaiian Crow (Burr et al. 1982), Palila (Berger et al. 1977), and the forest birds of Hawaii (Scott et al. 1983), Maui (Kepler et al. 1984), Molokai (Kepler et al. 1984), and Kauai (Sincock et al. 1984). Here we present an integrated overview of the strategies necessary to ensure the continued survival of Hawaiian forest bird species (Table 75). Many of the strategies will be appropriate to other parts of the world where major portions of avifaunas are threatened with extinction.

Legal habitat protection

Once key areas have been identified for most species, the primary conservation action needed

TABLE 75

STATUS AND MANAGEMENT RECOMMENDATIONS FOR NATIVE HAWAIIAN FOREST BIRDS

Island/species	Present status[a]	Total population	Management recommendations
Hawaii			
Hawaiian Crow (Alala)	E	75	Intensive management and captive propagation are absolutely essential in concert with habitat protection.
Ou	E	400	Probably little can be done in immediate future. Use of radio transmitters could prove useful in learning more about habitat requirements and limiting factors.
Hawaiian Goose (Nene)	E	340	Only current means of ensuring survival is captive propagation. Proposed research on food and predation may provide some relief.
Akiapolaau	E	1500	Long-term survival requires that several tracts of koa-ohia forest on windward Mauna Kea and Mauna Loa above 1500 m elevation be set aside and managed as ecosystem preserves.
Palila	E	2000	Removal of mouflon and implementation of fire management program should increase habitat quality. Long-term survival will be enhanced if width of mamane forest is increased.
Hawaiian Hawk (Io)	E	2000	Species is widespread, very adaptable in habitat and prey use; has good reproduction, high population densities for a raptor. In no immediate danger of extinction.
Hawaii Creeper	E	12,500	Large populations bode well for long-term survival, but habitat is declining in quality. Most severe habitat losses are in koa-ohia forests above 1500 m, where ecosystem preserves should be established and managed.
Hawaii Akepa	E	14,000	
Omao	N	170,000	Large numbers and broad distributions bode well for continued existence of these species. Mauna Kea Elepaio race, however, has restricted range, and small population (2500) should be monitored.
Elepaio	N	215,000	
Iiwi	N	340,000	
Common Amakihi	N	870,000	
Apapane	N	1,100,000	
Maui			
Hawaiian Goose (Nene)	E	50	Status is the same as on Hawaii.
Nukupuu	E	30	Pigs and goats have caused severe erosion on steep slopes above 1500 m, threatening long-term stability of forests and thus the future of all forest birds. Existing preserves are adequate for survival, if state forest reserves are included in a badly needed ungulate control program. Core habitat of Poo-uli should be fenced immediately and pigs removed. If habitat improvement does not result in increased numbers, captive propagation will be necessary. Research with radio-tagged birds has high potential in identifying additional limiting factors.
Poo-uli	E	140	
Maui Akepa	E	230	
Maui Parrotbill	E	500	
Crested Honeycreeper (Akohekohe)	E	3800	Large population and broad distribution bode well for continued existence. Management program for pigs and goats needed in essential habitat.
Iiwi	N	19,000	Large populations and broad distributions bode well for continued existence.
Maui Creeper	N	35,000	
Common Amakihi	N	47,000	
Apapane	N	110,000	
Molokai			
Molokai Creeper	E	?	The Nature Conservancy is actively managing significant proportion of essential habitat. Molokai Creeper may be extinct. See comments for Kauai birds.
Olomao	E	20	
Iiwi	N	80	
Common Amakihi	N	1800	Larger numbers and apparent disease resistance indicate no immediate threat of extinction.
Apapane	N	39,000	

TABLE 75
CONTINUED

Island/species	Present status[a]	Total population	Management recommendations
Lanai			
Common Amakihi	N	?	Possibility of using Molokai birds to reestablish population.
Apapane	N	540	Best hope is to control axis deer and prevent introduction of new exotics.
Kauai			
Kauai Akialoa	E	?	Only hope for long-term survival of endangered species on Kauai and Molokai is captive propagation. Disease appears to be the primary factor responsible for their desperate status and continued decline. Except for Ou, there may be no place to safely translocate birds within their historical ranges. Kauai Akialoa may be extinct.
Nukupuu	E	?	
Kauai Oo (Ooaa)	E	2	
Ou	E	<10	
Kamao	E	20	
Puaiohi[b]	E	180	
Kauai Creeper[b]	N	6800	Appears to have undergone significant decline in numbers and contraction in range in past 15 years.
Kauai Akepa[b]	N	5000	Large numbers and broad distribution bode well for continued existence.
Common Amakihi[b]	N	11,000	
Anianiau[b]	N	24,000	
Iiwi[b]	N	26,000	
Elepaio[b]	N	40,000	
Apapane[b]	N	163,000	

[a] Status: E = endangered; T = threatened; N = not endangered.

[b] Population numbers based on 1968–1973 survey by J. L. Sincock (unpub. data), for species known to occur widely outside our study area.

is habitat protection. A critical step in this process is consultation with the involved landowners to discuss management for natural values (Kepler and Scott 1985). Except for those species with desperately low populations, the most effective way to ensure the long-term survival of native birds is actively to protect intact ecosystems from further degradation and restore them as nearly as possible to their natural state. Commercial use and conservation management may be compatible on a rotational basis on rangeland (Scott et al. 1983); however, elimination of commercial activities in many areas of essential habitat in the Hawaiian Islands must precede intensive management of such areas. Because birds have the largest home ranges among the Hawaiian land biota, they provide a suitable base for deciding the minimum size of the managed area (see Eisenberg (1980) for a similar argument based on neotropical mammals).

Through the HFBS we have identified those areas most crucial to the long-term survival of native Hawaiian forest birds in the various recovery plans. The key areas on Maui, Kauai, and much of Molokai already enjoy legal protection as reserves. On much of Hawaii, however, the majority of the prime forest bird habitat has no protection, is threatened with commercial exploitation, and is declining in quality at an alarming rate. If the chance for long-term survival of forest birds is to be increased significantly, prime areas must be protected and managed for the benefit of their native ecosystems. Key areas that presently are not legally protected and that appear critical to the long-term survival of the Hawaiian Crow (Burr et al. 1982, Burr 1984) and Palila (Scott et al. 1984) have been identified on Hawaii and are reviewed below.

The best areas for Akiapolaau, Hawaii Creeper, and Akepa are the koa-ohia forests above 1300 m in the Hamakua, Kipukas, and Kau study areas; those in Hamakua are threatened by feral pigs, feral cattle, ranching, and planned timber harvest. The long-term survival chances of Akiapolaau, Hawaii Creeper, and Akepa would be enhanced significantly by legal protection of these lands. The information needed to design such a group of preserves is available. Action is needed by the concerned federal, state, and private agencies.

The relationship between montane forests and adequate water supply is a potent selling point for habitat protection. Agricultural, commercial, residential, and resort development on leeward Hawaii and Maui is impeded by inadequate water availability. A historical parallel occurred when many coastal Hawaiian villages were deserted after the water supply (streams, springs) failed.

At Lapakahi site on Hawaii and Nuu site on Maui, the water failure was connected with the clearing of dry and mesic woodlands above the sites on Kohala Mountain and on the Kahikinui Tract (Newman 1969). Preservation of forested areas on leeward Hawaii and eventual reforestation of areas like Kahikinui thus offer an economic incentive of a more dependable water supply, and would provide habitat suitable for native forest birds and other endemic plants and animals. The key selling point in negotiations for a conservation easement with the landowner over the Waikamoi Preserve on Maui was that the proposed conservation activities would improve water supply quality.

Habitat management

Once areas enjoy legal protection as conservation areas, they must be fenced, domestic and feral ungulates removed, introduced plants controlled or eradicated, and human access restricted. Although simple in principle, these four steps are often difficult to implement. Because of the vulnerability of native vegetation to destruction by introduced ungulates and plants, a policy of active management—not benign neglect (Soulé et al. 1971, Kepler and Scott 1985)—is imperative in some areas and desirable in most others to preserve the integrity of native ecosystems. Although we emphasize the importance of protecting montane forests to ensure the survival of endangered birds, natural communities at lower elevations often have significant biological value as well, and these communities may eventually be colonized by endangered birds as adaptations to introduced stress evolve.

Endangered bird species frequently occur on ranchlands, suggesting that they have a fair degree of adaptability to habitat modification, at least in its initial stages. However, the history of many of these lands is one of steady loss of canopy cover and native understory species while the number and impact of introduced plants increase (Warshauer and Jacobi 1982). Thus disturbed areas that now harbor endangered birds are not stable habitats and may not be suitable for endangered species indefinitely.

The lands of the U.S. National Park Service and The Nature Conservancy are the only major forest bird habitats in the Hawaiian Islands that are actively managed to protect native ecosystems. State activities on the Mauna Kea Game Management Area have resulted in the removal of goats, sheep, banana poka, and *Eupatorium riparium* and in limited control of mouflon. Other areas designated as state natural area reserves or forest reserves have no program to control introduced species, except public hunting. The need to control feral ungulates and exotic plants in existing preserves cannot be overstated. It is the most cost-effective way to increase the survival chances of native species and to reduce the number of extinct, endangered, and threatened species 100 years from now. Preserving native ecosystems now would avoid overwhelming conservation agencies in the future with species requiring clinical management to prevent extinction.

Intensive management of individual species

Manipulation of vegetation configuration, predator control, nest site manipulation, captive propagation (Conway 1980, Carpenter and Derrickson 1981), and translocation are costly but usually effective measures appropriate as a last resort for populations facing imminent extinction (Temple 1978). For species not yet on the brink, management dollars would be better spent on habitat protection and management.

Planting food crops has been proposed as a management strategy for the Hawaiian Goose (Kosaka et al. 1983) and Hawaiian Crow (Burr et al. 1982). Planting succulent grasses and fruit trees would benefit these species only in the long-term and only in conjunction with other intensive management measures. Moreover, the modification of an ecosystem for the benefit of one species and possible detriment of several other native species, possibly even endangered ones, raises philosophical concerns.

Control of predators, especially cats and mongooses, can be effective when concentrated in the area of nest sites. Mongoose predation of young takes a significant toll of Dark-rumped Petrels, Townsend's (Newell's) Shearwaters, Hawaiian Geese, endemic waterbirds, and Hawaiian Crows. For these species, saturating breeding sites with traps or poison bait may be an effective control measure.

Nest site manipulation includes multiple clutching (removing one clutch to obtain another), removing young from the nest and raising them in captivity, vaccinating birds against disease, and providing nest sites for cavity breeders. The key consideration is whether increased reproductive success will mitigate the factors limiting the population. On Kauai, for example, our data suggest that many species may become extinct by the year 2000 if avian disease has recently penetrated the Alakai Swamp. Funds and manpower would be ill-spent attempting to increase reproductive output of endangered passerines on Kauai if this is the case. The only clear case we see where nest site manipulation is justified is that of the Hawaiian Crow, and even here it is best combined with captive propagation to get through a population bottleneck (Burr 1984). These measures will not increase the survival chances for the Hawaiian Crow in the wild, however, unless there is a commitment to habitat protection and management.

Captive propagation has proved successful in reviving the Hawaiian Goose population (Kear 1975, Kear and Berger 1980); however, a self-sustaining natural population has not yet resulted (Devick 1981a, 1981b). Temple (1978) recommended captive propagation as the last resort for wild populations with little immediate hope of improving their reproductive output through habitat improvement, and for repopulating the original range. Because of the lack of success in reestablishing extirpated bird populations from captive-bred birds, captive propagation should proceed while endangered populations are still available to receive captively produced stock that can augment an existing population through cross-fostering. Among Hawaiian honeycreepers, the Nihoa Finch, Hawaii and Kauai races of Common Amakihi, Anianiau, Kauai Creeper, and Apapane have been kept in captivity (Berger 1981). Perkins (1903) noted that Hawaii Oo could easily be kept in captivity indefinitely. Hawaiian Crows have been bred in captivity and are prime candidates for captive propagation. For rare species, such as the Akiapolaau, for which probable stresses have been identified and which are subject to control, populations may increase sufficiently with habitat improvements so as to make captive propagation unnecessary. Habitat improvement for the Akiapolaau would also improve survival chances for other endangered native species. Captive propagation in connection with translocation may be feasible to reestablish the Ou from the windward Hawaii population to areas of its former range, such as Kona, Kau, and East Maui.

The extremely endangered birds on Kauai and Molokai are on a runaway course to extinction. If these species are to be preserved, extraordinary efforts are necessary. Captive propagation may be the only way to ensure survival of the Kamao, Olomao, and, if not too late, the Kauai Oo, Kauai Akiloa, Kauai Nukupuu, and Molokai Creeper. There is little hope that these species will survive without a commitment to this type of intensive management, and no guarantee that they will survive with it.

The New Zealand Wildlife Service has developed a successful strategy of transferring birds to new islands where the critical limiting factors are absent (Williams 1977); this strategy was pioneered with the Kakapo (*Strigops habroptilus*) (Oliver 1955), a flightless lekking parrot (Merton et al. 1984). Interisland transfer is unequivocally credited with saving the Saddleback (*Creadion carunculatus*), one of the two extant species of wattlebird, from extinction (Merton 1966, 1975; King 1978) and almost certainly the Black Robin (*Petroica traversi*) as well (Flack 1978, Diamond 1984). Transfers that are possible for this type of recovery effort among Hawaiian species include the Hawaiian Crow to Kau; Olomao to East Maui; Ou to Kona, Kau, and East Maui; Nihoa Millerbird to Laysan Island; Nihoa Finch to Necker Island; Common Amakihi to Lanai; Palila to Kona and the northern slopes of Mauna Kea; Maui Parrotbill, Nukupuu, Maui Creeper, and Akepa to Kahikinui; and Akiapolaau, Hawaii Creeper, and Akepa to koa forests in Hawaii Volcanoes National Park. By analyzing vegetation structure, resource levels, and natural history, the probability of a successful transplant can be increased by identifying optimal release sites.

Public education

Public support for conservation is essential for ultimate success in restoring native ecosystems. This has been strongly stated in all recovery plans prepared for Hawaiian birds. Radio and television spots, newspaper releases, filmstrips, brochures, and other printed materials are currently used to raise public awareness. A 30-min film for elementary and secondary schools would be very helpful. Professional wildlife biologists need to explain their perspective in non-technical terms to state legislators, regulatory officials, and the general public. Hunters need to understand that the endemic geese, hawks, owls, and crows are inappropriate targets. Visitors and travelling residents need to understand that thoughtless or inadvertent importations of organisms alien to the islands may create disastrous problems of enormous proportions. In the final analysis it is the people of the Hawaiian Islands who will save the forest birds, but they need to become better informed of the natural heritage under their stewardship. Informing the public may be our biggest challenge in attempting to save native Hawaiian ecosystems.

Importation control

Many of the stresses experienced by native bird populations derive from such introduced organisms as aggressive plants, pathogens, insects, predatory molluscs, and competing birds. Solving such problems usually entails a substantial commitment of resources. A cost-effective strategy to prevent the occurrence of these problems is to place more rigorous and restrictive controls on importations to ensure that organisms potentially disruptive to native ecosystems or detrimental to native birds are not permitted to enter the Hawaiian Islands. Many of the most serious problems are caused by deliberate, thoughtless importations (e.g., fountain grass, banana poka)

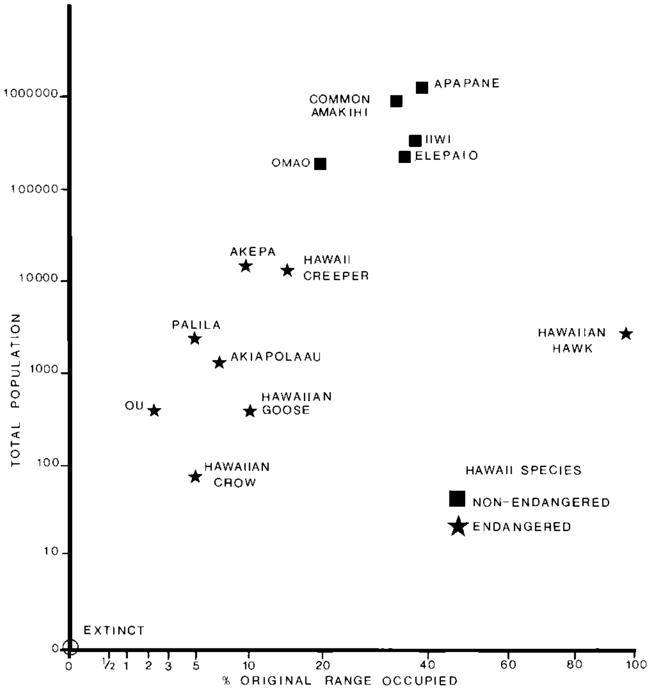


FIGURE 334. Extinction model for bird species on Hawaii.

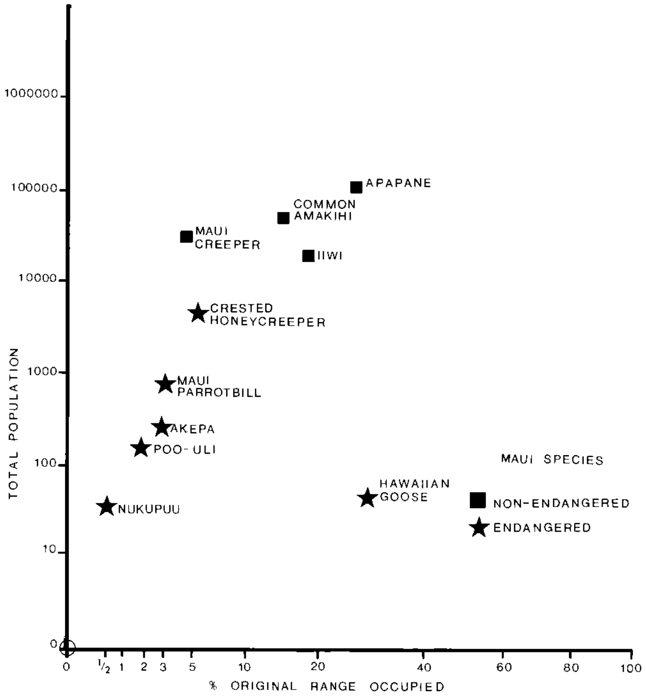


FIGURE 335. Extinction model for bird species on Maui.

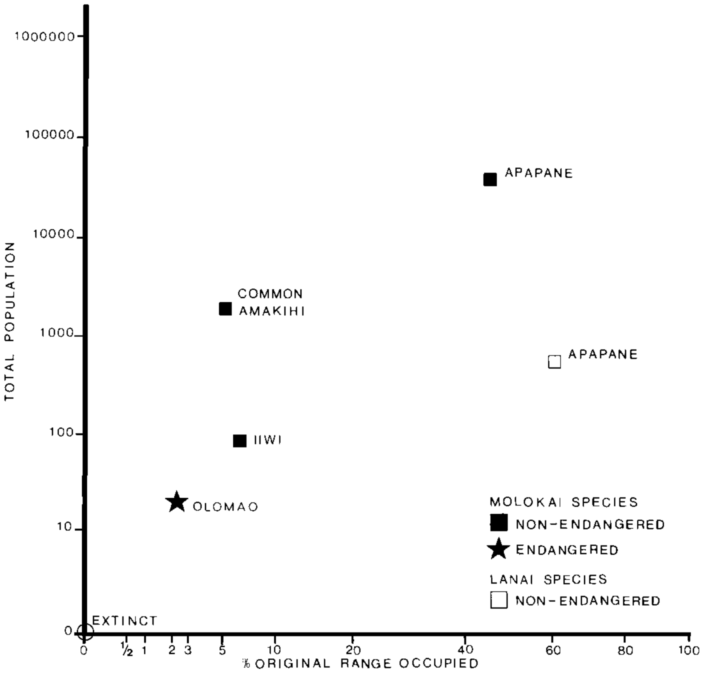


FIGURE 336. Extinction model for bird species on Molokai and Lanai.

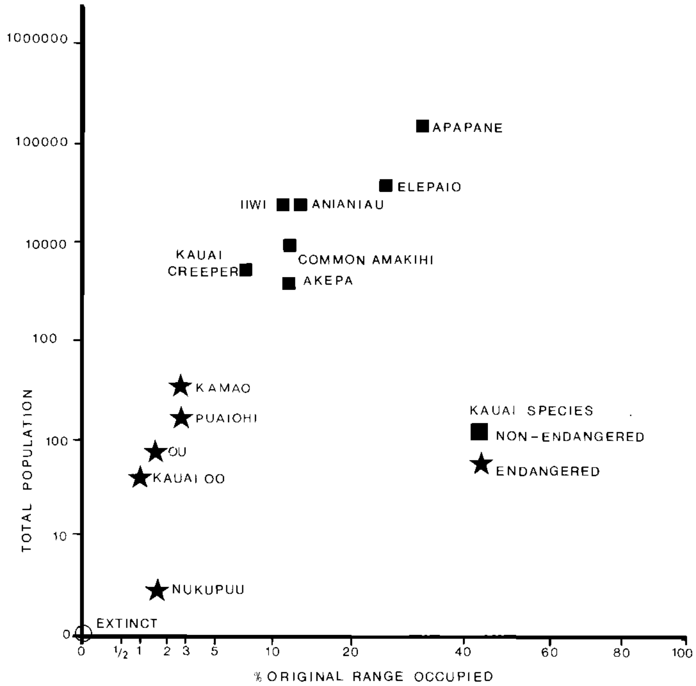


FIGURE 337. Extinction model for bird species on Kauai.

that could have been avoided had state officials looked beyond narrow agricultural interests in permitting these organisms entry. A comprehensive, well designed, fully implemented system of importation controls is of a high priority in averting unnecessary future problems.

Future research needs

The major refugia for native forest birds should be surveyed at least decennially to monitor long-term population trends. Surveys to study seasonal and annual variation in distribution and habitat response are also important. A systematic survey of forest bird habitats on Oahu would be desirable. These efforts should be planned so that useful information is gathered on the behavior, habitat response, and biology of the rarer species. Research on the diet and habitat response patterns of the Puaiohi would help to maximize the chances of a successful captive propagation program for that species. Paired high- and low-elevation tests manipulating food sources and predators would yield insight on the limiting factors of the Hawaiian Goose. More information is needed on the regeneration patterns and role of introduced organisms in native ecosystems once feral ungulate pressure is removed.

Radiotelemetry studies on endangered passerines have high potential for yielding valuable insights on breeding behavior, movement patterns, limiting factors (in conjunction with translocation), optimal preserve designs, and the most appropriate management techniques. Radiotelemetry studies are needed on the Hawaiian Crow to compare habitat utilization and resource availability on a seasonal basis, to maximize reproductive output, and to determine the effectiveness of disease vaccinations. Studies on seasonal movement patterns with radiotagged Ou, Palila, Maui Parrotbill, Akiapolaau, and Crested Honeycreeper would also aid in the development of optimal management strategies. An intensive study of distributional anomalies identified in this study would be valuable in further determination of limiting factors of endangered Hawaiian forest birds. Endangered and surrogate species translocated to areas of unexpectedly low densities in aviaries or released with radio transmitters can have their behavior and survival rates easily compared with birds similarly treated in occupied areas.

EXTINCTION MODELS

As a means of identifying those species most in need of attention, we constructed "status graphs" for the native avifauna of each island (Figs. 334–337). These graphs plot the current population of each species against the percent of the species' range still occupied. At a glance the graphs show how many birds are left and how restricted their ranges have become. The species nearest the lower left-hand corner (the point of extinction) are the most endangered; those farther away are less threatened, while those appearing in the upper right-hand corner are fairly safe.

ISLAND RECOMMENDATIONS

Hawaii

The native avifauna is most intact in four refugia: the Mauna Kea mamane-naio woodland, the windward rainforest, the Kau forest, and the mesic forest on the north slopes of Hualalai (Fig. 338). In addition, the main population of the Hawaiian Crow and very low populations of other endangered species inhabit the mesic to wet forest of central Kona. The habitat response graphs (Fig. 331) show that koa-ohia forest above 1500 m elevation supports the highest density of endangered birds, with a secondary population center lying in the mamane-naio woodland. Endangered bird density declines dramatically with decreasing vegetation biomass within a habitat type.

Hawaiian Geese populations are presently maintained principally by releases of captive-bred birds. Captive propagation has begun and will be essential for the Hawaiian Crow; it may also prove necessary for the Ou. Our status graph (Fig. 334) indicates that these species are the ones most threatened with extinction on Hawaii.

The main threats to the mamane and naio woodland on Mauna Kea are fire and feral ungulates (mouflon and formerly sheep, goats, and cattle). Removal of mouflon and the few remaining sheep from the upper elevations of Mauna Kea is recommended, as is developing a fire management program that includes eliminating fountain grass, establishing fire breaks, controlling activity in the Hale Pohaku corridor, educating the public, and increasing surveillance during high-risk periods.

Management of the Kau Forest Reserve epitomizes benign neglect. Fencing the forest reserve above 1300 m elevation and removal of feral pigs are recommended. The mouflon and feral sheep at timberline should be extirpated. Feral cattle are found in Kau at higher elevations within and above the koa-ohia forest. Long-term stability of the forest requires that domestic and feral cattle be eliminated from the area. The long-term survival chances of the endangered birds in Kau would be further increased if feral ungulates were removed from the Kapapala Forest Reserve. That area would then serve as a corridor linking the Kau and Hamakua populations of Akiapolaau, Hawaii Creeper, and Akepa. This

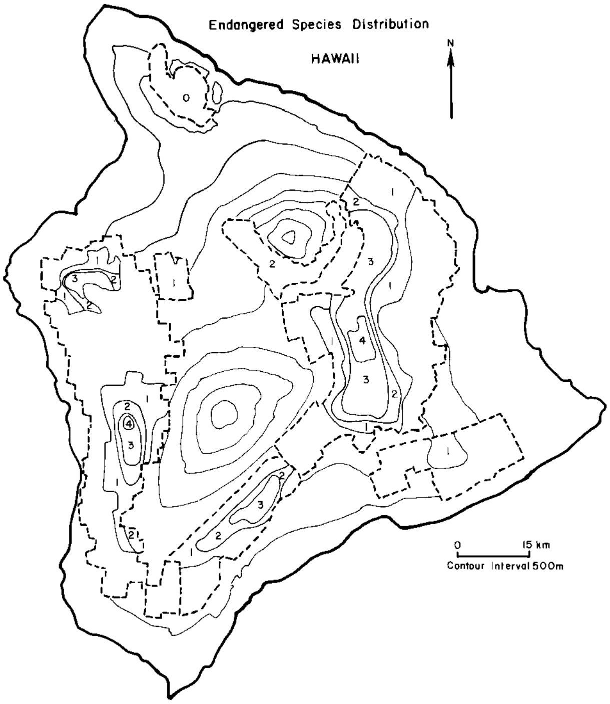


FIGURE 338. Distribution of endangered passerine bird species richness on Hawaii.

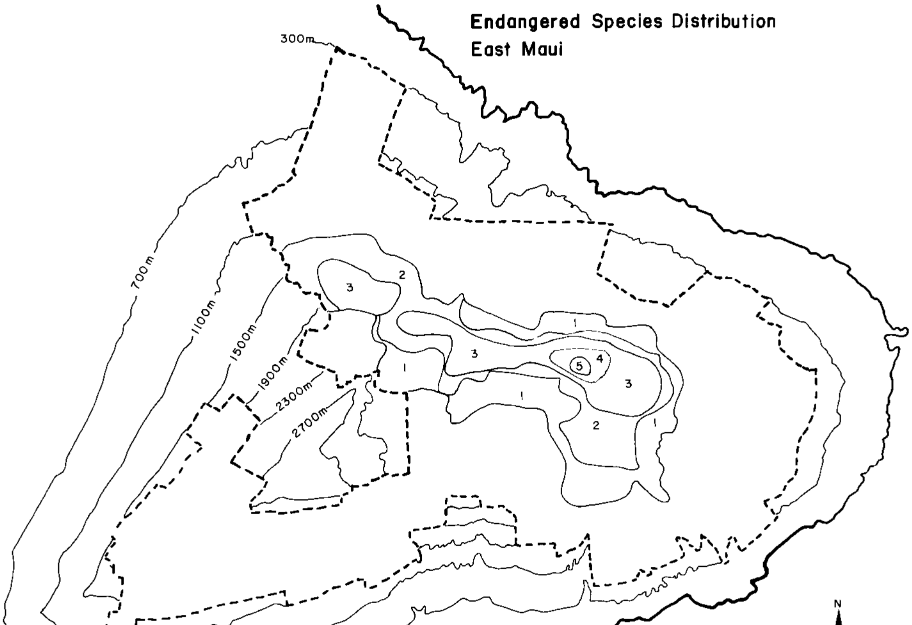


FIGURE 339. Distribution of endangered passerine bird species richness on East Maui.

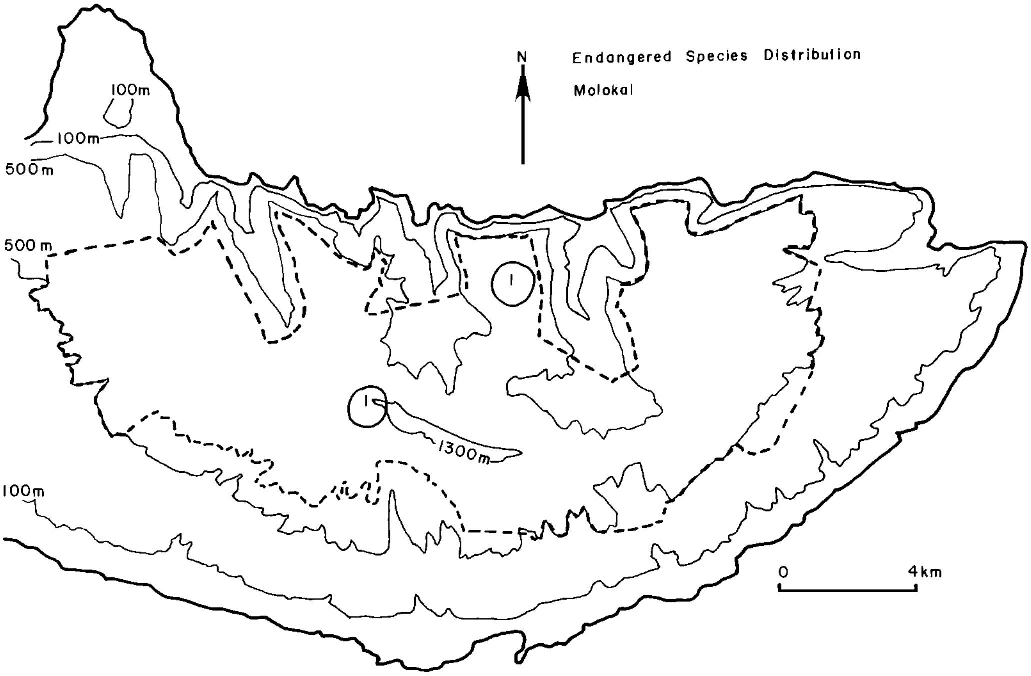


FIGURE 340. Distribution of endangered passerine bird species richness on Molokai.

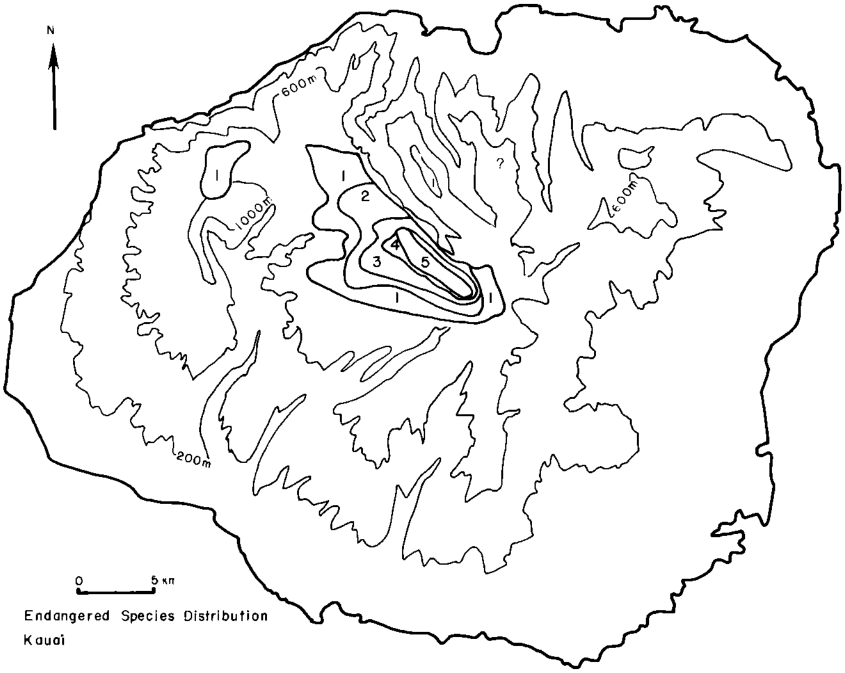


FIGURE 341. Distribution of endangered passerine bird species richness on Kauai.

management strategy would be strengthened if the lands of Keauhou above 1500 m north of Hawaii Volcanoes National Park were similarly managed. Their suitability as forest bird habitat, however, has steadily declined during the last 30 years, because of ranching and clearing (Warshauer and Jacobi 1982).

On windward Hawaii, acquisition of a long-term mandate for conservation management is especially important for the montane forests above 1300 m elevation. Koa-ohia forests at 1500–2000 m on Mauna Kea and northwest of Kilauea Crater are threatened with commercial harvesting. These areas support the core of the Akiapolaau, Hawaii Creeper, and Akepa populations. Reforesting the mesic koa-ohia forests on the windward slopes of Mauna Kea may make it possible to reestablish the link between the populations of Akiapolaau in the Hamakua and Mauna Kea study areas. Extensive areas of well-managed habitat in Hawaii Volcanoes National Park benefit many native biota, including Hawaiian Geese and Hawaiian Hawks, but other than an occasional Ou, virtually no endangered passerines occur within the park boundaries. Control measures are needed for banana poka, which threatens significant portions of essential forest bird habitat on windward Hawaii. High priority should be placed on controlling further spread of banana poka in the vicinity of Hawaii Volcanoes National Park.

On leeward Hawaii, the koa-ohia forest on Hualalai that supports Hawaiian Crows, Hawaii Creepers, and Akepa is heavily grazed and portions were unlawfully logged. A reserve is being established in this area, as has long been proposed by the Hawaii Division of Forestry and Wildlife. In central Kona, the koa-ohia forests that Hawaiian Crows occupy are a mosaic of grazed and undisturbed lands. Portions of the prime Hawaiian Crow habitat in this area are being logged at present. Dedicating some of these lands to conservation management is essential in the near future, or Hawaiian Crows and much of the koa-ohia forest ecosystem in central Kona will disappear.

In conclusion, the top priorities on Hawaii are (1) securing ownership of, conservation easements to, or management agreements for several koa-ohia forest areas that are essential for the survival of the Hawaiian Crow, Akiapolaau, Hawaii Creeper, and Akepa; (2) removal of feral ungulates from the Mauna Kea Game Management area; (3) intensive management of the Hawaiian Crow population; (4) control of banana poka in essential habitat; and (5) control of pigs in essential habitat.

Maui

The native avifauna of Maui is best represented in the high-elevation rainforest of northwest Haleakala and upper Kipahulu Valley (Fig. 339). The Olomao and Ou have apparently become extinct. The habitat response graphs (Fig. 331) indicate that the montane ohia rainforest supports the highest density of endangered birds. Nukupuu, Maui Akepa, and Poo-uli are the species most threatened with extinction on Maui (Fig. 335). The Hawaiian Goose population on Haleakala is maintained chiefly by release of captive bred birds (Devick 1981b).

We would expect to see a significant increase in the densities of the Maui Parrotbill and Poo-uli by fencing and then eliminating feral pigs and goats from the high montane rainforest in the Hanawi and Kuhiwa watersheds. These areas are national park and state forest reserve lands; recently, Haleakala National Park has begun fencing essential forest bird habitat. The area with the highest priority for fencing is the watershed between the two forks of the Hanawi, where the greatest numbers of Poo-uli are known to occur. All other endangered Maui forest birds also occur in this area. The Waikamoi Reserve supports a fairly intact koa-ohia forest west of Koolau Gap with key populations of Maui Parrotbill, Maui Akepa, and Crested Honeycreeper; management rights to this area have been recently acquired by The Nature Conservancy, which will be fencing it and eliminating feral ungulates. Management rights to the Haiku Uka lands, owned by East Maui Irrigation Co. and lying between Waikamoi Reserve and the Koolau Forest Reserve, also need to be acquired so that this essential connecting forest can be similarly managed.

The dry side of East Maui, Kahikinui, has been overgrazed to a scrubland with vestiges of the original forest. Portions of Kahikinui were fenced in 1983 by the Hawaii Department of Land and Natural Resources and the National Park Service as the first step in regenerating this ecosystem. Here the plan is to enlist the cooperation of local hunters to radically reduce goat herds on the south slope of Haleakala (W. Wong, L. Loope, pers. comm.). The revegetation of Kahikinui offers an exciting prospect in the management of endangered species. As earlier mentioned, the dry koa-mamane-ohia woodland that would eventually develop above 1400 m elevation would provide good habitat for Maui Parrotbill, Nukupuu, and Akepa. The Kahikinui forest would connect to the koa forests on Kuiki Peak by a corridor of dry forest in Kaupo Gap. Because Maui Parrotbill and Nukupuu often flock with Maui Creeper, which tend to wander, we would expect Maui

Creeper flocks to repopulate the regenerated Kahikinui woodland in time, and that some of the flocks would include birds of the two endangered species, thus seeding new populations.

Perhaps as much as 80% of the benefits that are to be derived from management efforts would result from exclusion of feral ungulates and prevention of the establishment of new populations of exotic plants and animals. Additional research is needed in the montane rainforest of East Maui on seasonal and annual variation in distribution, abundance, and habitat response of the endangered passerines. The results of these studies should help in the design and management of reserves. They should also help us to gain a more detailed understanding of the operation of the factors that limit the rarest species.

Molokai

The avifauna of Molokai is much reduced, but Olomao and possibly Molokai Creeper still survive (Fig. 340). These species and the Iiwi are near extinction (Fig. 336) and are confined to remote rainforests. Captive propagation and translocation are the best hope for the continued survival of the endangered Molokai forest birds. The Nature Conservancy has begun active management to preserve the native forest on its Kamakou Preserve, but the area needs to be expanded eastward to include all the remnant rainforest. The Olokui Plateau is almost inaccessible to feral ungulates and supports the least disturbed native forest in Hawaii (Fig. 329); a short stretch of fencing across a certain treacherous ridge would close the only possible access for pigs and axis deer. The native vegetation on vast tracts of east Molokai and the southwest edge of our study area is utterly devastated. If our assessment of the impact of avian disease is correct, the outlook for the long-term survival of Olomao and Molokai Creeper, even with intensive habitat protection and management, seems bleak.

Lanai

The Lanai avifauna has been almost totally extirpated by habitat destruction and probably avian disease. The Apapane may be the only native passerine extant (Fig. 336). Fencing would help protect the remaining forest. If, as we suspect, disease is the principal factor responsible for the massive extinctions on Molokai and Lanai, then the long-term survival chances for reintroduced native species are negligible. One bright spot would be reintroducing Common Amakihi on Lanai, using birds from the apparently disease-resistant lowland populations on Molokai.

Kauai

Most of the native birds of Kauai have retreated to the Alakai Swamp since the 1890s (Fig. 341). After the 1960 survey (Richardson and Bowles 1964), it was hoped that the Alakai would serve as a permanent refuge for the six endangered species, but Kauai Akialoa were last sighted in 1965, and Nukupuu in 1975 (Sincock et al. 1984). Our survey shows that none of the endangered Kauai passerines has a population of even 50 birds; we estimated fewer than 10 Kauai Oo and Ou. In addition, the Kauai Creeper population appears to have declined in the past decade (Fig. 337). Disease is one probable cause for these declines. Distribution and density maps for the endangered passerines show a general retreat to the remote south edge of the Alakai, suggesting that an inimical factor is entering from the lower north edge. If present trends continue unabated, by the year 2000 several of the six endangered Kauai passerines could be extinct in the wild. Captive propagation seems to be the only way to sustain these species. In many ways the situation on Kauai replays the pattern of retreat and extinction that must have occurred on Molokai, Lanai, and Oahu. Despite the continued declline of endangered birds, the Alakai Swamp should be protected from introduced plant invasion and feral ungulates because of its rich diversity of native plants and the outside chance that some species may yet evolve genetic resistance to avian diseases. Dams, ditches, and other potential breeding sites for mosquitoes should not be permitted on the high plateau.

CONCLUSION

Much has been learned about endangered Hawaiian forest birds in the last decade. Available information is now adequate to define essential habitat. Although numerous factors may have potential negative impacts on Hawaiian species, we feel that those having the greatest impact are clearly identified on each island. In many cases, the management actions and means to eliminate or significantly reduce these negative factors are known. Implementation of these actions should result in significant increases in the numbers of many endangered birds while increasing the long-term survival chances of the native ecosystems in which they live. For some limiting factors such as mosquito-borne diseases, effective means of abatement may not exist, although reduction in exposure may be possible and effective control techniques may be discovered. The long-term survival chances of Palila, Maui Parrotbill, Maui Nukupuu, Akiapolaau, Hawaii Creeper, Akepa, Crested Honeycreeper, and Poo-uli can be increased significantly by protection, restoration, and management of their essential habitat. If we fail to act on available information, their survival chances will be reduced significantly. Other species will require intensive management with no guarantee of success. For some species little can be done beyond maintaining a captive population, and for birds like Olomao, Kauai Oo, Kauai Akialoa, Maui and Kauai Nukupuu, and Molokai Creeper, it may be too late to establish a captive flock. Much progress has been made through the combined actions of federal, state, and private agencies, as well as by university workers and concerned individuals. Much more needs to be achieved. We hope that the data presented in this monograph will encourage the cooperation of all interested parties towards further conservation action in the Hawaiian Islands.

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Survey Participants and Habitats

John Sincock and Mike Scott are all smiles as they are picked up after a difficult transect. Tonnie Casey and Rich Warshauer peer out truck cab, Kau 1976.

Jim Jacobi and Mike Scott discuss procedures during the critical early stages in Kau.

John Sincock, relieved after exiting from a Kau transect.

Mark Collins in a forest clearing.

Tonnie Casey hikes down Transect 3, Kau survey.

Although resting at his camp on Transect 2 on Hawaii, Charlie van Riper looks ready to continue.

The 1977 Forest Bird Survey Team (L to R): Carter Atkinson, Larry Katahira, Tonnie Casey, Phil Ashman, Mark Collins, Tim Burr, Peter Pyle, Avery Taylor, Mike Scott and Cam Kepler.

Radio checks with the outside world were undertaken daily to assure our safety: Cam Kepler calling from Kilauea Forest, Hawaii.

The team that surveyed the forests of Leeward Hawaii: (L to R), 1st Row: Jack Jeffrey, Matthew Ednie, Tim Bertrand, Philip Ashman, Rick Warshauer; L to R, standing: Tonnie Casey, Howard Hunt, Ted Bodner, Carter Atkinson, Rich McArthur, Tim Burr, Peter Pyle, Milton Kealoha, Mike Scott, Cam Kepler, Holly McEldowney, Heather Fortner and Jim Jacobi. Not shown: Miles Nakahara and Dick Davis.

Some members of the bird team undergoing training, Keahou Ranch, May 1977 (L to R): Carter Atkinson, Avery Taylor, Mike Scott, Cam Kepler, Phil Ashman and Peter Pyle.

Hamakua Transects often ended abruptly in cane fields that looked much alike. Carter Atkinson studies his map after leaving Transect 19.

A small group from the bird team during training at Keauhou Ranch, May 1978 (L to R): Howard Hunt, Cam Kepler, Ted Bodner, Jack Jeffrey and Carter Atkinson.

Philip Ashman relaxes at campsite on Hualalai's south slope (4920'). Transect 39, 23 June 1978.

Rich MacArthur enjoying lunch at camp in mamane forest on Mauna Loa (5800'). Transect 58, 14 June 1978.

Training at Keauhou Ranch, May 1978 (L to R): Carter Atkinson, Jack Jeffrey, Mike Scott and Ted Bodner.

Usually only a dream, Tim Burr snatches a rare moment of rest after a hard day on Mauna Loa: campsite, sta. 19, Transect 51, June 1978.

A last map check at the drop-off point for Maui transects 5 and 6, 6 hours and 5000' in elevation change away: L to R, Rob Hansen, Ted Rodriguez, and Mike Scott, May 1980.

Looking elf-like in his rain gear, Botanist Rick Warshauer prepares to move downslope during a very wet afternoon on Maui, Tr. 8, 4700', June 1980.

The Maui Trail Crew heads to Haleakala's north slope after sitting out 50″ of rain at Paliku Cabin, Haleakala National Park: L to R, Sam Kalalau, Mark Tanaka-Saunders, Terry Lind, Talmadge Magno, Mike Hoffman and Greg Cameron, March 1980.

Action as crew prepares to board helicopter for flight to training base camp on Maui, May 1980: L to R, Tom Hauptman (pilot), Carol Beadle (USNPS), Kay Kepler, and Peter Pyle.

Steve Mountainspring negotiates a very narrow stretch on Puu Hoi Ridge (Tr. 25), Pelekunu Valley, Molokai, August 1980.

Malcolm Harrison (New Zealand Wildlife Service) photographs Pelekunu Valley and the isolated Olokui Plateau, Molokai, from top of Tr. 7, May 1979.

Wet but happy, Kay Kepler pauses on Tr. 19, Olokui, Molokai, at 4000′, Aug. 1980.

Statisticians Valerie Wildman (L) and Fred L. Ramsey checking out sampling methods on Maui.

Tired and muddy after a week in the Alakai, the six members of the bird team manage a smile at the pick-up point: (L to R), Phil Ashman, John Engbring, Marie Morin, Mike Scott, Cam Kepler, and Kay Kepler.

Sheila Doyle recording observations in heavily grazed pasture on Mauna Kea, Tr. 112, Feb. 1982.

Trail crew chief Dick Davis checks compass heading while laying transect in windward Hawaii.

Whenever and wherever possible, Mike Scott kept track of the myriad details needing attention during the 7 years required to complete the Hawaii Forest Bird Survey: Kokee, Kauai, June 1981.

Drying equipment was always necessary between extended trips into the Alakai: here Cam Kepler, Dave Boynton and Phil Ashman discuss the survey amidst gear at state facility, Kokee.

Mike Scott and Cam Kepler are delighted to have completed the surveys: Kokee, Kauai, June 1981.

The Nature Conservancy showed great interest in the forest bird survey. Here, Kelvin Taketa checks out a privately owned section of Haleakala's north slope, February 1981. Kelvin later helped secure the area as TNC's 5230 acre Waikamoi Preserve harboring 6 endangered species.

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APPENDIX TABLE 1[a]

ELEVATION [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY STRATUM, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Elevation												
100–300 m	···	···	290 (4)	···	240 (16)	···	···	···	···	259 (7)	300 (0)	···
300–500 m	···	471 (5)	413 (5)	···	437 (15)	···	490 (0)	481 (7)	···	425 (9)	456 (12)	···
500–700 m	680 (4)	616 (4)	616 (4)	···	634 (5)	···	615 (16)	616 (8)	656 (9)	611 (6)	582 (7)	···
700–900 m	829 (6)	802 (3)	815 (5)	···	805 (3)	···	796 (15)	818 (6)	792 (9)	801 (4)	730 (20)	···
900–1100 m	1008 (5)	1000 (3)	1004 (4)	1080 (20)	1008 (3)	···	1045 (11)	1004 (5)	1000 (9)	999 (5)	···	···
1100–1300 m	1202 (4)	1204 (3)	1130 (5)	1217 (9)	1207 (3)	···	1218 (7)	1206 (5)	1200 (9)	1190 (5)	···	1253 (4)
1300–1500 m	1408 (4)	1406 (3)	···	1420 (7)	1407 (2)	···	1355 (5)	1401 (5)	1382 (11)	1346 (7)	···	1350 (4)
1500–1700 m	1611 (5)	1598 (3)	···	1590 (6)	1592 (3)	···	1585 (7)	1603 (6)	1606 (15)	···	···	1510 (0)
1700–1900 m	1798 (5)	1791 (4)	···	1807 (5)	1799 (4)	···	···	1810 (5)	1730 (5)	···	···	···
1900–2100 m	1983 (7)	1977 (6)	···	1998 (5)	1993 (4)	2028 (5)	···	2008 (5)	···	···	···	···
2100–2300 m	2120 (6)	2160 (13)	···	2152 (9)	2176 (5)	2211 (9)	···	2208 (5)	···	···	···	···
2300–2500 m	···	···	···	···	2338 (6)	2411 (7)	···	2390 (9)	···	···	···	···
2500–2700 m	···	···	···	···	···	2601 (6)	···	2567 (14)	···	···	···	···
2700–2900 m	···	···	···	···	···	2787 (7)	···	2760 (23)	···	···	···	···
2900–3100 m	···	···	···	···	···	2972 (18)	···	···	···	···	···	···
Habitat												
Ohia	1370 (16)	1236 (8)	711 (9)	1842 (15)	1301 (11)	···	1185 (18)	1309 (17)	1083 (23)	903 (12)	···	1298 (5)
Koa-ohia	1456 (16)	1144 (15)	···	1484 (24)	1358 (9)	···	···	1148 (22)	···	···	···	···
Koa-mamane	···	1995 (16)	···	1671 (19)	1672 (13)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	1880 (0)	2374 (21)	···	···	···	···	···	···
Mamane	···	···	···	···	1694 (31)	2593 (17)	···	2187 (16)	···	···	···	···
Other natives	···	···	···	···	1066 (42)	···	···	1819 (43)	···	904 (22)	516 (18)	···
Intro. trees	···	791 (26)	···	···	851 (47)	···	1065 (62)	1306 (65)	640 (0)	685 (27)	579 (11)	···
Treeless	1414 (35)	993 (18)	1005 (53)	1962 (91)	1656 (58)	···	···	2110 (21)	1337 (81)	···	492 (28)	1370 (0)

[a] Values are given in meters; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 2[a]
MOISTURE [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	3 (+)	···	4 (0)	···	···	···	···	5 (+)	4 (0)	···
300–500 m	···	6 (0)	5 (+)	···	4 (+)	···	4 (0)	6 (0)	···	5 (+)	4 (+)	···
500–700 m	6 (0)	6 (+)	6 (+)	···	4 (+)	···	5 (+)	6 (0)	6 (+)	5 (+)	5 (+)	···
700–900 m	6 (+)	6 (+)	5 (+)	···	4 (+)	···	6 (+)	6 (+)	5 (+)	5 (+)	6 (0)	···
900–1100 m	6 (+)	6 (+)	4 (+)	2 (0)	5 (+)	···	6 (0)	6 (+)	5 (+)	5 (+)	···	···
1100–1300 m	6 (+)	6 (+)	4 (+)	2 (+)	4 (+)	···	6 (+)	6 (+)	6 (+)	6 (+)	···	6 (0)
1300–1500 m	6 (+)	6 (+)	···	2 (+)	3 (+)	···	6 (0)	5 (+)	6 (0)	6 (0)	···	6 (0)
1500–1700 m	5 (+)	5 (+)	···	2 (0)	3 (+)	···	6 (0)	5 (+)	6 (0)	···	···	6 (0)
1700–1900 m	4 (+)	4 (+)	···	2 (+)	2 (+)	···	···	4 (+)	6 (0)	···	···	···
1900–2100 m	2 (+)	3 (+)	···	2 (0)	2 (+)	2 (0)	···	3 (+)	···	···	···	···
2100–2300 m	2 (0)	2 (0)	···	2 (0)	2 (0)	2 (0)	···	2 (+)	···	···	···	···
2300–2500 m	···	···	···	···	2 (0)	2 (0)	···	2 (0)	···	···	···	···
2500–2700 m	···	···	···	···	···	2 (0)	···	2 (0)	···	···	···	···
2700–2900 m	···	···	···	···	···	2 (0)	···	2 (0)	···	···	···	···
2900–3100 m	···	···	···	···	···	2 (0)	···	···	···	···	···	···
Habitat												
Ohia	5 (+)	6 (+)	5 (+)	2 (+)	3 (+)	···	6 (+)	6 (+)	6 (+)	6 (+)	···	6 (0)
Koa-ohia	5 (+)	5 (+)	···	2 (+)	4 (+)	···	···	5 (+)	···	···	···	···
Koa-mamane	···	2 (+)	···	2 (0)	2 (+)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	4 (0)	2 (0)	···	···	···	···	···	···
Mamane	···	···	···	···	2 (+)	2 (0)	···	2 (0)	···	···	···	···
Other natives	···	···	···	···	2 (0)	···	···	2 (+)	···	2 (+)	4 (+)	···
Intro. trees	···	6 (+)	···	···	3 (+)	···	6 (+)	4 (+)	2 (0)	3 (+)	5 (+)	···
Treeless	4 (+)	4 (0)	2 (+)	2 (0)	2 (+)	···	···	2 (+)	6 (0)	···	4 (+)	6 (0)

[a] Values are given in mean moisture index (2 = dry, 4 = mesic, 6 = wet); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 3[a]

CROWN COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	...	...	48 (4)	...	56 (5)	...	...	...	...	95 (8)	81 (0)	...
300–500 m	...	66 (4)	58 (2)	...	96 (16)	...	110 (0)	99 (18)	...	93 (8)	33 (8)	...
500–700 m	75 (0)	63 (1)	83 (2)	...	73 (4)	...	95 (6)	68 (5)	59 (8)	53 (3)	25 (3)	...
700–900 m	58 (2)	57 (1)	83 (2)	...	63 (2)	...	82 (9)	86 (5)	61 (4)	43 (2)	40 (30)	...
900–1100 m	45 (2)	50 (1)	73 (2)	50 (10)	75 (2)	...	74 (5)	93 (3)	77 (8)	55 (3)	...	...
1100–1300 m	38 (2)	54 (1)	58 (7)	52 (8)	58 (2)	...	75 (4)	97 (3)	104 (5)	90 (3)	...	123 (3)
1300–1500 m	41 (1)	62 (1)	...	36 (3)	52 (1)	...	93 (4)	85 (4)	93 (6)	92 (6)	...	120 (3)
1500–1700 m	53 (2)	58 (1)	...	45 (3)	57 (1)	...	73 (4)	90 (4)	57 (9)	...	...	134 (0)
1700–1900 m	58 (2)	55 (2)	...	45 (3)	47 (2)	...	...	72 (4)	58 (11)	...	...	...
1900–2100 m	21 (2)	38 (2)	...	28 (2)	34 (2)	38 (2)	...	46 (4)	...	...	...	...
2100–2300 m	15 (0)	42 (0)	...	16 (3)	26 (2)	37 (2)	...	8 (1)	...	...	...	...
2300–2500 m	...	...	...	...	21 (4)	39 (1)	...	3 (1)	...	...	...	...
2500–2700 m	...	...	...	...	...	37 (1)	...	5 (3)	...	...	...	...
2700–2900 m	...	...	...	...	...	25 (2)	...	0	...	...	...	...
2900–3100 m	...	...	...	...	...	17 (5)	...	...	...	...	...	...
Habitat												
Ohia	42 (1)	51 (1)	76 (1)	35 (1)	55 (1)	...	80 (2)	89 (1)	82 (3)	64 (2)	...	123 (2)
Koa-ohia	52 (1)	64 (1)	...	45 (4)	68 (1)	...	...	117 (3)	...	...	...	...
Koa-mamane	...	32 (2)	...	41 (4)	52 (2)	...	...	...	...	...	...	...
Mamane-naio	...	...	...	...	50 (0)	38 (1)	...	...	...	...	...	...
Mamane	...	...	...	...	38 (2)	30 (1)	...	8 (3)	...	...	...	...
Other natives	...	...	...	...	27 (2)	...	...	26 (2)	...	21 (4)	23 (7)	...
Intro. trees	...	54 (2)	...	...	61 (6)	...	93 (6)	77 (4)	31 (0)	75 (4)	30 (3)	...
Treeless	54 (3)	0	21 (6)	0	8 (4)	...	...	6 (1)	18 (4)	...	24 (15)	0

[a] Values are given in percent cover (and may exceed 100 due to multiple crown layers); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 4[a]

CANOPY HEIGHT [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	7 (2)	···	25 (0)	···	···	···	···	5 (1)	17 (0)	···
300–500 m	···	20 (1)	6 (+)	···	19 (2)	···	17 (0)	16 (3)	···	5 (+)	7 (2)	···
500–700 m	17 (0)	17 (+)	12 (+)	···	15 (1)	···	9 (1)	6 (+)	4 (+)	5 (+)	8 (1)	···
700–900 m	17 (0)	19 (+)	9 (+)	···	16 (+)	···	8 (1)	7 (+)	4 (+)	5 (+)	4 (1)	···
900–1100 m	17 (+)	20 (+)	8 (+)	4 (1)	16 (+)	···	7 (1)	8 (+)	4 (+)	5 (+)	···	···
1100–1300 m	17 (+)	20 (+)	11 (2)	7 (1)	14 (+)	···	7 (1)	7 (+)	5 (+)	7 (+)	···	5 (+)
1300–1500 m	17 (+)	21 (+)	···	7 (1)	13 (+)	···	8 (1)	7 (+)	5 (+)	5 (1)	···	5 (+)
1500–1700 m	16 (+)	19 (+)	···	7 (+)	12 (+)	···	7 (1)	8 (1)	5 (+)	···	···	5 (0)
1700–1900 m	13 (+)	17 (1)	···	5 (+)	12 (+)	···	···	7 (1)	7 (1)	···	···	···
1900–2100 m	5 (1)	13 (1)	···	5 (+)	10 (+)	7 (+)	···	4 (+)	···	···	···	···
2100–2300 m	3 (0)	17 (0)	···	4 (1)	7 (+)	6 (+)	···	2 (+)	···	···	···	···
2300–2500 m	···	···	···	···	6 (+)	6 (+)	···	1 (+)	···	···	···	···
2500–2700 m	···	···	···	···	···	5 (+)	···	1 (+)	···	···	···	···
2700–2900 m	···	···	···	···	···	5 (+)	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	5 (1)	···	···	···	···	···	···
Habitat												
Ohia	15 (+)	19 (+)	10 (+)	5 (+)	13 (+)	···	7 (+)	6 (+)	5 (+)	5 (+)	···	5 (+)
Koa-ohia	17 (+)	21 (+)	···	8 (1)	14 (+)	···	···	9 (+)	···	···	···	···
Koa-mamane	···	17 (0)	···	8 (1)	14 (+)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	17 (0)	6 (+)	···	···	···	···	···	···
Mamane	···	···	···	···	9 (+)	5 (+)	···	3 (1)	···	···	···	···
Other natives	···	···	···	···	10 (1)	···	···	6 (+)	···	3 (+)	4 (1)	···
Intro. trees	···	17 (+)	···	···	12 (1)	···	11 (2)	11 (1)	3 (0)	9 (1)	10 (1)	···
Treeless	14 (1)	0	5 (1)	0 (+)	2 (1)	···	···	1 (+)	3 (+)	···	5 (3)	1 (0)

[a] Values are given in meters; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 5[a]

FOLIAGE VOLUME (TREE BIOMASS INDEX) [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	234 (16)	···	1378 (126)	···	···	···	···	716 (79)	1379 (0)	···
300–500 m	···	788 (44)	474 (36)	···	1712 (240)	···	1170 (0)	1887 (451)	···	728 (98)	385 (128)	···
500–700 m	969 (0)	858 (23)	978 (30)	···	1141 (79)	···	895 (109)	602 (84)	293 (49)	354 (43)	265 (38)	···
700–900 m	751 (28)	778 (18)	904 (36)	···	1014 (42)	···	977 (145)	804 (67)	315 (32)	277 (26)	226 (124)	···
900–1100 m	599 (26)	623 (19)	811 (35)	590 (190)	1113 (41)	···	694 (96)	966 (57)	497 (65)	404 (37)	···	···
1100–1300 m	520 (26)	682 (16)	706 (104)	653 (163)	836 (30)	···	639 (60)	986 (53)	711 (52)	669 (38)	···	1152 (41)
1300–1500 m	577 (18)	802 (15)	···	302 (44)	673 (19)	···	764 (67)	857 (49)	637 (66)	479 (36)	···	1215 (44)
1500–1700 m	725 (28)	788 (20)	···	311 (31)	688 (23)	···	449 (42)	864 (47)	393 (103)	···	···	1393 (0)
1700–1900 m	713 (33)	726 (28)	···	327 (34)	537 (26)	···	···	748 (57)	472 (117)	···	···	···
1900–2100 m	155 (33)	383 (25)	···	173 (18)	316 (24)	245 (13)	···	365 (39)	···	···	···	···
2100–2300 m	45 (0)	507 (0)	···	100 (25)	178 (15)	238 (18)	···	40 (7)	···	···	···	···
2300–2500 m	···	···	···	···	132 (33)	224 (12)	···	12 (6)	···	···	···	···
2500–2700 m	···	···	···	···	···	183 (10)	···	17 (8)	···	···	···	···
2700–2900 m	···	···	···	···	···	112 (9)	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	61 (13)	···	···	···	···	···	···
Habitat												
Ohia	519 (14)	591 (9)	830 (18)	205 (12)	782 (17)	···	683 (36)	795 (21)	529 (27)	391 (19)	···	1191 (29)
Koa-ohia	781 (17)	947 (9)	···	524 (69)	999 (20)	···	···	1317 (46)	···	···	···	···
Koa-mamane	···	375 (27)	···	300 (33)	551 (21)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	396 (0)	224 (8)	···	···	···	···	···	···
Mamane	···	···	···	···	316 (17)	152 (8)	···	44 (19)	···	···	···	···
Other natives	···	···	···	···	251 (25)	···	···	168 (18)	···	105 (23)	167 (61)	···
Intro. trees	···	587 (31)	···	···	832 (96)	···	1068 (126)	1086 (97)	143 (0)	818 (50)	356 (51)	···
Treeless	725 (48)	0	151 (50)	6 (3)	72 (39)	···	···	27 (6)	85 (20)	···	282 (198)	24 (0)

[a] Values are given in units of meters (height) times percent (cover); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 6[a]

KOA FOLIAGE VOLUME [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	0	···	···	···	···	0	0	···
300–500 m	···	100 (24)	0	···	0	···	0	0	···	0	12 (8)	···
500–700 m	0	332 (15)	0	···	2 (2)	···	0	4 (3)	0	0	0	···
700–900 m	0	283 (12)	0	···	13 (4)	···	0	290 (53)	0	0	0	···
900–1100 m	70 (14)	135 (11)	0	102 (68)	74 (10)	···	0	231 (29)	0	0	···	···
1100–1300 m	119 (14)	18 (4)	0	112 (60)	83 (8)	···	0	216 (27)	0	0	···	0
1300–1500 m	132 (13)	117 (11)	···	150 (37)	111 (8)	···	0	103 (21)	0	0	···	0
1500–1700 m	178 (18)	249 (13)	···	89 (22)	184 (13)	···	0	34 (10)	0	···	···	0
1700–1900 m	87 (15)	283 (17)	···	45 (12)	115 (15)	···	···	14 (6)	0	···	···	···
1900–2100 m	23 (10)	162 (22)	···	10 (4)	37 (9)	0	···	5 (3)	···	···	···	···
2100–2300 m	0	357 (0)	···	0	1 (1)	0	···	0	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	2 (1)	0	0	2 (2)	3 (1)	···	0	3 (1)	0	0	···	0
Koa-ohia	330 (10)	425 (4)	···	152 (31)	310 (10)	···	···	582 (32)	···	···	···	···
Koa-mamane	···	258 (19)	···	178 (31)	177 (15)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	12 (4)	0	···	0	···	···	···	···
Other natives	···	···	···	···	0	···	···	41 (11)	···	0	0	···
Intro. trees	···	14 (5)	···	···	5 (5)	···	0	94 (25)	0	0	4 (3)	···
Treeless	253 (25)	0	0	0	17 (17)	···	···	0	0	···	0	0

[a] Values are given in units of meters (height) times percent (cover); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 7[a]

OHIA FOLIAGE VOLUME [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	163 (40)	···	1375 (125)	···	···	···	···	336 (51)	0	···
300–500 m	···	111 (28)	382 (23)	···	1418 (209)	···	680 (0)	89 (79)	···	352 (55)	25 (9)	···
500–700 m	765 (0)	377 (12)	798 (25)	···	815 (73)	···	607 (103)	230 (37)	183 (39)	105 (17)	36 (8)	···
700–900 m	592 (22)	396 (8)	788 (32)	···	821 (37)	···	835 (126)	224 (24)	220 (25)	63 (7)	6 (6)	···
900–1100 m	420 (17)	391 (10)	746 (31)	488 (258)	906 (36)	···	513 (92)	368 (24)	359 (49)	172 (17)	···	···
1100–1300 m	321 (15)	509 (12)	592 (83)	306 (49)	635 (25)	···	413 (47)	495 (30)	501 (45)	438 (29)	···	876 (37)
1300–1500 m	361 (10)	546 (10)	···	121 (19)	476 (15)	···	600 (57)	516 (38)	442 (56)	299 (28)	···	916 (38)
1500–1700 m	446 (17)	424 (11)	···	158 (25)	347 (16)	···	348 (42)	524 (40)	277 (88)	···	···	689 (0)
1700–1900 m	506 (25)	348 (18)	···	254 (25)	294 (22)	···	···	423 (37)	293 (61)	···	···	···
1900–2100 m	118 (23)	158 (21)	···	161 (18)	130 (13)	0	···	182 (28)	···	···	···	···
2100–2300 m	45 (0)	0	···	100 (25)	80 (10)	0	···	10 (4)	···	···	···	···
2300–2500 m	···	···	···	···	16 (6)	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	408 (11)	472 (7)	705 (15)	198 (11)	684 (15)	···	521 (31)	513 (16)	369 (21)	239 (13)	···	899 (26)
Koa-ohia	381 (7)	430 (5)	···	265 (35)	585 (14)	···	···	448 (25)	···	···	···	···
Koa-mamane	···	0	···	26 (7)	54 (9)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	21 (6)	0	···	0	···	···	···	···
Other natives	···	···	···	···	29 (8)	···	···	52 (10)	···	52 (15)	49 (10)	···
Intro. trees	···	97 (7)	···	···	305 (66)	···	280 (104)	72 (21)	110 (0)	115 (19)	25 (5)	···
Treeless	400 (26)	0	151 (50)	6 (3)	55 (31)	···	···	14 (4)	52 (13)	···	49 (49)	12 (0)

[a] Values are given in units of meters (height) times percent (cover); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 8[a]

NAIO FOLIAGE VOLUME [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	0	···	···	···	···	0	0	···
300–500 m	···	0	0	···	0	···	0	0	···	0	0	···
500–700 m	0	0	0	···	+ (+)	···	0	0	0	0	0	···
700–900 m	0	0	0	···	0	···	0	0	0	+ (+)	0	···
900–1100 m	0	0	0	0	+ (+)	···	0	0	0	0	···	···
1100–1300 m	0	0	0	2 (2)	2 (1)	···	0	0	0	0	···	0
1300–1500 m	0	0	···	5 (3)	14 (2)	···	0	0	0	0	···	0
1500–1700 m	0	0	···	0	37 (3)	···	0	0	0	···	···	0
1700–1900 m	0	0	···	0	31 (4)	···	···	0	0	···	···	···
1900–2100 m	0	0	···	0	26 (4)	108 (9)	···	0	···	···	···	···
2100–2300 m	0	0	···	0	11 (3)	96 (13)	···	0	···	···	···	···
2300–2500 m	···	···	···	···	0	69 (10)	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	38 (7)	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	14 (3)	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	4 (2)	···	···	···	···	···	···
Habitat												
Ohia	0	0	0	0	4 (1)	···	0	0	0	0	···	0
Koa-ohia	0	0	···	4 (2)	11 (1)	···	···	0	···	···	···	···
Koa-mamane	···	0	···	0	70 (5)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	30 (0)	110 (5)	···	···	···	···	···	···
Mamane	···	···	···	···	54 (5)	0	···	0	···	···	···	···
Other natives	···	···	···	···	10 (5)	···	···	0	···	+ (+)	0	···
Intro. trees	···	0	···	···	2 (2)	···	0	0	0	0	0	···
Treeless	0	0	0	0	0	···	···	0	0	···	0	0

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[a] Values are given in units of meters (height) times percent (cover); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 9[a]

MAMANE FOLIAGE VOLUME [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	0	···	···	···	···	0	0	···
300–500 m	···	0	0	···	0	···	0	0	···	0	0	···
500–700 m	0	0	0	···	8 (2)	···	0	0	0	0	0	···
700–900 m	0	0	+ (+)	···	4 (1)	···	0	0	0	+ (+)	0	···
900–1100 m	0	0	0	0	8 (3)	···	0	0	0	0	···	···
1100–1300 m	0	0	0	0	14 (2)	···	0	0	0	0	···	0
1300–1500 m	0	0	···	12 (5)	14 (2)	···	0	3 (2)	0	0	···	0
1500–1700 m	0	0	···	23 (5)	66 (5)	···	0	3 (1)	0	···	···	0
1700–1900 m	0	2 (1)	···	12 (4)	67 (8)	···	···	3 (1)	0	···	···	···
1900–2100 m	0	46 (8)	···	2 (1)	73 (8)	136 (9)	···	11 (3)	···	···	···	···
2100–2300 m	0	150 (0)	···	0	81 (14)	134 (14)	···	22 (4)	···	···	···	···
2300–2500 m	···	···	···	···	116 (38)	154 (10)	···	12 (6)	···	···	···	···
2500–2700 m	···	···	···	···	···	145 (9)	···	10 (5)	···	···	···	···
2700–2900 m	···	···	···	···	···	98 (8)	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	57 (13)	···	···	···	···	···	···
Habitat												
Ohia	0	0	+ (+)	1 (1)	4 (1)	···	0	0	0	0	···	0
Koa-ohia	0	0	···	4 (2)	15 (2)	···	···	2 (1)	···	···	···	···
Koa-mamane	···	107 (8)	···	52 (8)	184 (9)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	44 (0)	112 (3)	···	···	···	···	···	···
Mamane	···	···	···	···	160 (10)	152 (8)	···	42 (19)	···	···	···	···
Other natives	···	···	···	···	40 (6)	···	···	31 (4)	···	0	0	···
Intro. trees	···	0	···	···	15 (5)	···	0	5 (3)	0	+ (+)	0	···
Treeless	0	0	0	0	+ (+)	···	···	2 (1)	0	···	0	0

[a] Values are given in units of meters (height) times percent (cover); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 10[a]
INTRODUCED TREES FOLIAGE VOLUME [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	11 (11)	···	0	···	···	···	···	303 (79)	1379 (0)	···
300–500 m	···	452 (72)	26 (6)	···	223 (88)	···	490 (0)	1751 (442)	···	142 (36)	328 (132)	···
500–700 m	0	68 (13)	8 (2)	···	152 (28)	···	162 (88)	190 (57)	12 (9)	151 (38)	201 (37)	···
700–900 m	0	18 (3)	+ (+)	···	31 (7)	···	52 (52)	44 (22)	0	150 (27)	221 (129)	···
900–1100 m	0	5 (2)	1 (1)	0	6 (3)	···	46 (40)	117 (40)	0	153 (36)	···	···
1100–1300 m	0	24 (8)	0	0	10 (4)	···	49 (23)	13 (5)	0	61 (27)	···	0
1300–1500 m	0	1 (1)	···	0	4 (3)	···	0	1 (1)	0	0	···	0
1500–1700 m	0	22 (6)	···	0	0	···	0	67 (28)	0	···	···	0
1700–1900 m	0	0	···	0	0	···	···	130 (43)	57 (57)	···	···	···
1900–2100 m	0	0	···	0	37 (18)	0	···	84 (21)	···	···	···	···
2100–2300 m	0	0	···	0	0	0	···	6 (4)	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	0	0	8 (1)	0	7 (1)	···	10 (4)	5 (2)	5 (4)	16 (4)	···	0
Koa-ohia	0	6 (1)	···	0	3 (1)	···	···	35 (13)	···	···	···	···
Koa-mamane	···	0	···	0	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	3 (1)	0	···	0	···	···	···	···
Other natives	···	···	···	···	13 (9)	···	···	3 (2)	···	37 (13)	80 (58)	···
Intro. trees	···	392 (31)	···	···	457 (65)	···	712 (166)	854 (95)	33 (0)	658 (53)	308 (52)	···
Treeless	0	0	0	0	0	···	···	0	0	···	201 (198)	0

[a] Values are given in units of meters (height) times percent (cover); + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 11[a]

TOTAL SHRUB COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	37 (13)	···	12 (9)	···	···	···	···	63 (9)	95 (0)	···
300–500 m	···	94 (3)	31 (3)	···	48 (10)	···	6 (0)	49 (12)	···	36 (4)	32 (5)	···
500–700 m	100 (0)	93 (1)	54 (3)	···	46 (4)	···	57 (10)	45 (5)	56 (6)	34 (3)	45 (3)	···
700–900 m	98 (2)	82 (1)	52 (3)	···	43 (2)	···	33 (6)	50 (3)	41 (3)	50 (3)	22 (8)	···
900–1100 m	90 (2)	79 (1)	43 (3)	40 (0)	46 (3)	···	37 (5)	59 (4)	45 (4)	56 (3)	···	···
1100–1300 m	97 (1)	93 (1)	48 (9)	34 (5)	41 (2)	···	50 (5)	49 (3)	61 (5)	74 (4)	···	53 (3)
1300–1500 m	99 (1)	95 (1)	···	47 (4)	33 (1)	···	61 (5)	50 (3)	68 (4)	73 (9)	···	56 (3)
1500–1700 m	93 (1)	72 (2)	···	47 (3)	25 (1)	···	50 (5)	56 (3)	48 (8)	···	···	65 (0)
1700–1900 m	86 (2)	55 (2)	···	49 (3)	38 (2)	···	···	50 (3)	60 (9)	···	···	···
1900–2100 m	62 (3)	50 (5)	···	43 (2)	47 (2)	29 (3)	···	43 (2)	···	···	···	···
2100–2300 m	50 (0)	0	···	34 (4)	40 (2)	32 (3)	···	40 (3)	···	···	···	···
2300–2500 m	···	···	···	···	24 (6)	31 (1)	···	48 (3)	···	···	···	···
2500–2700 m	···	···	···	···	···	36 (1)	···	54 (4)	···	···	···	···
2700–2900 m	···	···	···	···	···	35 (+)	···	45 (8)	···	···	···	···
2900–3100 m	···	···	···	···	···	35 (1)	···	···	···	···	···	···
Habitat												
Ohia	93 (1)	89 (1)	47 (2)	42 (2)	49 (1)	···	49 (3)	51 (1)	54 (2)	56 (2)	···	54 (2)
Koa-ohia	98 (1)	78 (1)	···	49 (3)	24 (1)	···	···	64 (3)	···	···	···	···
Koa-mamane	···	14 (4)	···	50 (3)	13 (1)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	35 (1)	···	···	···	···	···	···
Mamane	···	···	···	···	24 (2)	31 (1)	···	21 (6)	···	···	···	···
Other natives	···	···	···	···	26 (2)	···	···	43 (3)	···	58 (5)	45 (5)	···
Intro. trees	···	72 (2)	···	···	37 (4)	···	49 (10)	36 (3)	110 (0)	39 (3)	43 (3)	···
Treeless	63 (4)	50 (0)	16 (6)	20 (6)	33 (4)	···	···	43 (2)	29 (8)	···	25 (8)	37 (0)

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 12[a]

TOTAL GROUND COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	64 (25)	···	1 (1)	···	···	···	···	80 (12)	0	···
300–500 m	···	0	22 (3)	···	8 (3)	···	117 (0)	19 (7)	···	80 (10)	24 (9)	···
500–700 m	0	+ (+)	23 (2)	···	36 (4)	···	53 (11)	49 (6)	62 (9)	44 (4)	7 (2)	···
700–900 m	2 (2)	5 (1)	29 (2)	···	49 (2)	···	107 (5)	58 (5)	36 (6)	54 (3)	8 (8)	···
900–1100 m	8 (2)	9 (1)	44 (3)	82 (2)	41 (2)	···	64 (8)	50 (3)	52 (6)	45 (3)	···	···
1100–1300 m	3 (1)	4 (1)	33 (6)	49 (7)	57 (2)	···	50 (4)	61 (3)	60 (7)	56 (4)	···	68 (4)
1300–1500 m	0	3 (1)	···	68 (4)	50 (2)	···	46 (5)	72 (3)	87 (9)	71 (9)	···	75 (3)
1500–1700 m	4 (1)	19 (2)	···	52 (4)	51 (2)	···	61 (8)	75 (3)	75 (11)	···	···	89 (0)
1700–1900 m	5 (1)	41 (2)	···	35 (2)	44 (3)	···	···	79 (4)	99 (16)	···	···	···
1900–2100 m	6 (2)	49 (5)	···	21 (2)	38 (3)	69 (3)	···	73 (3)	···	···	···	···
2100–2300 m	0	99 (0)	···	11 (2)	21 (3)	54 (4)	···	62 (5)	···	···	···	···
2300–2500 m	···	···	···	···	20 (9)	50 (3)	···	77 (8)	···	···	···	···
2500–2700 m	···	···	···	···	···	40 (2)	···	45 (3)	···	···	···	···
2700–2900 m	···	···	···	···	···	40 (1)	···	17 (8)	···	···	···	···
2900–3100 m	···	···	···	···	···	40 (4)	···	···	···	···	···	···
Habitat												
Ohia	1 (+)	5 (+)	29 (1)	26 (2)	28 (1)	···	57 (3)	62 (2)	62 (3)	54 (2)	···	71 (3)
Koa-ohia	1 (1)	16 (1)	···	63 (4)	81 (1)	···	···	80 (3)	···	···	···	···
Koa-mamane	···	86 (4)	···	61 (3)	75 (2)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	3 (0)	47 (1)	···	···	···	···	···	···
Mamane	···	···	···	···	49 (3)	49 (2)	···	43 (15)	···	···	···	···
Other natives	···	···	···	···	62 (5)	···	···	77 (3)	···	46 (4)	10 (6)	···
Intro. trees	···	4 (1)	···	···	52 (5)	···	63 (12)	51 (5)	83 (0)	58 (5)	9 (3)	···
Treeless	33 (4)	0	24 (10)	2 (2)	16 (4)	···	···	61 (3)	40 (11)	···	24 (12)	124 (0)

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 13[a]

NATIVE SHRUB COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	26 (7)	···	11 (9)	···	···	···	···	3 (1)	0	···
300–500 m	···	29 (3)	17 (1)	···	8 (5)	···	3 (0)	4 (3)	···	7 (1)	23 (4)	···
500–700 m	40 (0)	42 (1)	19 (1)	···	15 (2)	···	13 (2)	22 (3)	35 (6)	20 (2)	31 (2)	···
700–900 m	39 (1)	43 (1)	25 (1)	···	12 (1)	···	18 (4)	32 (3)	27 (2)	36 (2)	15 (0)	···
900–1100 m	40 (1)	45 (1)	31 (2)	37 (0)	18 (1)	···	15 (2)	32 (2)	35 (3)	46 (2)	···	···
1100–1300 m	45 (1)	55 (1)	23 (4)	37 (4)	25 (1)	···	30 (3)	37 (2)	53 (4)	50 (2)	···	52 (2)
1300–1500 m	48 (1)	51 (1)	···	50 (4)	28 (1)	···	32 (3)	46 (3)	65 (4)	62 (4)	···	54 (3)
1500–1700 m	59 (2)	51 (1)	···	51 (3)	23 (1)	···	27 (3)	54 (3)	53 (7)	···	···	62 (0)
1700–1900 m	81 (2)	51 (2)	···	53 (2)	37 (2)	···	···	50 (3)	59 (9)	···	···	···
1900–2100 m	62 (3)	50 (5)	···	49 (2)	47 (2)	29 (3)	···	43 (2)	···	···	···	···
2100–2300 m	50 (0)	0	···	36 (4)	40 (2)	32 (3)	···	39 (3)	···	···	···	···
2300–2500 m	···	···	···	···	24 (6)	31 (1)	···	49 (3)	···	···	···	···
2500–2700 m	···	···	···	···	···	36 (1)	···	54 (4)	···	···	···	···
2700–2900 m	···	···	···	···	···	35 (+)	···	45 (8)	···	···	···	···
2900–3100 m	···	···	···	···	···	35 (1)	···	···	···	···	···	···
Habitat												
Ohia	52 (1)	55 (1)	23 (1)	49 (1)	34 (1)	···	26 (1)	46 (1)	45 (2)	37 (1)	···	53 (2)
Koa-ohia	56 (2)	43 (1)	···	50 (2)	13 (1)	···	···	38 (2)	···	···	···	···
Koa-mamane	···	14 (4)	···	50 (3)	13 (1)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	35 (1)	···	···	···	···	···	···
Mamane	···	···	···	···	23 (2)	31 (1)	···	21 (6)	···	···	···	···
Other natives	···	···	···	···	18 (2)	···	···	35 (3)	···	55 (4)	37 (4)	···
Intro. trees	···	31 (1)	···	···	4 (1)	···	11 (4)	11 (2)	95 (0)	23 (2)	27 (2)	···
Treeless	58 (3)	50 (0)	15 (5)	20 (6)	33 (4)	···	···	45 (2)	23 (6)	···	16 (5)	37 (0)

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 14[a]

INTRODUCED SHRUB COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	17 (5)	···	2 (1)	···	···	···	···	53 (10)	95 (0)	···
300–500 m	···	64 (5)	18 (2)	···	39 (9)	···	0	40 (13)	···	24 (4)	9 (3)	···
500–700 m	0	17 (2)	14 (1)	···	22 (2)	···	25 (7)	27 (3)	6 (2)	11 (2)	15 (3)	···
700–900 m	0	6 (1)	2 (+)	···	14 (1)	···	1 (1)	15 (2)	6 (2)	3 (1)	8 (8)	···
900–1100 m	0	1 (+)	5 (1)	3 (0)	4 (1)	···	1 (+)	12 (2)	4 (2)	3 (1)	···	···
1100–1300 m	0	1 (+)	6 (2)	6 (3)	2 (+)	···	+ (+)	6 (1)	3 (1)	+ (+)	···	2 (1)
1300–1500 m	0	0	···	2 (2)	+ (+)	···	+ (+)	4 (1)	2 (1)	0	···	+ (+)
1500–1700 m	0	0	···	+ (+)	+ (+)	···	0	4 (1)	+ (+)	···	···	0
1700–1900 m	0	+ (+)	···	0	0	···	···	3 (1)	0	···	···	···
1900–2100 m	0	0	···	0	0	0	···	3 (1)	···	···	···	···
2100–2300 m	0	0	···	0	0	0	···	3 (1)	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	1 (+)	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	0	+ (+)	10 (1)	+ (+)	4 (+)	···	2 (1)	5 (1)	3 (1)	5 (1)	···	1 (1)
Koa-ohia	0	3 (+)	···	3 (1)	2 (+)	···	···	12 (1)	···	···	···	···
Koa-mamane	···	0	···	+ (+)	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	1 (+)	0	···	1 (1)	···	···	···	···
Other natives	···	···	···	···	8 (2)	···	···	12 (2)	···	6 (3)	8 (3)	···
Intro. trees	···	41 (2)	···	···	33 (4)	···	8 (2)	22 (3)	15 (0)	15 (3)	18 (4)	···
Treeless	0	0	2 (1)	0	0	···	···	1 (1)	3 (2)	···	9 (4)	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 15[a]

GROUND FERN COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	20 (14)	···	0	···	···	···	···	34 (7)	0	···
300–500 m	···	0	3 (1)	···	4 (2)	···	0	10 (5)	···	30 (4)	0	···
500–700 m	0	0	4 (1)	···	7 (1)	···	10 (4)	15 (3)	11 (4)	14 (2)	0	···
700–900 m	0	0	5 (1)	···	5 (1)	···	3 (2)	15 (2)	9 (2)	12 (1)	0	···
900–1100 m	0	0	+ (+)	0	10 (1)	···	6 (1)	20 (2)	17 (2)	14 (2)	···	···
1100–1300 m	0	0	0	1 (+)	11 (1)	···	16 (2)	35 (2)	28 (4)	28 (3)	···	29 (2)
1300–1500 m	0	0	···	+ (+)	7 (1)	···	11 (2)	34 (3)	48 (5)	28 (6)	···	26 (2)
1500–1700 m	0	0	···	1 (+)	7 (1)	···	31 (4)	36 (3)	49 (7)	···	···	37 (0)
1700–1900 m	0	0	···	3 (1)	4 (1)	···	···	40 (3)	56 (10)	···	···	···
1900–2100 m	0	0	···	1 (+)	4 (1)	0	···	25 (2)	···	···	···	···
2100–2300 m	0	0	···	1 (+)	3 (1)	0	···	16 (2)	···	···	···	···
2300–2500 m	···	···	···	···	2 (1)	0	···	21 (2)	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	19 (3)	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	7 (4)	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	0	0	3 (+)	2 (+)	6 (+)	···	12 (1)	36 (1)	27 (2)	20 (1)	···	28 (1)
Koa-ohia	0	0	···	1 (+)	14 (1)	···	···	32 (2)	···	···	···	···
Koa-mamane	···	0	···	1 (+)	1 (+)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	1 (+)	0	···	11 (3)	···	···	···	···
Other natives	···	···	···	···	0	···	···	15 (1)	···	5 (1)	0	···
Intro. trees	···	0	···	···	3 (1)	···	32 (8)	9 (2)	15 (0)	19 (2)	0	···
Treeless	0	0	0	1 (1)	4 (2)	···	···	14 (1)	17 (4)	···	0	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 16[a]
MATTED FERN COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	44 (18)	···	64 (22)	···	···	···	···	27 (8)	0	···
300–500 m	···	6 (3)	58 (3)	···	37 (11)	···	0	25 (11)	···	34 (6)	15 (5)	···
500–700 m	0	6 (1)	23 (2)	···	7 (2)	···	30 (10)	35 (4)	39 (7)	40 (3)	44 (4)	···
700–900 m	0	13 (1)	30 (3)	···	9 (1)	···	1 (1)	33 (3)	56 (4)	15 (2)	15 (0)	···
900–1100 m	1 (1)	10 (1)	33 (3)	0	14 (2)	···	14 (4)	32 (3)	33 (5)	20 (2)	···	···
1100–1300 m	0	3 (1)	25 (7)	+ (+)	4 (1)	···	16 (3)	32 (3)	32 (7)	17 (3)	···	8 (2)
1300–1500 m	0	1 (+)	···	0	1 (+)	···	3 (1)	19 (2)	21 (6)	5 (3)	···	2 (1)
1500–1700 m	0	1 (+)	···	0	+ (+)	···	5 (3)	9 (2)	12 (4)	···	···	0
1700–1900 m	0	0	···	+ (+)	0	···	···	+ (+)	4 (2)	···	···	···
1900–2100 m	0	0	···	0	0	0	···	0	···	···	···	···
2100–2300 m	0	0	···	0	0	0	···	0	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	+ (+)	6 (+)	34 (1)	+ (+)	6 (1)	···	12 (2)	28 (1)	36 (3)	27 (2)	···	6 (1)
Koa-ohia	0	3 (+)	···	+ (+)	4 (1)	···	···	16 (2)	···	···	···	···
Koa-mamane	···	0	···	0	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	0	0	···	0	···	···	···	···
Other natives	···	···	···	···	0	···	···	0	···	2 (2)	26 (5)	···
Intro. trees	···	22 (1)	···	···	1 (1)	···	5 (4)	13 (3)	0	10 (2)	45 (5)	···
Treeless	0	0	17 (9)	0	0	···	···	0	9 (5)	···	0	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 17[a]

TREE FERN COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	0	···	···	···	···	7 (3)	0	···
300–500 m	···	1 (1)	9 (1)	···	1 (+)	···	3 (0)	5 (3)	···	7 (2)	0	···
500–700 m	60 (0)	34 (2)	46 (2)	···	9 (2)	···	21 (5)	7 (1)	16 (4)	7 (1)	0	···
700–900 m	59 (1)	32 (1)	43 (3)	···	16 (2)	···	13 (4)	11 (1)	11 (2)	19 (2)	0	···
900–1100 m	50 (2)	33 (1)	18 (2)	0	24 (2)	···	25 (3)	17 (2)	6 (2)	11 (1)	···	···
1100–1300 m	52 (1)	38 (1)	20 (5)	+ (+)	15 (1)	···	29 (3)	11 (2)	5 (2)	27 (2)	···	3 (+)
1300–1500 m	51 (1)	44 (1)	···	0	5 (1)	···	33 (4)	3 (1)	2 (1)	16 (4)	···	3 (+)
1500–1700 m	34 (2)	21 (2)	···	0	2 (+)	···	27 (4)	1 (+)	0	···	···	3 (0)
1700–1900 m	5 (1)	4 (1)	···	1 (+)	+ (+)	···	···	+ (+)	1 (+)	···	···	···
1900–2100 m	0	0	···	0	0	0	···	0	···	···	···	···
2100–2300 m	0	0	···	0	0	0	···	0	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	41 (1)	33 (1)	32 (1)	+ (+)	12 (1)	···	27 (2)	6 (+)	7 (1)	20 (1)	···	3 (+)
Koa-ohia	42 (2)	32 (1)	···	1 (+)	9 (1)	···	···	14 (2)	···	···	···	···
Koa-mamane	···	0	···	0	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	0	0	···	0	···	···	···	···
Other natives	···	···	···	···	0	···	···	0	···	1 (1)	0	···
Intro. trees	···	0	···	···	1 (1)	···	30 (7)	4 (1)	0	2 (1)	0	···
Treeless	5 (2)	0	0	0	0	···	···	0	4 (2)	···	0	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 18[a]

IEIE COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	0	···	···	···	···	2 (+)	0	···
300–500 m	···	0	0	···	6 (4)	···	0	0	···	2 (1)	1 (1)	···
500–700 m	0	0	2 (1)	···	4 (1)	···	0	1 (+)	3 (1)	1 (+)	+ (+)	···
700–900 m	0	0	+ (+)	···	7 (1)	···	0	1 (+)	3 (1)	0	0	···
900–1100 m	0	0	0	0	4 (1)	···	0	1 (+)	7 (2)	+ (+)	···	···
1100–1300 m	0	0	0	0	+ (+)	···	0	2 (+)	2 (1)	1 (+)	···	2 (+)
1300–1500 m	0	0	···	0	0	···	0	1 (+)	+ (+)	3 (1)	···	1 (+)
1500–1700 m	0	0	···	0	0	···	0	2 (+)	0	···	···	0
1700–1900 m	0	0	···	0	0	···	···	1 (+)	0	···	···	···
1900–2100 m	0	0	···	0	0	0	···	1 (+)	···	···	···	···
2100–2300 m	0	0	···	0	0	0	···	0	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	0	0	1 (1)	0	2 (+)	···	0	2 (+)	3 (1)	1 (+)	···	1 (+)
Koa-ohia	0	0	···	0	1 (+)	···	···	1 (+)	···	···	···	···
Koa-mamane	···	0	···	0	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	0	0	···	0	···	···	···	···
Other natives	···	···	···	···	0	···	···	0	···	0	1 (1)	···
Intro. trees	···	0	···	···	1 (1)	···	0	+ (+)	0	+ (+)	+ (+)	···
Treeless	0	0	0	0	0	···	···	0	0	···	0	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 19[a]

PASSIFLORA COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	...	...	0	...	1 (1)	...	...	...	...	5 (2)	0	...
300–500 m	...	0	0	...	0	...	0	0	...	2 (1)	0	...
500–700 m	0	0	0	...	1 (+)	...	0	+ (+)	0	0	0	...
700–900 m	0	0	0	...	3 (+)	...	0	+ (+)	+ (+)	+ (+)	0	...
900–1100 m	0	0	0	0	1 (+)	...	0	+ (+)	0	0	...	...
1100–1300 m	0	0	0	0	1 (+)	...	0	+ (+)	0	0	...	0
1300–1500 m	0	1 (+)	...	0	1 (+)	...	+ (+)	0	0	0	...	0
1500–1700 m	0	6 (1)	...	0	2 (+)	...	0	0	0	...	...	0
1700–1900 m	0	3 (1)	...	0	2 (1)	...	...	0	0	...	...	...
1900–2100 m	0	0	...	0	1 (+)	0	...	0	...	...	...	...
2100–2300 m	0	0	...	0	0	0	...	0	...	...	...	...
2300–2500 m	...	...	...	...	0	0	...	0	...	...	...	...
2500–2700 m	...	...	...	...	...	0	...	0	...	...	...	...
2700–2900 m	...	...	...	...	...	0	...	0	...	...	...	...
2900–3100 m	...	...	...	...	...	0	...	...	...	...	...	...
Habitat												
Ohia	0	0	0	0	1 (+)	...	+ (+)	0	+ (+)	+ (+)	...	0
Koa-ohia	0	2 (+)	...	0	3 (+)	...	...	0	...	...	...	...
Koa-mamane	...	0	...	0	1 (1)	...	...	...	...	...	...	...
Mamane-naio	...	...	...	...	3 (0)	0	...	...	...	...	...	...
Mamane	...	...	...	...	1 (+)	0	...	0	...	...	...	...
Other natives	...	...	...	...	0	...	...	1 (+)	...	0	0	...
Intro. trees	...	1 (1)	...	...	4 (1)	...	0	+ (+)	0	1 (+)	0	...
Treeless	0	0	0	0	+ (+)	...	...	0	0	...	0	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 20[a]

NATIVE HERB COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	21 (13)	···	0	···	···	···	···	1 (+)	0	···
300–500 m	···	0	+ (+)	···	0	···	0	2 (2)	···	4 (2)	0	···
500–700 m	0	0	5 (1)	···	0	···	0	1 (+)	2 (1)	2 (1)	0	···
700–900 m	0	0	1 (+)	···	0	···	5 (2)	2 (1)	3 (1)	8 (1)	0	···
900–1100 m	0	0	12 (1)	0	+ (+)	···	3 (1)	5 (1)	19 (4)	11 (2)	···	···
1100–1300 m	0	0	3 (1)	4 (1)	+ (+)	···	10 (2)	8 (1)	27 (5)	22 (2)	···	34 (3)
1300–1500 m	0	0	···	2 (1)	0	···	14 (4)	8 (1)	21 (3)	36 (8)	···	32 (3)
1500–1700 m	0	0	···	1 (+)	0	···	0	9 (1)	20 (2)	···	···	37 (0)
1700–1900 m	0	0	···	13 (2)	0	···	···	8 (1)	37 (8)	···	···	···
1900–2100 m	0	0	···	5 (1)	2 (1)	0	···	4 (1)	···	···	···	···
2100–2300 m	0	0	···	1 (+)	1 (1)	0	···	3 (1)	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	3 (1)	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	3 (1)	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	1 (1)	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	0	0	5 (+)	5 (1)	+ (+)	···	8 (1)	8 (+)	18 (2)	13 (1)	···	33 (2)
Koa-ohia	0	0	···	8 (2)	+ (+)	···	···	4 (1)	···	···	···	···
Koa-mamane	···	0	···	1 (+)	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	0	0	···	4 (3)	···	···	···	···
Other natives	···	···	···	···	0	···	···	2 (+)	···	6 (3)	0	···
Intro. trees	···	0	···	···	0	···	1 (+)	1 (+)	0	1 (+)	0	···
Treeless	0	0	1 (1)	0	0	···	···	4 (1)	8 (2)	···	0	62 (0)

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 21[a]

INTRODUCED HERB COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	1 (1)	···	···	···	···	17 (5)	0	···
300–500 m	···	0	7 (1)	···	5 (2)	···	37 (0)	6 (3)	···	17 (3)	0	···
500–700 m	0	0	2 (1)	···	9 (2)	···	13 (4)	11 (2)	9 (3)	9 (2)	0	···
700–900 m	0	0	2 (+)	···	8 (1)	···	60 (9)	11 (1)	4 (1)	4 (1)	0	···
900–1100 m	0	0	1 (+)	2 (2)	4 (1)	···	33 (6)	5 (1)	3 (2)	3 (1)	···	···
1100–1300 m	0	0	0	6 (2)	5 (1)	···	11 (2)	4 (1)	2 (1)	1 (+)	···	1 (+)
1300–1500 m	0	0	···	7 (1)	3 (+)	···	9 (3)	6 (1)	4 (2)	0	···	+ (+)
1500–1700 m	0	0	···	4 (1)	5 (1)	···	7 (3)	5 (1)	+ (+)	···	···	0
1700–1900 m	0	0	···	1 (+)	1 (+)	···	···	7 (1)	0	···	···	···
1900–2100 m	0	0	···	1 (+)	4 (1)	0	···	11 (1)	···	···	···	···
2100–2300 m	0	0	···	1 (+)	1 (1)	0	···	11 (1)	···	···	···	···
2300–2500 m	···	···	···	···	1 (+)	0	···	12 (2)	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	7 (2)	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	3 (0)	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	0	0	3 (+)	1 (+)	3 (+)	···	18 (2)	4 (+)	3 (1)	5 (1)	···	1 (+)
Koa-ohia	0	0	···	6 (1)	5 (1)	···	···	10 (1)	···	···	···	···
Koa-mamane	···	0	···	5 (1)	7 (1)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	5 (1)	0	···	9 (3)	···	···	···	···
Other natives	···	···	···	···	11 (3)	···	···	12 (1)	···	4 (2)	0	···
Intro. trees	···	0	···	···	13 (3)	···	20 (5)	13 (2)	3 (0)	6 (1)	0	···
Treeless	0	0	0	0	0	···	···	10 (1)	4 (3)	···	0	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 22[a]

NATIVE GRASS COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	5 (3)	···	0	···	···	···	···	0	0	···
300–500 m	···	0	3 (1)	···	0	···	0	0	···	+ (+)	0	···
500–700 m	0	+ (+)	+ (+)	···	0	···	0	+ (+)	1 (+)	+ (+)	0	···
700–900 m	0	+ (+)	7 (1)	···	0	···	0	1 (+)	4 (1)	+ (+)	0	···
900–1100 m	0	2 (+)	7 (1)	0	+ (+)	···	1 (+)	3 (1)	6 (1)	1 (+)	···	···
1100–1300 m	0	+ (+)	4 (2)	3 (1)	1 (+)	···	5 (1)	8 (1)	3 (1)	2 (1)	···	8 (2)
1300–1500 m	0	0	···	17 (2)	2 (+)	···	9 (2)	15 (2)	8 (2)	7 (3)	···	15 (2)
1500–1700 m	+ (+)	+ (+)	···	27 (3)	5 (1)	···	21 (5)	15 (2)	11 (3)	···	···	15 (0)
1700–1900 m	+ (+)	3 (+)	···	18 (2)	7 (1)	···	···	16 (2)	6 (3)	···	···	···
1900–2100 m	2 (1)	3 (1)	···	15 (2)	4 (1)	0	···	14 (1)	···	···	···	···
2100–2300 m	0	0	···	7 (2)	2 (+)	0	···	19 (2)	···	···	···	···
2300–2500 m	···	···	···	···	2 (2)	0	···	24 (3)	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	14 (1)	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	6 (5)	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	+ (+)	1 (+)	4 (+)	16 (1)	2 (+)	···	6 (1)	11 (1)	5 (1)	1 (+)	···	11 (1)
Koa-ohia	0	+ (+)	···	13 (2)	4 (1)	···	···	5 (1)	···	···	···	···
Koa-mamane	···	0	···	28 (3)	+ (+)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	1 (1)	0	···	12 (5)	···	···	···	···
Other natives	···	···	···	···	0	···	···	15 (2)	···	1 (1)	0	···
Intro. trees	···	0	···	···	+ (+)	···	0	1 (+)	3 (0)	+ (+)	0	···
Treeless	+ (+)	0	2 (2)	1 (1)	8 (2)	···	···	17 (1)	4 (2)	···	0	62 (0)

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 23[a]

INTRODUCED GRASS COVER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	24 (15)	···	0	···	···	···	···	28 (5)	0	···
300–500 m	···	0	16 (2)	···	+ (+)	···	80 (0)	+ (+)	···	30 (4)	24 (9)	···
500–700 m	0	+ (+)	22 (1)	···	21 (3)	···	32 (7)	33 (4)	38 (6)	25 (3)	7 (2)	···
700–900 m	2 (2)	4 (1)	23 (2)	···	36 (2)	···	39 (8)	36 (4)	23 (4)	37 (2)	8 (8)	···
900–1100 m	8 (2)	7 (1)	35 (3)	80 (0)	27 (2)	···	28 (5)	20 (2)	6 (3)	21 (2)	···	···
1100–1300 m	3 (1)	3 (1)	27 (5)	47 (7)	40 (2)	···	15 (3)	13 (2)	+ (+)	5 (2)	···	3 (1)
1300–1500 m	0	3 (1)	···	48 (3)	38 (2)	···	6 (2)	15 (3)	7 (3)	2 (1)	···	4 (1)
1500–1700 m	3 (1)	19 (2)	···	25 (3)	35 (2)	···	7 (3)	16 (3)	1 (1)	···	···	0
1700–1900 m	5 (1)	39 (2)	···	3 (1)	32 (2)	···	···	15 (2)	0	···	···	···
1900–2100 m	4 (1)	46 (5)	···	1 (+)	25 (2)	69 (3)	···	24 (2)	···	···	···	···
2100–2300 m	0	99 (0)	···	+ (+)	14 (3)	54 (4)	···	16 (2)	···	···	···	···
2300–2500 m	···	···	···	···	16 (8)	50 (3)	···	17 (3)	···	···	···	···
2500–2700 m	···	···	···	···	···	40 (2)	···	2 (1)	···	···	···	···
2700–2900 m	···	···	···	···	···	40 (1)	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	40 (4)	···	···	···	···	···	···
Habitat												
Ohia	+ (+)	4 (+)	24 (1)	6 (1)	17 (1)	···	18 (2)	9 (1)	11 (2)	21 (1)	···	4 (1)
Koa-ohia	1 (1)	15 (1)	···	40 (3)	58 (1)	···	···	31 (3)	···	···	···	···
Koa-mamane	···	86 (4)	···	28 (4)	67 (2)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	3 (0)	47 (1)	···	···	···	···	···	···
Mamane	···	···	···	···	41 (3)	49 (2)	···	16 (8)	···	···	···	···
Other natives	···	···	···	···	51 (4)	···	···	41 (3)	···	32 (4)	10 (6)	···
Intro. trees	···	4 (1)	···	···	36 (4)	···	10 (4)	31 (4)	62 (0)	32 (3)	9 (3)	···
Treeless	32 (4)	0	20 (10)	0	4 (2)	···	···	19 (1)	7 (5)	···	24 (12)	0

[a] Values are given in percent cover; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 24[a]

OHIA FLOWER INDEX [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	104 (53)	···	1238 (1238)	···	···	···	···	463 (81)	0	···
300–500 m	···	+ (+)	93 (14)	···	3117 (586)	···	0	2 (2)	···	728 (170)	16 (7)	···
500–700 m	0	15 (4)	165 (21)	···	1253 (161)	···	33 (18)	16 (5)	26 (17)	77 (24)	6 (2)	···
700–900 m	145 (40)	29 (4)	317 (37)	···	587 (49)	···	114 (68)	35 (8)	21 (10)	10 (3)	0	···
900–1100 m	99 (21)	88 (10)	329 (30)	144 (103)	507 (55)	···	26 (11)	72 (13)	69 (25)	80 (13)	···	···
1100–1300 m	21 (4)	49 (7)	103 (40)	39 (9)	350 (28)	···	8 (3)	23 (4)	77 (22)	32 (7)	···	970 (100)
1300–1500 m	13 (2)	79 (10)	···	12 (2)	231 (14)	···	21 (11)	25 (6)	26 (10)	4 (2)	···	329 (54)
1500–1700 m	56 (9)	92 (11)	···	11 (2)	155 (13)	···	13 (7)	66 (14)	23 (16)	···	···	68 (0)
1700–1900 m	94 (18)	53 (12)	···	4 (+)	75 (11)	···	···	127 (24)	6 (4)	···	···	···
1900–2100 m	31 (11)	12 (2)	···	7 (1)	47 (10)	0	···	67 (16)	···	···	···	···
2100–2300 m	0	0	···	6 (1)	14 (3)	0	···	1 (1)	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	54 (8)	43 (4)	219 (14)	6 (1)	464 (24)	···	25 (6)	75 (8)	46 (9)	104 (20)	···	675 (65)
Koa-ohia	77 (9)	87 (6)	···	24 (4)	277 (14)	···	···	46 (7)	···	···	···	···
Koa-mamane	···	0	···	9 (+)	26 (8)	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	12 (6)	0	···	0	···	···	···	···
Other natives	···	···	···	···	18 (6)	···	···	29 (10)	···	34 (12)	19 (7)	···
Intro. trees	···	6 (4)	···	···	474 (128)	···	0	22 (15)	0	153 (35)	5 (2)	···
Treeless	51 (10)	0	71 (39)	5 (3)	8 (4)	···	···	5 (3)	11 (5)	···	0	0

[a] Values are given in units of foliage volume (meters heights × percent cover) times fraction of twigs in flower; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 25[a]

OLAPA FRUIT INDEX [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	···	···	0	···	0	···	···	···	···	0	0	···
300–500 m	···	0	+ (+)	···	0	···	0	0	···	+ (+)	0	···
500–700 m	0	+ (+)	+ (+)	···	0	···	0	+ (+)	0	+ (+)	0	···
700–900 m	+ (+)	+ (+)	+ (+)	···	0	···	+ (+)	1 (+)	+ (+)	+ (+)	0	···
900–1100 m	+ (+)	+ (+)	+ (+)	10 (0)	+ (+)	···	+ (+)	1 (+)	+ (+)	+ (+)	···	···
1100–1300 m	+ (+)	+ (+)	0	8 (1)	+ (+)	···	+ (+)	1 (+)	+ (+)	+ (+)	···	1 (+)
1300–1500 m	+ (+)	+ (+)	···	10 (+)	+ (+)	···	+ (+)	+ (+)	1 (+)	+ (+)	···	+ (+)
1500–1700 m	0	+ (+)	···	10 (+)	+ (+)	···	+ (+)	+ (+)	1 (+)	···	···	0
1700–1900 m	0	+ (+)	···	9 (+)	0	···	···	+ (+)	1 (+)	···	···	···
1900–2100 m	+ (+)	0	···	10 (0)	0	0	···	+ (+)	···	···	···	···
2100–2300 m	0	0	···	10 (0)	0	0	···	0	···	···	···	···
2300–2500 m	···	···	···	···	0	0	···	0	···	···	···	···
2500–2700 m	···	···	···	···	···	0	···	0	···	···	···	···
2700–2900 m	···	···	···	···	···	0	···	0	···	···	···	···
2900–3100 m	···	···	···	···	···	0	···	···	···	···	···	···
Habitat												
Ohia	+ (+)	+ (+)	+ (+)	10 (+)	+ (+)	···	+ (+)	1 (+)	+ (+)	+ (+)	···	+ (+)
Koa-ohia	+ (+)	+ (+)	···	9 (+)	+ (+)	···	···	1 (+)	···	···	···	···
Koa-mamane	···	0	···	10 (+)	0	···	···	···	···	···	···	···
Mamane-naio	···	···	···	···	0	0	···	···	···	···	···	···
Mamane	···	···	···	···	0	0	···	0	···	···	···	···
Other natives	···	···	···	···	0	···	···	0	···	0	0	···
Intro. trees	···	+ (+)	···	···	0	···	0	+ (+)	0	+ (+)	0	···
Treeless	0	0	0	10 (0)	+ (+)	···	···	0	+ (+)	···	0	1 (0)

[a] Values are given in percent of twigs in fruit; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.

APPENDIX TABLE 26[a]

MAMANE FLOWER [MEAN (SE)] ON THE HAWAIIAN ISLANDS BY ELEVATION, HABITAT, AND STUDY AREA

	Kau	Hamakua	Puna	Kipukas	Kona	Mauna Kea	Kohala	East Maui	West Maui	Molokai	Lanai	Kauai
Stratum												
100–300 m	...	...	0	...	0	...	...	...	...	0	0	...
300–500 m	...	0	0	...	0	...	0	0	...	0	0	...
500–700 m	0	0	0	...	0	...	0	0	0	0	0	...
700–900 m	0	0	0	...	0	...	0	0	0	0	0	...
900–1100 m	0	0	0	99 (0)	0	...	0	0	0	0	...	...
1100–1300 m	0	0	0	99 (0)	0	...	0	0	0	0	...	0
1300–1500 m	0	0	...	82 (5)	0	...	0	0	0	0	...	0
1500–1700 m	0	0	...	66 (5)	0	...	0	0	0	...	...	0
1700–1900 m	0	0	...	87 (4)	0	...	...	+ (+)	0	...	...	...
1900–2100 m	0	0	...	93 (2)	0	27 (3)	...	+ (+)	...	...	...	...
2100–2300 m	0	0	...	99 (0)	0	17 (3)	...	4 (2)	...	...	...	...
2300–2500 m	...	...	...	...	0	13 (2)	...	0	...	...	...	...
2500–2700 m	...	...	...	...	...	4 (1)	...	1 (1)	...	...	...	...
2700–2900 m	...	...	...	...	...	4 (1)	...	0	...	...	...	...
2900–3100 m	...	...	...	...	...	15 (5)	...	...	...	...	...	...
Habitat												
Ohia	0	0	0	98 (1)	0	...	0	0	0	0	...	0
Koa-ohia	0	0	...	87 (3)	0	...	...	0	...	...	...	...
Koa-mamane	...	0	...	30 (6)	0	...	...	...	...	...	...	...
Mamane-naio	...	...	...	...	0	18 (2)	...	...	...	...	...	...
Mamane	...	...	...	...	0	4 (+)	...	29 (15)	...	...	...	...
Other natives	...	...	...	...	0	...	...	+ (+)	...	0	0	...
Intro. trees	...	0	...	...	0	...	0	+ (+)	0	0	0	...
Treeless	0	0	0	99 (0)	0	...	...	1 (1)	0	...	0	0

[a] Values are given in units of foliage volume (meters height × percent cover) times percent of twigs in flower; + indicates stratum value is positive but under 0.5; ··· indicates stratum was not sampled in study area.