Prey Abundance, Space Use, Demography, and Foraging Habitat of Northern
Goshawks in Western Washington

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CHAPTER 1

Influence of La Niña on Prey Abundance, Space Use, and Demography of Northern

Goshawks

Abstract

I studied the prey abundance, space use, and demography of Northern Goshawks (*Accipiter gentilis*) during the breeding season from 1996-2000 in the mesic forests of western Washington. This time period included a strong La Niña event (late 1998/early 1999) which caused unusually high levels of winter precipitation followed by a cold spring. Abundance indices of nine prey species declined following the La Niña winter. Home range sizes of goshawks more than doubled. Survival rates of adult goshawks were reduced by about 36%, with most mortalities occurring during the winter months. Reproduction virtually ceased during the two post-La Niña years; mean number of young fledged per occupied territory declined by 94%. In this study, the use of radiotelemetry allowed me to gain a comprehensive understanding of the effects weather can have on the space use and demography of a generalist predator. I learned a lesson important for managers of goshawk habitat; weather effects may override habitat effects. Regardless of the quality and quantity of habitat provided in an area, goshawks may not breed if weather has impacted prey populations. Additionally, goshawks may not breed for a number of years while maintaining home ranges similar to (but larger than) those during breeding years.

KEY WORDS: Accipiter gentilis, *home range, La Niña, Northern Goshawk, prey abundance, reproduction, space use, survival, Washington, weather.*

Interannual variation in avian demographic parameters is often related to variation in weather (Elkins 1983). Some of the most profound effects of climate on birds (e.g. increased mortality or reduced production of young) are seen during El Niño years when the warming of ocean surface temperatures in the Equatorial Pacific inhibits cold water upwelling, thereby decreasing fish (prey) production (Cane 1983). This temporary significant decline in fish abundance impacts fish-eating seabirds in many areas throughout the eastern Pacific including Chile (Guerra et al. 1988), the Galapagos Islands (Boersma 1998), and western North America (Hodder and Graybill 1985, Bayer 1986, Hatch 1987, Wilson 1991, Massey et al. 1992). El Niño also affects landbirds, often by affecting rainfall (Jaksic et al. 1997, Sillett et al. 2000, Grant et al. 2000). These effects are pronounced in dry environments where moisture is a limiting factor for primary production. A sudden increase in precipitation increases available food resources for some of the regions' birds. While an increase in precipitation is generally favorable in arid regions, it can be detrimental to a population in a mesic region. Miskelly (1990) reports on decreased survival and reproduction in Snares Island Snipe (*Coenocorypha aucklandica huegeli*) and decreased reproduction in Black Tits (*Petroica macrocephala dannefaerdi*) due to increases in rainfall and cooler temperatures during El Niño years in the Snares Islands of New Zealand. In each of the above events, the primary mechanism driving changes in demography were the indirect effects of weather causing changes in

prey abundance as opposed to directly impacting the populations through acts such as hypothermia or freezing of eggs.

During 1998-99 I had an opportunity to document predator and prey responses to a strong weather event. During this time the Pacific Northwest had increased precipitation and decreased temperature in response to the cold-water counterpart of El Niño, La Niña. I studied the prey abundance, space use, survival, and reproduction of Northern Goshawks (*Accipiter gentilis*) from 1996-2000 in the mesic forests of western Washington, and here 1) describe the magnitude of the 1998-99 La Niña, 2) detail its direct effects on the prey base of goshawks, and 3) compare the space use patterns and demographic performance of goshawks before and after the event. In this paper I demonstrate the profound impact a short-term (< 1 yr) climatic challenge can have on a generalist raptor by reducing abundances of multiple prey species simultaneously.

METHODS

STUDY AREA

I studied goshawks at 23 territories throughout western Washington, primarily in the Olympic Mountains, Willapa Hills, and central Cascade Mountains west of the Cascade Crest (Figure 1.1). Goshawks in this area breed from near sea level up through the mid elevations in the Cascade and Olympic ranges (nests in this study ranged from 120 - 750 m elevation). A mild, moist maritime climate supports dense conifer forests in the region

and high forest productivity. Annual precipitation in the region is generally high on the windward sides of the Olympic and Cascade Mountains (250-365 cm/year); however, the northeast corner of the Olympic Peninsula is in a rain shadow and receives far less annual precipitation (80-150 cm/year; Franklin and Dyrness 1988). Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) are the most common overstory species in low elevation western Washington with western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), Pacific silver fir (*Abies amabilis*), and red alder (*Alnus rubra*) being common as well (Franklin and Dyrness 1988). Common understory and shrub species include western hemlock, western redcedar, swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and red huckleberry (*Vaccinium parvifolium*). Within goshawk territories natural openings (e.g. meadows, wetlands, rock outcrops) were rare and forest cover was relatively contiguous, albeit in varying stages of succession (Finn et al. 2002b). The territories ranged from intensively (State or privately owned land) to moderately (National Forest) managed forest, to areas where no timber harvest has occurred (National Parks; see Finn 2000, Finn et al. 2002a,b). The intensively managed landscape was a mosaic of relatively discrete patches ranging from recent clearcuts to harvest age forest (i.e., 35-80 years). Most territories were completely on either intensively, moderately, or unmanaged land, however, seven areas contained a mix of land use types.

WEATHER

Precipitation and temperature records were obtained through the National Oceanic and Atmospheric Administrations (NOAA) National Climatic Data Center (NCDC) website (National Climatic Data Center 1999a). I reviewed monthly summary tables of precipitation and temperature for two weather stations in western Washington (Quillayute Airport on the Pacific Coast and Seattle), as well as the statewide mean throughout Washington. The two stations in western Washington were chosen because they lie within the geographic area of study (Figure 1.1). I searched the tables for sustained periods of above average rainfall and below average temperature to help define the period of the La Niña and to quantify the proximate effects of the La Niña in terms of weather patterns and their deviation from normal conditions.

PREY SURVEYS

In western Washington, goshawks prey on a wide variety of forest birds and mammals (Watson et al. 1998, Chapter 2). I used estimates of Douglas' squirrel (*Tamiasciurus douglasii*), Gray Jay (*Perisoreus canadensis*), and Steller's Jay (*Cyanocitta stelleri*) abundance on the Olympic Peninsula each breeding season from 1995-1999 to infer changes in population levels following La Niña. A University of Washington (UW) field crew conducted point count surveys in 27 forested sites throughout the northern and western portions of the Peninsula (Luginbuhl et al. 2001). Using this dataset I assessed

differences in abundance between the pre-La Niña and post-La Niña periods with paired

t-tests (Zar 1996). Each of the 27 forested stands was surveyed in at least two pre-La

Niña years (range 2-4, $\bar{x}$ = 2.6 years) and again in the first post-La Niña year (1999).

In addition to these surveys, there were other survey or monitoring programs

being conducted in western Washington by other biologists that documented abundances

(or abundance indices) of goshawk prey during this time period. Bednarz et al. (2001)

conducted point count surveys on breeding forest birds (including five species of

goshawk prey: Steller's Jay, Hairy Woodpecker [*Picoides villosus*], Northern Flicker

[*Colaptes auratus*], American Robin [*Turdus migratorius*], Swainson's Thrush [*Catharus*

ustulatus]) during 1998 (pre-La Niña) and 1999 (post-La Niña) in western Washington.

The Washington Department of Fish and Wildlife (WDFW 2000, 2001) monitors hunter

harvest rates ('catch per unit effort' [number harvested per hunter-day]; an index of

abundance) for forest grouse (Blue [*Dendragapus obscurus*] and Ruffed [*Bonasa*

umbellus] Grouse combined) in all 20 western Washington counties. I compared the

average number harvested per hunter-day during 1999-2000 (post-La Niña) to the

number harvested per hunter-day during 1994-98 (pre-La Niña average) using paired t-

tests.

SPACE USE

Selection and capture of goshawks. Forestry workers, falconers, and wildlife surveyors

initially located all of the territories used in this study (Finn 2000, Finn et al. 2002a,b). I

returned to reported locations and used standard broadcast methods (Kennedy and

Stahlecker 1993) to locate active goshawk nests. Of the 23 territories used in this study,

nine were used to assess spatial use patterns of foraging adult goshawks (Table 1.1,

Figure 1.1). The remaining 14 territories were either too inaccessible for continual

radiotelemetry work or I was not able to capture the adults. Eight of the nine territories

were dominated by intensively managed forest (private and State land), while a single

territory was solely on National Forest which had been subjected to low levels of forest

management (Table 1.1).

Adult goshawks were captured at their nests using Dho-gaza nets and a live Great

Horned Owl (*Bubo virginianus*) as lure (Bloom et al. 1992). All hawks were fitted with

an 18 g backpack style transmitter-harness package (Buehler et al. 1995; 2-3% of body

weight, Advanced Telemetry Systems, Isanti, MN). Transmitter batteries lasted up to

four years and no premature failures were confirmed out of the 35 birds radiotagged

during the study. I returned to evaluate the behavior of the bird within 72 hours to

determine whether the transmitter was causing any obvious adverse effects (Withey et al.

2001).

Radiotracking. From a vehicle and on foot, I tracked 17 (nine male, eight female)

adult goshawks for at least one year (i.e., breeding season) between 1996-2000. Seven

birds were tracked in ≥ 2 yr (Table 1.1). All hawks were tracked for at least 1 day per

week (range = 1-3 days/week) from the time of tagging (generally late May to early June)

until the end of the fledgling dependency period (mid to late August). I attempted to

track hawks from sunrise to sunset, however locations were often unknown for short

periods throughout the day as I drove to find them. The number of locations obtained per

day per bird ranged from 1 to 16 ($\bar{x}$ = 3.3) and were not considered to be independent for

statistical purposes (Otis and White 1999, Kernohan et al. 2001). I often recorded single

locations per day while conducting other aspects of the study. The average number of

fixes (± SE) per bird per breeding season was 45 ± 5.1. My goal was to obtain as

complete an understanding as possible of the foraging behavior of goshawks during each

day of study by tracking individuals continuously during foraging bouts.

I used triangulation techniques (White and Garrott 1990) to obtain initial location

estimates, and then homed to within 100-200 m of the hawk's location by foot. If I did

not see a hawk I assumed I was within 100 m if I detected its signal without an antenna

under normal topographic conditions ("box signal"; approximate distance determined by

a beacon test of transmitters hung in trees [Withey et al. 2001]). If a bird flew from an

area before I could home in on its location I estimated the location using the initial

triangulation fixes. Birds were located on > 98% of attempts due to the extensive

network of roads in managed forests.

Home range analysis. I estimated home range sizes with the 100% minimum

convex polygon (MCP; Mohr 1947) and 95% fixed kernel (Worton 1989) methods using

the Animal Movements extension (Hooge and Eichenlaub 1997) to ArcView GIS. I used

Least Squares Cross Validation (LSCV) to determine the appropriate smoothing

parameter for the kernel estimates (Seaman et al. 1999). I only used ranges based on ≥

30 locations as recommended by Seaman et al. (1999). In addition to the 30 location

minimum requirement, I also set a minimum of ten tracking days per breeding season to provide representation throughout the breeding season.

Core area(s) were analyzed to see whether or not hawks were using their home ranges evenly or if they were clustering their activity into a few portions of it. In addition, I calculated the size of each bird's range at 5% increments (5-95%) of the utilization distribution (UD) to look for differences in how they utilized space between pre- and post-La Niña.

I investigated effects of sex, breeding status, and time period (pre- vs. post-La Niña) on home range size using t-tests with alpha level set to 0.05. I used repeated measures ANOVA to compare the effects of time period on range size for 5% increments of fixed kernel estimates. Each 5% increment of the utilization distribution was treated as a repeated measure. Only one nest failed among the pairs studied and this pair was grouped with non-breeders because the failure occurred before radiotracking began. The pre-La Niña period includes 1996-1998 breeding seasons while the post-La Niña period includes 1999 and 2000 breeding seasons (National Climatic Data Center 1999b). Some birds were tracked during multiple years ($n = 7$) while others were only tracked in a single year ($n = 10$) (Table 1.1). Ranges for those birds tracked in multiple years were averaged within each category tested before analysis.

DEMOGRAPHY

In addition to the 17 birds radiotagged for space use monitoring, I tagged an additional 12 goshawks to add to my sample for adult survivorship analysis (Table 1.1, Figure 1.1). Due to small sample sizes of both sexes I was not able to assess intersexual differences in overall survival or sex-specific effects of La Niña on survival. Therefore, I grouped adult males and females together for analysis. I constructed a Kaplan-Meier survival function, modified for staggered entry of animals over time (Pollock et al. 1989), for the adult population from June 1997-November 2000. I assigned all winter mortalities to the month of January, because I generally did not recover birds that died overwinter until spring. I then compared the slope of the function before and after the La Niña winter using simple linear regression (comparison of two slopes; Zar 1996). I assumed that tagging did not interact with climate to influence the survival of adult goshawks, however, I did not have a control population of non-tagged goshawks on which I could monitor survival for comparison (Withey et al. 2001).

I monitored all 23 territories (Table 1.1, Figure 1.1) to determine occupancy status and reproductive success rates. Most territories were monitored for at least a three-year period (spanning both pre- and post-La Niña years). However, five territories were only monitored for two years because they were found during the latter part of the study (Table 1.1). Thirteen territories were occupied (had at least one adult present, and vocal, during the breeding season) in at least one pre-La Niña year and at least one post-La Niña year. To compare reproductive output between pre- and post-La Niña at these thirteen

territories, I compared the average number of young fledged per year for each time period using a Wilcoxon signed-rank test (Zar 1996).

RESULTS

WEATHER

The winter (December-February) of 1998-99 was classified as a "strong period" of La Niña (National Centers for Environmental Prediction/Climate Prediction Center 1999). Washington received record setting levels of precipitation followed by the coldest spring in decades. The statewide mean for winter precipitation in 1998-99 was over 20 cm above the historic mean - setting a new 106 year record (Figure 1.2a). The spring of 1999 was the coldest since 1982 for Washington State (Figure 1.2b) and it is this combination of high precipitation and low temperature that characterizes La Niña winters in the Pacific Northwest. The effect of La Niña was even more apparent when data from the two western Washington weather stations were examined (the 'wet side' of the state), particularly the coastal forest region around Quillayute (Figure 1.1). The La Niña winter brought 160 cm of rainfall to this area, an area that receives an average of 103 cm per winter (Figure 1.2a). Additionally, the spring that followed was about 2º C cooler than normal (Figure 1.2b). Precipitation and temperature returned to normal the winter/spring following La Niña; in fact the winter of 1999-2000 was drier than normal in Seattle and throughout the state as a whole (Figure 1.2a).

PREY ABUNDANCE

All three species of goshawk prey that were monitored on the Olympic Peninsula by the UW field crew declined in abundance following the La Niña winter (Figure 1.3a). In 1999, Douglas' squirrel detection rates (mean number detected per 10 minute point count) were only 17% of their pre-La Niña average ($\bar{x}_{pre}$ = 0.55 se = 0.08 vs. $\bar{x}_{post}$ = 0.09 se = 0.02, t = 5.22, df = 26, P < 0.001; Figure 1.3a). Gray Jay detection rates decreased by 50% ($\bar{x}_{pre}$ = 0.22 se = 0.05 vs. $\bar{x}_{post}$ = 0.11 se = 0.03, t = 3.06, df = 26, P = 0.01; Figure 1.3a), while Steller's Jay detection rates decreased to a lesser extent (about 16%) in the year following La Niña ($\bar{x}_{pre}$ = 0.64 se = 0.06 vs. $\bar{x}_{post}$ = 0.54 se = 0.05, t = 2.17, df = 26, P = 0.04; Figure 1.3a). Although the crew did not continue prey surveys at these 27 stands in 2000, four stands were surveyed in 2000 as well as in at least two pre-La Niña years. The results from this limited sample suggests that abundances of these three species remained low on the Olympic Peninsula during 2000 relative to their pre-La Niña values.

Bednarz et al. (2001) found significant declines in all five species of goshawk prey surveyed in western Washington (Cascades and Olympics) following the La Niña winter (Figure 1.3b). They found a 72% reduction in Steller's Jay detections. Declines for two species of thrush and two piciformes ranged from 35-88%. They did not conduct surveys during the 2000 field season.

Forest grouse (Blue and Ruffed combined) were hunted in 18 of 20 western Washington counties in 1999 and 2000 (Washington Department of Fish and Wildlife 2000, 2001). In both years success rates of hunters were lower in all 18 counties (range of declines 23-91%) relative to their 1994-98 (pre-La Niña) averages (Figure 1.3c). Overall, grouse hunter success rates decreased by an average of 52% in western Washington following the La Niña winter ($\bar{x}_{pre}$ = 0.48 harvested per hunter-day, se = 0.03 vs. $\bar{x}_{post}$ = 0.23 harvested per hunter-day, se = 0.02, t = 9.75, df = 17, P < 0.001; Figure 1.3c).

SPACE USE

Nine male and five female goshawks were tracked sufficiently to obtain at least 100% MCP home range estimates in at least one year; two of those females were not tracked intensively enough to calculate 95% fixed kernel estimates. Breeding period home range size estimates for all goshawks combined (including non-breeders) during the study ranged from 643 to 10,730 ha using the 100% MCP method ($\bar{x}$ = 3,710 se = 688), and from 844 to 8,676 ha using 95% fixed kernels ($\bar{x}$ = 3,516 se = 516). Goshawks traveled 2.2 km on average, and an average maximum of 5.0 km, from their nests while breeding. The farthest a breeding goshawk was ever detected from the nest in this study was 10.2 km. Goshawks did not use their ranges in an even manner. They used 1-4 core areas in which 50% of the utilization distribution was confined to an average of 15% of the home range area (95% fixed kernel).

Male ranges were generally larger than females and those of non-breeders tended to be larger than breeders (Figure 1.4). However, the only significant differences were between ranges in the pre- and post-La Niña periods regardless of breeding status. Average range size more than doubled during the two years following the La Niña winter (100% MCP: t = -3.79, df = 17, P = 0.001, Figure 1.5a; 95% fixed kernel: t = -3.37, df = 12, P = 0.01, Figure 1.5b).

Hawks were more likely to breed pre-La Niña than post, so breeding status was a confounding factor with time period (home ranges may have been larger because birds were not breeding, not because of La Niña effects). However, there are four birds that did not follow the pattern in at least one year and provide cases to assess the relative importance of breeding status versus time period on spatial use characteristics (Figure 1.5). One bird that was tracked in all five years of study did not breed during one of the pre-La Niña and both of the post-La Niña years. In the pre-La Niña non-breeding year his range size was as small as the breeding pre-La Niña years and not large as they were in the two post-La Niña years. The three birds (2 male, 1 female) that bred during the post-La Niña period all had unusually large home ranges, more than twice the size of pre-La Niña breeders. The two males had ranges 3-4 times larger than those males that bred pre-La Niña reflecting the need for males, in particular, to increase the size of their home ranges in response to a reduction in prey density. The results from these four cases adds further support to the idea that La Niña had a greater effect on range size than did breeding status. Five individual birds (four male, one female) were tracked in at least one pre- and at least one post-La Niña year and provide a within-bird comparison of changes

in home range size (Figure 1.6). All five had increases in range size following the La

Niña winter (increases ranged from 36-370%).

Size of core areas (50% fixed kernel estimators) tended to be larger following the

La Niña winter as well, remaining approximately 15% of the total home range area,

however differences were not significant due to small sample sizes and large variation

among individuals ($\bar{x}_{pre}$ = 423 ha, se = 116.0 vs. $\bar{x}_{post}$ = 701 ha, se =154.9, t = -1.35, df =

12, P = 0.20). In fact, post-La Niña ranges were larger at all levels of the utilization

distribution calculated by the fixed kernel method (repeated measures ANOVA,

interaction of utilization distribution percent and time period; F = 8.22, P = 0.01; Figure

1.7), suggesting that goshawks needed to expand use of their entire range – not just core

areas. However, the differences were much greater at the higher percentage levels, which

correspond to the outer, less-utilized portions of the home range. Post-La Niña ranges

were consistently twice the size of pre-La Niña ranges at every level of the utilization

distribution calculated, resulting in a substantial difference in area of the landscape used

outside of the inner core areas.

This substantial increase in space use is further exemplified by the change in

average foraging distance from the nest and average maximum foraging distance of

breeders following La Niña. Average distance from the nest increased from 2.0 to 3.3 km

(t = -5.30, df = 10, P < 0.001), while average maximum distance increased from 4.2 to

9.5 km (t = -8.55, df = 10, P < 0.001).

DEMOGRAPHY

Survivorship. During a 41-month period (June 1997-November 2000), I monitored a total of 29 individual goshawks (15 male, 14 female). The number of birds "at risk" at any given time ranged from 5 to 18 ($\bar{x} = 11$). Twelve birds died during this period (six males, six females), eleven were censored from analysis (presumably due to emigration), and six remained alive and trackable at the end of the monitoring period. The rate of mortality was nearly twice as great during post-La Niña than it was during pre-La Niña ($\beta_{pre} = -0.017$, $\beta_{post} = -0.029$, $t = 3.52$, df = 38, $P = 0.001$; Figure 1.8b). Estimated annual probability of survival of adult goshawks declined from 88.9% during pre-La Niña (Range of possible values: 80.0-90.0%) to 57.1% during post-La Niña (46.5-65.0%). Most (67%) of the deaths occurred during the winter months when my monitoring was sparse. These goshawks were generally not found until spring and it was difficult to determine when they died based on condition.

Reproduction. During the pre-La Niña period I monitored 19 occupied territories for 33 territory-years (number of territories times the number of years each was monitored); during post-La Niña I monitored 17 occupied territories for 24 territory-years. The success rate (percentage of occupied territories that fledged ≥ 1 young) during pre-La Niña was 73% while post-La Niña occupied territories were successful 17% of the time. This trend was also apparent when examining radiotagged males (regardless of occupancy status). They successfully reared young 50% of the time during pre-La Niña

(n = 7 males for 8 male-years), while during post-La Niña they were only successful 10%

of the time (n = 5 males for 10 male-years).

Of the thirteen territories that were occupied in at least one pre-La Niña year <u>and</u>

at least one post-La Niña year, nine (69%) were successful at least once during pre-La

Niña, but not post. Only two (15%) failed to fledge young during the entire period and

two (15%) territories were successful at least once during both time periods. No

territories were successful only during post-La Niña. Within these thirteen territories,

mean annual number of young fledged per occupied territory declined from 1.27 to 0.08

following the La Niña winter ($z = -2.97$, df $= 12$, $P = 0.003$; Figure 1.9). This disparity

was due to both high rate of nest failure (by pairs that laid eggs) and nest desertion prior

to egg-laying by some pairs during the post-La Niña years.

DISCUSSION

The unusually wet winter of 1998-99 and cool spring that followed had a substantial

impact on the western Washington goshawk population that lasted for at least two years.

Populations of many goshawk prey declined during the extended periods of cold, wet

weather. The declines following the La Niña winter were consistent among taxa and

extreme in some cases (e.g. Douglas' squirrels declined by 83%). In total, at least nine

species of goshawk prey from three different studies in western Washington showed

declines in abundance the year following La Niña while none showed increases or

stability. Collectively, these nine species comprise about 60% of the goshawk diet during the breeding season in western Washington (Watson et al. 1998, Chapter 2).

This sharp decline in prey abundance was correlated with substantial changes in the way goshawks hunted. Home range sizes in this study during the pre-La Niña period were comparable to other breeding period home range sizes reported for the contiguous western U.S. (range 569-3774 ha; Austin 1993, Bright-Smith and Mannan 1994, Kennedy et al. 1994, Hargis et al. 1994, Keane 1999, Boal et al. 2000). Post-La Niña ranges, however, expanded considerably and rival those of southeast Alaska (Iverson et al. 1996) in size. The widespread daily movements of goshawks I detected were not just cases of wandering behavior by non-breeders, but were also extended trips in search of food by breeders. In fact, the greatest distance I recorded of a breeder from its nest during the post-La Niña time period (10.2 km) was of a male who captured a Ruffed Grouse and subsequently returned a portion of it to the incubating female. Under normal conditions (i.e., pre-La Niña), forays >4 km from the nest were rare.

The decline in prey abundance also was correlated with substantial changes in survival and reproduction of this population, likely because hawks had to expend more time and energy to search for and acquire food. Mortality rates nearly doubled and reproductive output was a fraction of pre-La Niña levels. As in the case of home range size, survival and reproductive rates in this population during pre-La Niña were comparable to those reported elsewhere in the western U.S. (survival [annual]: 69-87%, Iverson et al. 1996, Ingraldi 1998, Reynolds and Joy 1998; reproduction [fledglings per active nest]: 0.94-2.2, see review in Squires and Reynolds 1997, Younk and Bechard

1994). During the course of the study mortality occurred primarily in the winter. It was especially prevalent during the La Niña winter and the one that followed (1999/2000). Goshawks on nearby Vancouver Island also apparently suffered unusually high mortality during the La Niña winter (11 of 17 radiotagged goshawks died; E. McClaren, pers. comm.). Kenward et al. (1993) suggest that starvation is a major factor in winter mortality of goshawks. While I generally recovered hawks too late to assess cause of death, my data on prey abundances during the post-La Niña period support the idea that much of the mortality was caused by starvation.

As expected, reproductive effort and output of those goshawks that survived the La Niña winter was markedly reduced, showing a disparity even greater than that for survival. Goshawks generally abandoned reproductive attempts during the pre-laying stage or failed during incubation. Reproductive rates were similarly low during post-La Niña at territories of both radiotagged and untagged (i.e., control) goshawks and similarly normal during pre-La Niña. Therefore, I do not believe that tagging had a substantial cumulative effect on reproductive success in addition to the effects of La Niña (Withey et al. 2001).

Evidence from other sources supports my findings that the La Niña had a major impact on goshawk reproduction in the Pacific Northwest. Surveys for nesting goshawks were conducted throughout parts of the Olympic Mountains (Figure 1.1) during the 1999 breeding season (Vulgares et al. 2000). After 99 hrs of field effort throughout 62 sites, they did not find a single active goshawk nest, and only a single site with any evidence of recent goshawk activity. McClaren et al. (2002) found reduced reproductive output on

Vancouver Island in 1999 ($\bar{x}$ = 0.67 young fledged per nest) but not in 2000. Vancouver

Island receives similar weather patterns as western Washington and bird and mammal

species were likely impacted there as well in a similar fashion. However, prey species

were not surveyed on the island, so it is not clear if the apparent quick recovery in 2000

was due to a recovery in prey abundance or not. In addition to goshawks, Northern

Spotted Owls (*Strix occidentalis caurina*) on the Olympic Peninsula also suffered

reduced reproduction (Gremel 2001). Following La Niña, owls experienced two

consecutive years with little or no reproduction. Over the last decade this population

generally had "good" reproduction during even years and poor reproduction during odd

years. The breeding seasons of 1999 and 2000 represent the first known instance where

this population suffered back-to-back seasons of poor reproduction. Not only was

fecundity reduced in 1999, so were site occupancy rates. In 1999, roughly twice as many

known owl territories were unoccupied relative to the average from 1992-2001. This

suggests that owls either suffered higher overwinter mortality or that they were foraging

further from their territory centers and, therefore, went undetected during surveys.

The impact of the La Niña on birds and mammals was not limited to western

Washington. In coastal Oregon, which also received record setting levels of precipitation

(National Climatic Data Center 1999a), Douglas' squirrel and corvid detection rates

decreased to very similar levels as on the Olympic Peninsula (J. Luginbuhl, unpub. data).

I monitored the hunting activities of breeding males in good prey years and bad,

and it was clear that they had to travel farther during the bad years to acquire the food

resources needed for a successful nest. Females generally stayed at the nest incubating

eggs or tending nestlings until males no longer returned with prey. At four territories I observed the behavior of the females during this crucial period. After a few days with no visits by the male, the females either abandoned the eggs or consumed the dead nestlings and began hunting fulltime themselves. The same pattern was seen in pairs that abandoned the breeding attempt during courtship – before incubation. Females would continue calling for males in the morning hours for a few days after males stopped returning and then abandon the territory themselves.

In this study, the use of radiotelemetry has allowed me to gain a comprehensive understanding of the effects weather can have on the space use and demography of a highly secretive bird. In some years, the impact of sustained inclement weather may be greater on a population than that of degraded habitat. Weather affects goshawks regardless of measures to manage forest habitat for goshawk population stability. Managers should prepare for significant variation in goshawk occupancy, reproduction, survivorship, and population size in their study areas and not assume a territory is no longer used just because it has not been occupied in a couple of years. Surveys should be done over several years and weather conditions should be factored in (Schueck and Marzluff 1995) to effectively guide population management.

While it appears goshawk prey were impacted throughout the Pacific Northwest during 1998-99, it is important to remember that this is an unreplicated study with respect to La Niña events. It is possible that other factors, and not La Niña, were responsible for the decline in birds and mammals. Therefore, continued monitoring of goshawk populations and their prey during future La Niña events may provide further insight into the importance of this type of climatic variation. Also, variation in climate associated

with the Pacific Decadal Oscillation (PDO), a measure of ocean temperatures across

thousands of kilometers, may be a better predictor of goshawk performance.

Table 1.1. Years each goshawk (or territory) was studied for space use, survivorship, and reproduction from 1996-2000 in western Washington.

Territory	Sex	Landscape History[†]	Year(s) studied for:		
			Space Use	Survivorship	Reproduction (by territory)
Burnt Mountain	♂ *	2,3	1998	1997-1999	1996-1999
Burnt Mountain	♀ *	2,3	1998	1997-1999	
Dungeness	♂ *	2	1997,2000	1997-2000	1996-2000
Dungeness	♀ *	2	1997	1997-1998	
Raney Creek	♂ *	3	1996-2000	1996-2000	1996-2000
Raney Creek	♀ *	3	1996-1997	1996-1997	
The Hole	♂ *	3	1998-1999	1998-2000	1996-2000
The Hole	♀ *	3	1998	1998-1999	
Lily Creek	♂ *	3	1997,1999-2000	1997-2000	1997-2000
Lily Creek	♀ *	3	1997	1997-1999	
Rushingwater Creek	♂ *	3	1998	1998	1998-2000
Rushingwater Creek	♀ *	3	1998-1999	1997-1999	
Swift Creek	♂ *	1,3	2000	2000	1998-2000
Swift Creek	♀ *	1,3	2000	2000	
Snoqualmie	♂ *	2,3	1999-2000	1997-2000	1997-2000
Snoqualmie	♀1*	2,3	-	1997-1998	
Snoqualmie	♀2*	2,3	2000	2000	
Big River	♂ *	3	1999	1999-2000	1999-2000
Big River	♀	3	-	-	
Mt. Zion	♂	2	-	-	1997-2000
Mt. Zion	♀ *	2	-	1997-2000	
St. Paul's Lookout	♂ *	3	-	1997-1999	1997-2000
Lake Cavanaugh	♂ *	3	-	1999-2000	1999-2000
Lake Cavanaugh	♀ *	3	-	1999-2000	
Calawah/Sitkum	♂ *	1,2	-	1997-1998	1996-1998
Calawah/Sitkum	♀	1,2	-	-	
North Fork Solduc	♂ *	1,2	-	1997-1998	1997-2000
North Fork Solduc	♀ *	1,2	-	1997-1998	
Lillian River	♂ *	1	-	2000	1998-2000
Lillian River	♀ *	1	-	2000	
Mueller Creek	♂ *	1,2	-	1997-1998	1997-1998
Mueller Creek	♀ *	1,2	-	1997	
Mowich River	N/A	1,3	-	-	1998-2000
Thunder Lake	N/A	3	-	-	1999-2000
Donkey Creek	N/A	3	-	-	1996-2000
Boundary Creek	N/A	2	-	-	1998-2000
Bowman Creek	N/A	1	-	-	1998-2000
Klahowya	N/A	2	-	-	1998-2000
Elbe Hills	N/A	3	-	-	1999-2000

* radiotagged birds
[†] 1 = National Park; no history of commercial logging
  2 = National Forest; low to moderate levels of logging in the past
  3 = State (Department of Natural Resources) or private land; subjected to moderate to high levels of logging
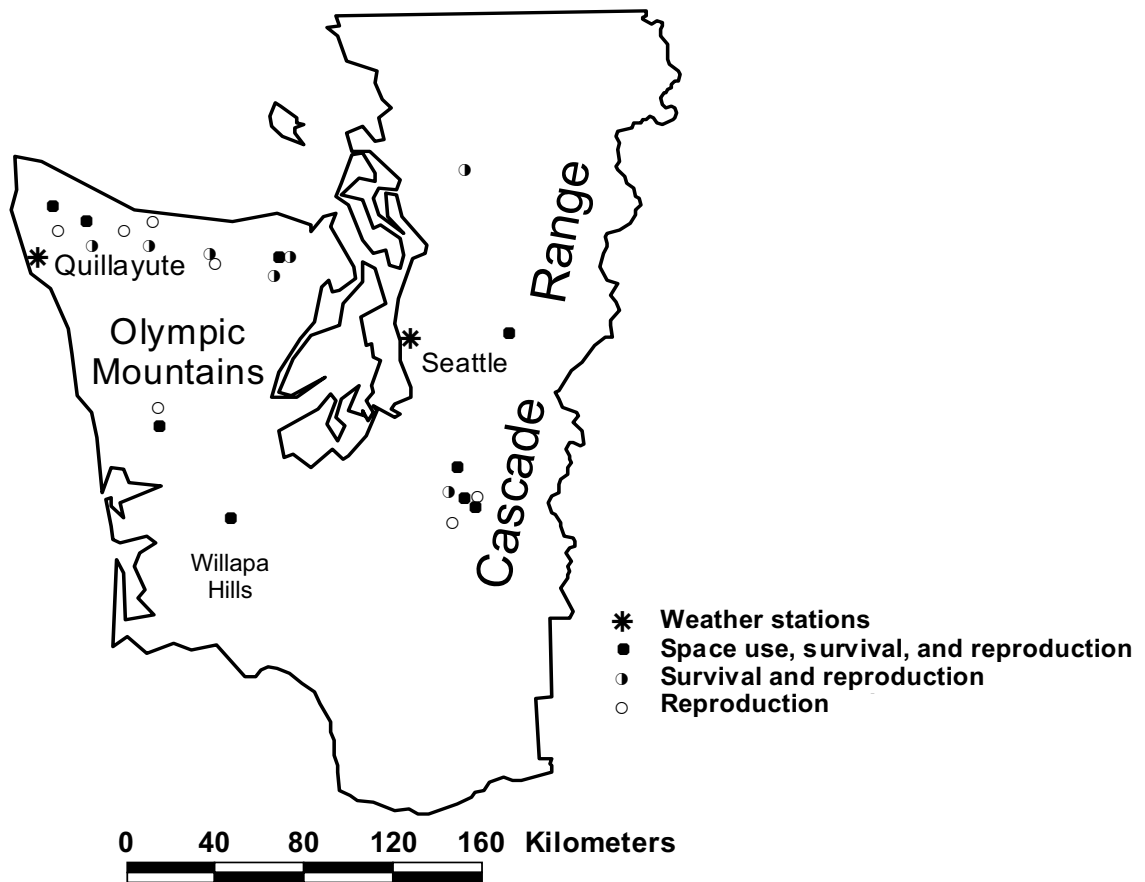
Figure 1.1 Map of western Washington showing locations of 23 goshawk territories where the study took place. Asterisks denote weather stations; various circles represent the type(s) of data collected at each territory. At a minimum, reproductive output (o) was monitored at each territory.

25
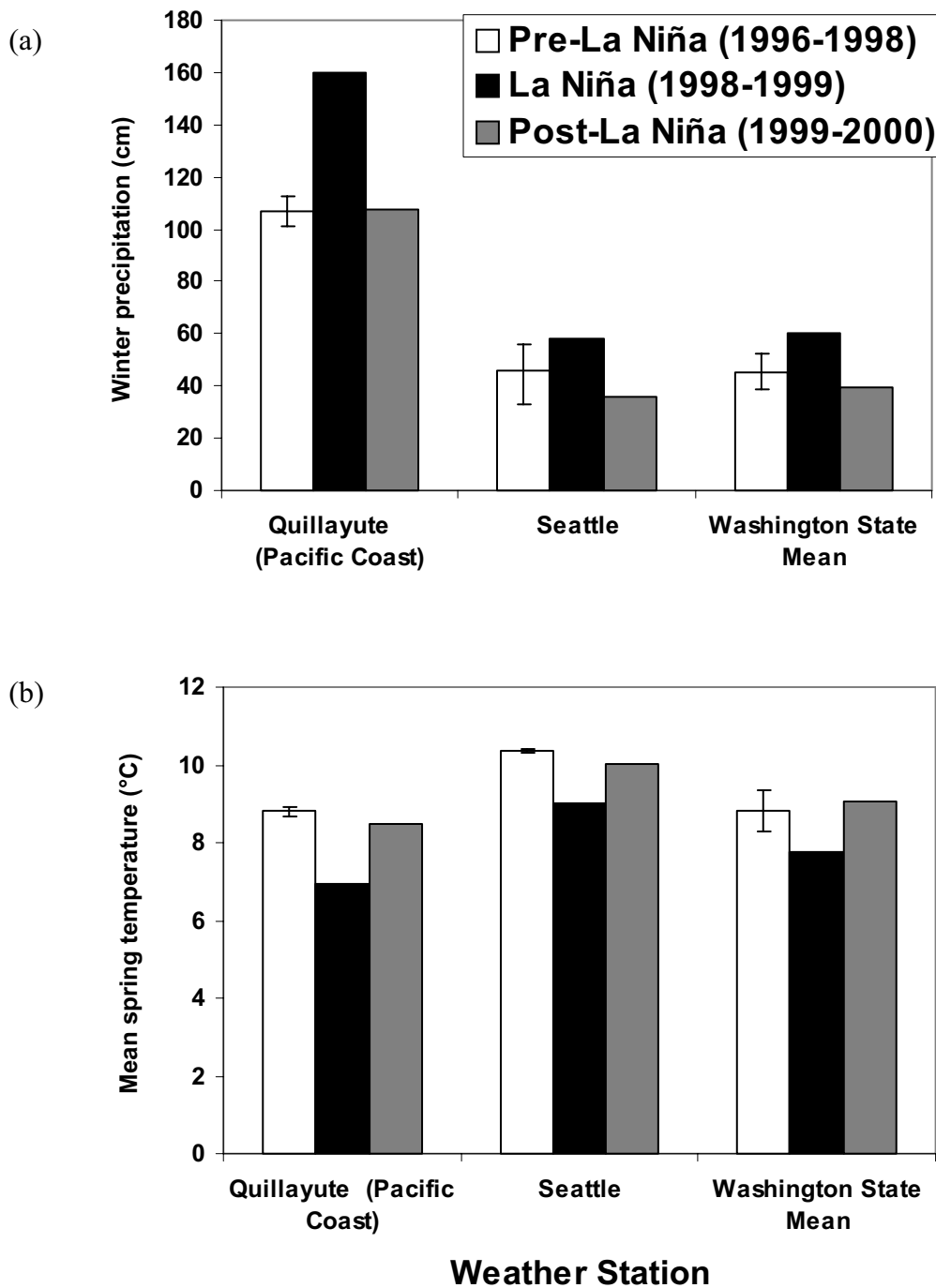
Figure 1.2 Interannual variation in (a) winter precipitation and (b) spring temperature for two western Washington weather stations and the overall state mean. Bars indicate range of values during the pre-La Niña period of this study (National Climatic Data Center 1999a).

(a)

(b)

(c)
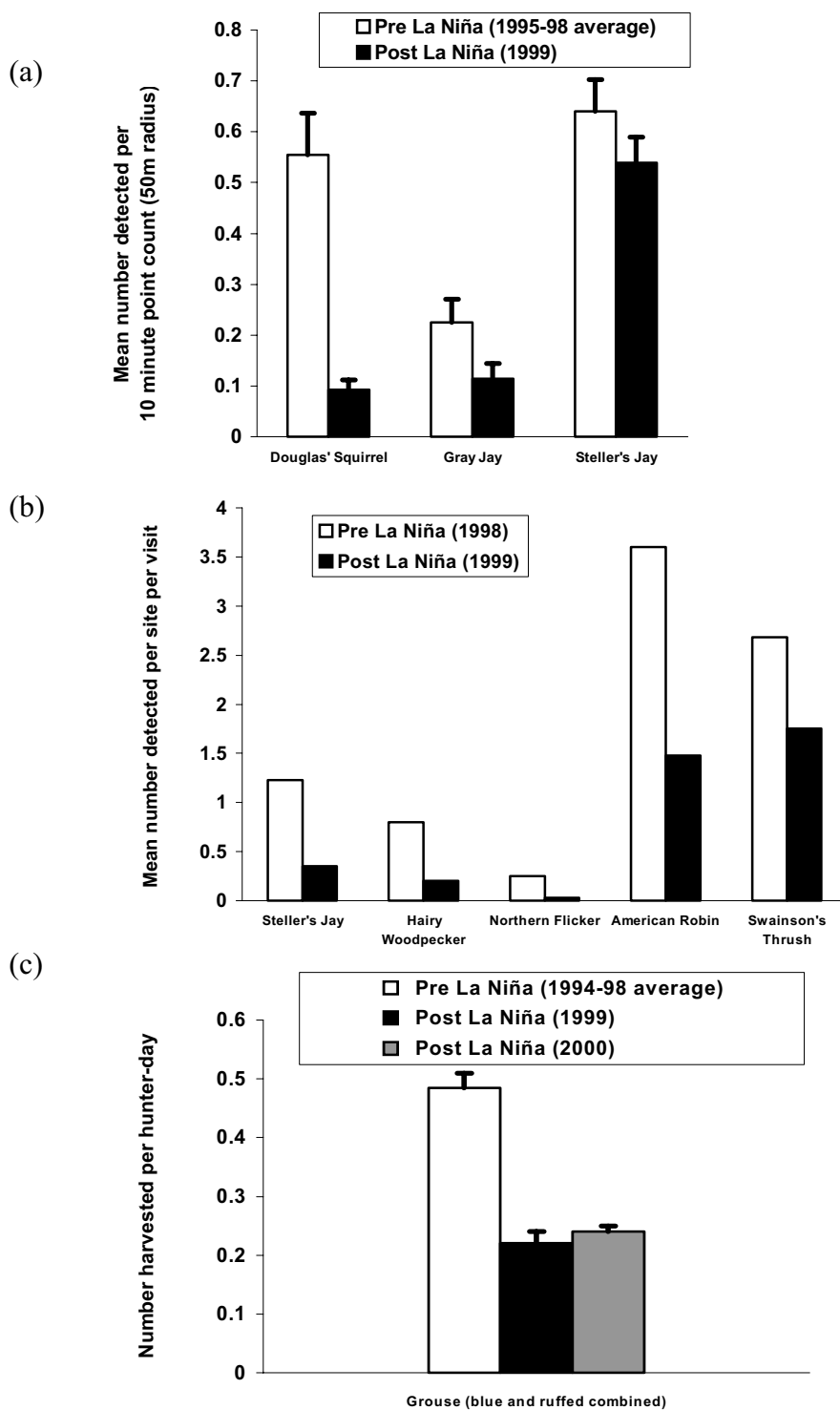
Figure 1.3 Change in relative abundance of selected goshawk prey in western Washington following the La Niña winter of 1998-99. Data were obtained from three sources: (a) this study, (b) Bednarz et al. 2002, and (c) Washington Department of Fish and Wildlife 2000, 2001. Bars represent variation (SE) among (a) 27 study sites, or (c) 18 counties.

(a)

(b)
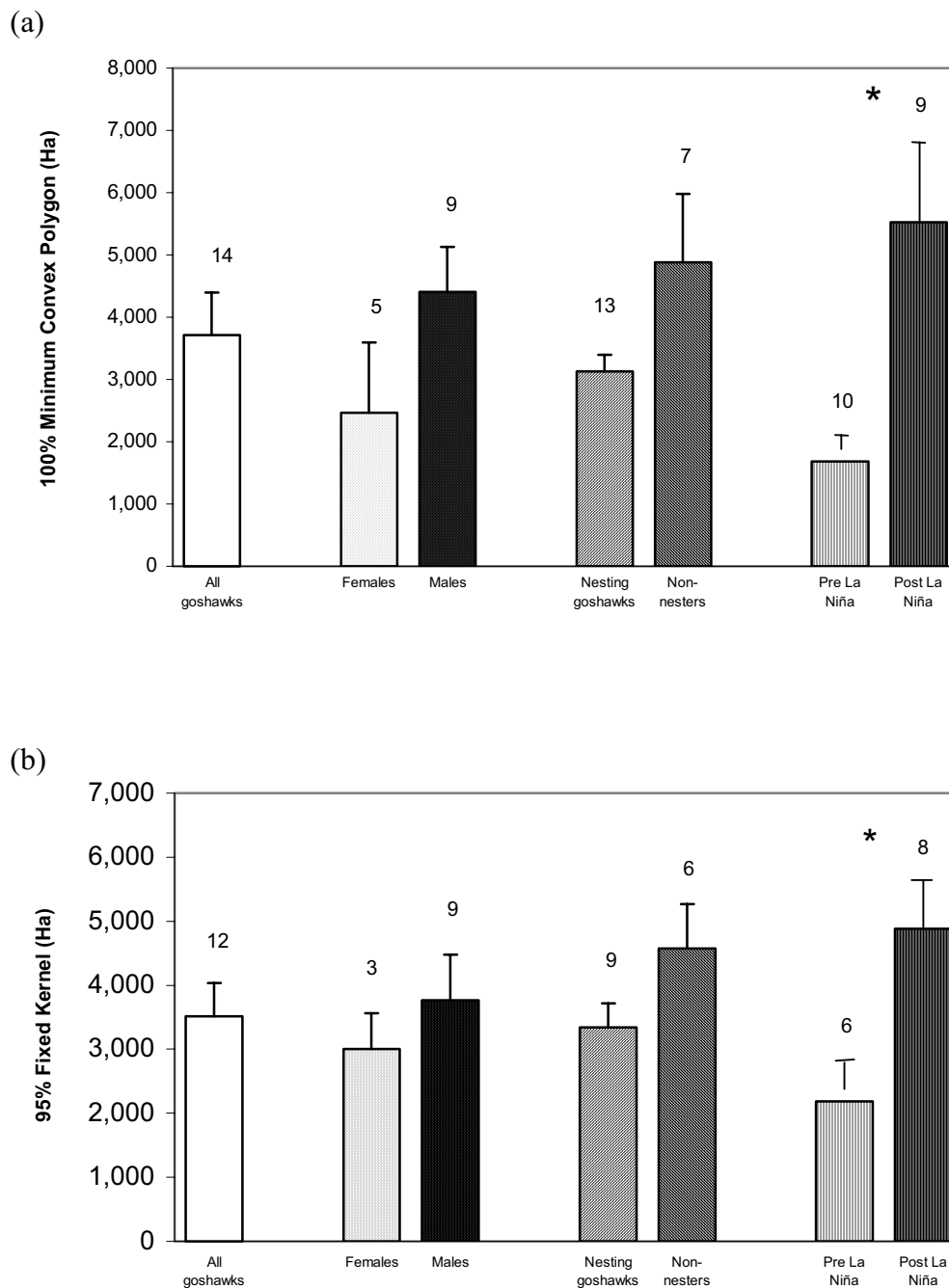
Figure 1.4 Mean sizes of Northern Goshawk home ranges during the breeding season in managed forests of western Washington using (a) 100% minimum convex polygon (MCP) and, (b) 95% fixed kernel methods. Bars represent 1 SE (sample size shown above bars). Asterisk denotes significant difference ($P < 0.05$) between pairs.

(a)
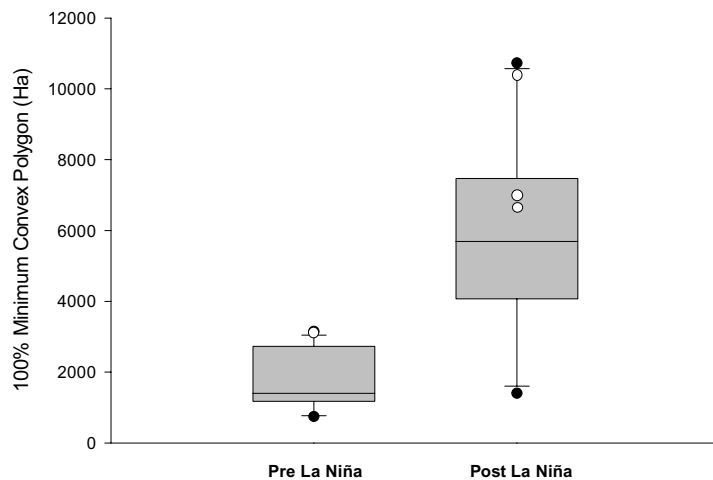
(b)
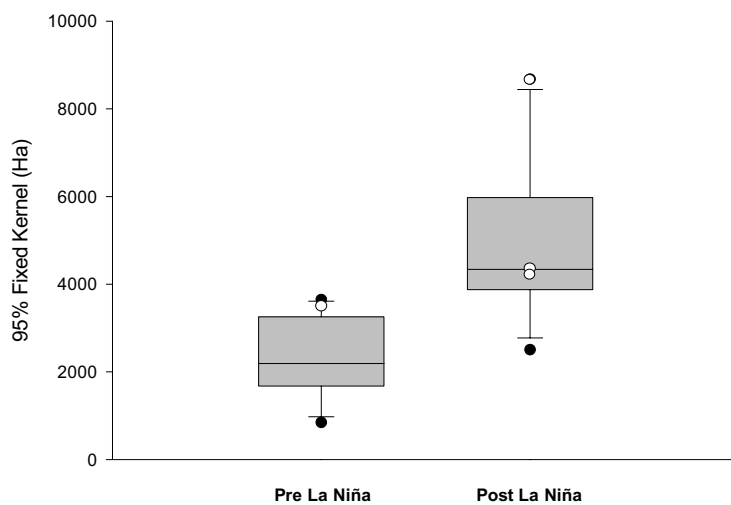
Figure 1.5 Box and whisker plots showing differences between pre- and post-La Niña home range sizes of Northern Goshawks using the (a) 100% minimum convex polygon (MCP) and (b) 95% fixed kernel methods. White dots represent birds that either did not breed during one of the pre-La Niña years ($n = 1$) or did breed during one of the post-La Niña years ($n = 3$). Boxes depict the median score and 25% and 75% quartiles. Whiskers represent the 10th and 90th percentiles and black dots represent the 5th and 95th percentiles.
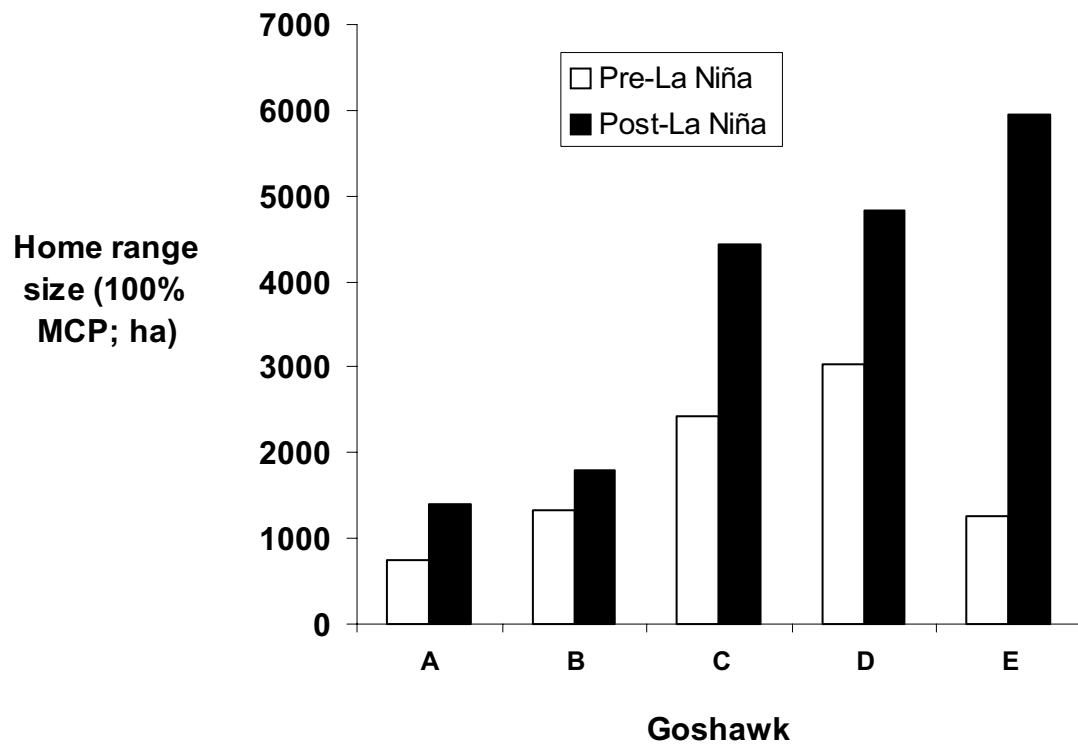
Figure 1.6 Home range size before and after La Niña for five Northern Goshawks (A-E).
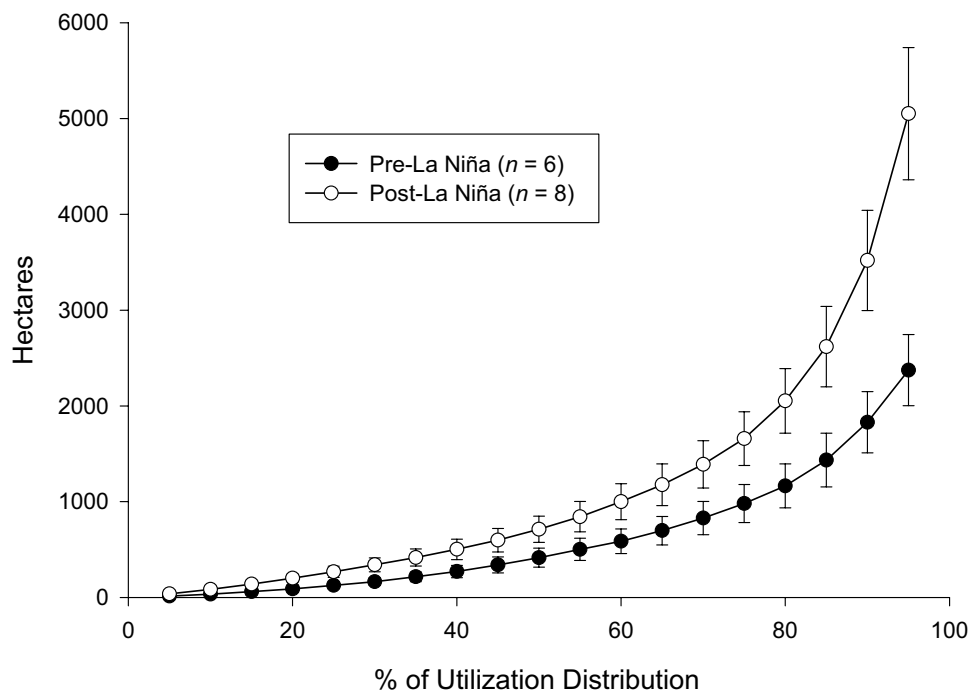
Figure 1.7 Comparison of pre- and post-La Niña home ranges (95% fixed kernel) at 5% increments of the utilization distribution.

(a)

(b)
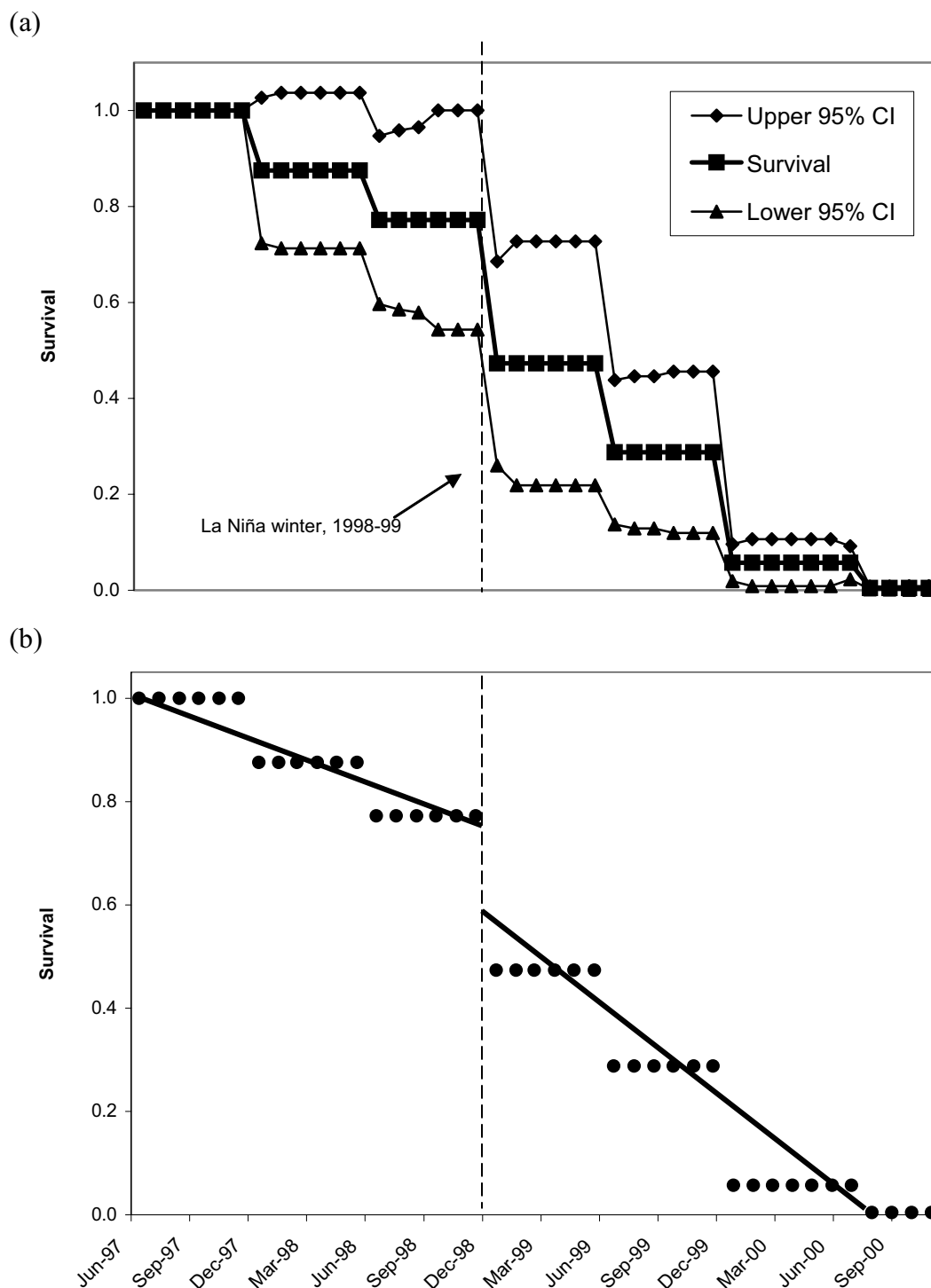
Figure 1.8 Kaplan-Meier survival function (a) and pre-/post-La Niña fitted regression lines (β_{pre} = -0.017, β_{post} = -0.029) of the survival function (b) for Northern Goshawks radiotagged in western Washington, June 1997-November 2000. The survival function was modified using staggered entry of animals.
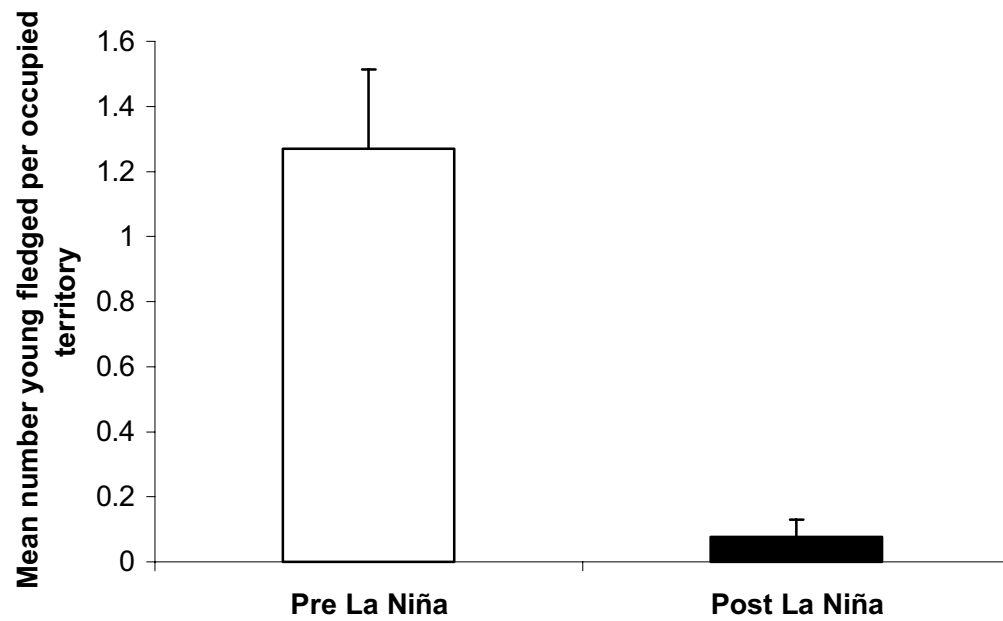
Figure 1.9 Mean annual number of young fledged per occupied territory before and after La Niña for goshawk territories (*n* = 13) that were occupied in at least one pre-La Niña year <u>and</u> at least one post-La Niña year. Bars represent 1 SE.

CHAPTER 2

Foraging Behavior and Habitat Use by Northern Goshawks in Managed Forests of

Western Washington

Abstract

I used radiotelemetry to study the foraging behavior and habitat use patterns of

Northern Goshawks (*Accipiter gentilis*) in managed forests of western Washington from

1997-2000. Goshawks primarily hunted using the 'short-stay perched-hunting' method,

but also hunted "on the wing" ('low soaring' method) when in areas dominated by

younger forest where below-canopy flight space was limited. Medium to large birds such

as Blue Grouse (*Dendragapus obscurus*), Ruffed Grouse (*Bonasa umbellus*), and Band-

tailed Pigeons (*Columba fasciata*) dominated the diet of this goshawk population.

Important mammal species include snowshoe hare (*Lepus americanus*), Douglas' squirrel

(*Tamiasciurus douglasii*), and northern flying squirrel (*Glaucomys sabrinus*). Of 104

identified prey items, 75% were avian and 25% mammalian species. I identified 52 kill

sites of 13 individual goshawks. Kills occurred in stands ranging from relatively open,

13-yr-old regeneration units (pre-canopy stage) to 200-yr-old complex, old-growth

forests. Stands ranged from small (0.5 ha) and isolated to large (> 100 ha) and

contiguous. Goshawks hunted in all forest types and successional stages except for

recent clearcuts and shrub/sapling stages. Univariate comparisons between kill sites and

paired random sites showed that goshawks tended to hunt in stands with larger diameter

trees and avoided areas composed primarily of small trees (sapling/pole). Kill sites had

an average of 35% less tall (≥ 3 m) understory cover than random sites. Low (< 3 m)

understory cover varied considerably at both kill and random sites and did not differ

statistically. Managers of relatively young (< 60 yr) forests in western Washington can

promote use of stands for hunting by goshawks by thinning to reduce densities of small

trees and increase remaining tree diameters while maintaining canopy closure and

abundance of snags.

KEY WORDS: Accipiter gentilis, *central place foraging, diet, foraging behavior,*
foraging habitat, forest structure, forest management, matched-pairs logistic regression,
Northern Goshawk, thinning, Washington

In determining whether or not a population requires special conservation

attention, biologists generally either assess the state of the population directly via

demographic studies (by estimating λ) or by assessing habitat use patterns to see if the

population relies on rare or declining habitats or habitat features within landscapes. For

species that are elusive and occur naturally at very low densities it is often difficult to

adequately quantify population size and rate of change. Under these conditions, it is

increasingly important to conduct well-designed habitat studies throughout the

population's range, which may provide the necessary information to determine what, if

any, special measures need to be taken to conserve the species. The Northern Goshawk

(*Accipiter gentilis*) fits this pattern. Goshawks have been at the center of debate between

environmental groups and biologists in western North America over the past decade. At

issue is whether or not goshawks require mature and old-growth forests and whether or not logging has caused substantial declines in the western U.S. goshawk population (Kennedy 1997).

While it is difficult to assess a population trend due to the nature of goshawks (low density, difficult to survey over large areas, etc.), biologists can conduct studies on habitat use of goshawks to ascertain whether or not they rely on certain forest types and/or successional stages for breeding, feeding, roosting, and dispersal. In addition to identifying which habitats are used more or less than expected based on occurrence, it is also important to study how goshawks use various habitats (foraging behavior) so that we understand the mechanisms that are determining their disproportionate use (Marzluff et al. 2001).

Many studies have quantified habitats used by goshawks for nesting in the western U.S. (see review in Squires and Reynolds 1997), but few have addressed habitats used for foraging (Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994, Beier and Drennan 1997, Good 1998). Further, no published studies have described the behavior of goshawks while hunting in North America. Kenward (1978, 1982) and Widén (1984, 1989) have written extensively on both topics in Europe. Similarities between foraging habitat use in North America and Europe include selection for older, closed-canopied forest containing larger trees and greater basal area. Goshawk habitat use in Europe, however, appears more varied with some populations adapted to anthropogenic conditions such as edges of agriculture and woodland (Kenward 1982, 1996) and utilization of city landfills (Tornberg and Colpaert 2001).

To add to our understanding of goshawk ecology, I addressed the question of foraging behavior and habitat use by Northern Goshawks in the Pacific Northwest at the finest of scales by using radio-telemetry to monitor hunting forays and to identify kill sites. My goal was to determine whether or not goshawks require certain types of forest conditions for hunting in managed forests of western Washington and, if so, make specific recommendations to public and private forest managers regarding goshawk habitat management. My objectives were to: 1) describe the behavior of goshawks while hunting in managed forests of western Washington, and 2) quantify foraging habitat use in terms of within-stand forest structure. My null hypothesis was that goshawks would hunt in all available forest conditions equally, regardless of overstory and understory characteristics. Finn et al. (2002a,b) suggest that understory development may impede use of stands for nesting on the Olympic Peninsula of Washington. Therefore, I was particularly interested in this variable with respect to goshawk hunting.

METHODS

STUDY AREA

The study took place during the breeding period (April – August) from 1997-2000. I studied goshawks from nine territories throughout western Washington, primarily in the Olympic Mountains, Willapa Hills, and central Cascade Mountains west of the Cascade crest (Figure 2.1). Goshawks breed in this area from near sea level up through the mid

elevations in the Cascade and Olympic ranges (nests in this study ranged from 120 - 750 m above sea level). A mild, moist, maritime climate supports dense conifer forests in the region with very high levels of forest productivity. Annual precipitation in the region is generally high on the windward sides of the Olympic and Cascade Mountains (250-365 cm); however, the northeast corner of the Olympic Peninsula is in a rain shadow and receives far less annual precipitation (80-150 cm; Franklin and Dyrness 1988). Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) are the most common overstory species in low elevation western Washington with western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), Pacific silver fir (*Abies amabilis*), and red alder (*Alnus rubra*) being common as well (Franklin and Dyrness 1988). Common understory and shrub species include western hemlock, western redcedar, swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and red huckleberry (*Vaccinium parvifolium*). Within goshawk territories, natural openings (e.g. meadows, wetlands, rock outcrops) were rare and forest cover was relatively contiguous, albeit in varying stages of succession. The territories were on lands intensively managed for timber production (State or privately owned land), except for one that was on moderately managed land (National Forest). The intensively managed landscape was a mosaic of relatively discrete patches ranging from recent clearcuts to harvest age forest (i.e., 35-80 years). Old-growth forest was rare in all areas (< 1%) except in the one territory on National Forest where it covered an estimated 10-15% of the landscape.

RADIOTELEMETRY

Selection and capture of goshawks. Forestry workers, falconers, or wildlife surveyors initially located all of the territories used in this study (Finn 2000, Finn et al. 2002a,b). I returned to reported locations and used standard broadcast methods (Kennedy and Stahlecker 1993) to locate active goshawk nests. Adult goshawks were captured at their nests using Dho-gaza nets and a live Great Horned Owl (*Bubo virginianus*) as lure (Bloom et al. 1992). All hawks were fitted with an 18-g backpack style transmitter-harness package (Buehler et al. 1995; 2-3% of body weight, Advanced Telemetry Systems, Isanti, MN). Transmitter batteries lasted up to three years and no premature failures were confirmed out of 35 birds radiotagged during the study. I returned to evaluate the behavior of the bird within 72 hours to ensure that the transmitter was not causing any obvious adverse effects (Withey et al. 2001).

    Radiotracking. I generally focused on a single goshawk for an entire day (0500-2100 hrs) to document as many hunting locations as possible as well as to accurately document its foraging behavior. Once a goshawk was located in the morning I would home in on its location and stay with it (remaining approximately 100-200m away) for as much of the day as possible, identifying sites where kills were made, determining how long it remained at each perch, how far it moved between perches, and other attributes of foraging behavior. To confirm that a kill was made I approached a hawk's location when the variation in the transmitter pulse rate indicated it was feeding (mercury tipswitches caused a slow pulse when vertical, fast when horizontal).

Determining kill locations. While I was tracking, a video camera (with time stamp) was recording the nest to confirm that prey was returned to the nest. During the fledgling period, when young were in nest stands but not at nests, I placed an observer in the stand to confirm prey deliveries. At least half of the identified kill sites (55%) were confirmed directly by either locating the prey remains or by seeing the goshawk leaving the immediate area with prey in talons, but on the remainder of occasions confirmation of the kill was not made until I reviewed the nest video or communicated with the nest observer. In these latter cases, the kill site location was estimated from my earlier tracking locations. To calibrate these location estimates I conducted a beacon test on transmitters hung in trees. The mean maximum error estimate of these remaining kill sites was 69 m (range = 30-200). I assumed that the goshawks last foraging position before a direct flight back to the nest was the kill site unless I had contrary evidence.

HABITAT ASSESSMENT

I collected stand structure data at all kill locations. I measured overstory characteristics in two 0.04 ha circular plots. One plot was centered on the site of the kill while the other was placed 100m away in the estimated direction of travel of the hawk before making the kill. My goal was to sample the habitat the hawk flew through on its way to making each kill. When I was not able to identify the direction of travel (approximately 50% of the time) I placed the second plot 100 m away in a random direction.

I measured the diameter at breast height (dbh) of all live conifers and hardwoods

≥ 2.5 cm dbh. For tree density calculations I grouped trees into three separate classes by

dbh: Sapling/Pole: <30 cm; Medium Tree: 30-50 cm; Large Tree: >50 cm. I calculated

basal area (m^2/ha) of all live conifers and hardwoods. I calculated the percent

composition of the overstory that was conifer versus hardwood by basal area. I measured

the dbh of all snags ≥ 12.5 cm dbh and ≥ 3 m in height. For snag density calculations I

grouped snags into two separate classes by dbh: Small Snags: 12.5-30 cm; Large Snags

>30 cm. I measured canopy closure (%) using a "Moosehorn" vertical sighting tube

(Robinson 1947) at each plot center as well as 5 m out in each of the cardinal directions

(10 measurements/kill site).

I measured understory vegetation along a 100 m line intercept transect (Mueller-

Dombois and Ellenberg 1974) extending between my two vegetation plot centers. I

recorded species, percent cover, and mean height for every sapling (<12.5 cm dbh),

shrub, and swordfern (*Polystichum munitum*) that intercepted the line. I grouped

understory plants into low (<3 m) and tall (≥ 3 m) categories. I also measured percent

cover of logs (≥ 30 cm diameter) and slash (<30 cm diameter wood) along understory

transects.

Univariate Analysis

I randomly selected a site to pair with each kill location that was 500-2,000 m from the

site of the kill in a random direction. This distance was chosen to insure that the paired

site was in a different stand, but within the same general part of the home range. I

compared paired sites that were in separate forest stands because stands are relatively

homogenous in managed forests. Also, I limited selection of these sites to forested areas

in which there were trees ≥ 12.5 cm dbh. This was done to exclude habitat types where I

never detected goshawks hunting (e.g. clearcuts, recently [<10 yr] planted stands, water

bodies). My goal was to compare stand structure at kill sites to potentially available sites

in the areas where the birds were currently hunting.

I compared each stand structure variable between paired kill and random sites

using conditional logistic regression for 1:1 matched data (Breslow and Day 1980,

Hosmer and Lemeshow 1989, Hershey et al. 1998). Hershey et al. (1998) provide a

thorough description of this method using Northern Spotted Owl (*Strix occidentalis

caurina*) nest sites to analyze stand structure variables similar to mine.

Multivariate Analysis

I also used conditional logistic regression for 1:1 matched data to determine if there were

particular combinations of variables that best distinguished kill sites from random sites

(Hershey et al. 1998). To reduce the number of variables to be considered in a

multivariate model, I excluded all variables with *P* values > 0.25 in univariate log-

likelihood ratio tests. I further reduced the list of variables by analyzing correlations

among them and retaining those that are more amenable to direct manipulation by forest

managers. I also assessed interactions among variables in the multivariate analysis. I

evaluated the full model of those remaining variables and only retained those variables whose P values again were < 0.25. I then used Akaikie's Information Criterion (AIC) to determine the most parsimonious model(s).

RESULTS

FORAGING BEHAVIOR

I observed two different hunting techniques and their relative use appeared to be related to habitat type. 'Short-stay perched-hunting' (Kenward 1982), where hawks occupy a perch, scan their surroundings for prey, then fly to another perch (usually 100-300 m away), was the most commonly used method overall (72% of foraging bouts) and in stands > 30 yr old (small sawtimber stage and older; 96% of foraging bouts). In addition to capturing adult and juvenile birds and mammals using this method, I also witnessed two cases of nest predation by goshawks (Steller's Jay [*Cyanocitta stelleri*] and Varied Thrush [*Ixoreus naevius*]) as well as attacks on fledglings of other raptor species at their nest sites (including a successful kill of a Barred Owl [*Strix varia*]). In areas dominated by younger, denser stages of sapling/pole forest (10-20 yr old), where below-canopy flight space is limited, goshawks tended to use a 'low soaring' technique (13% of total foraging bouts). This hunting technique was characterized by sustained flight < 100 m above the forest canopy generally in tight circles with little flapping of the wings. I generally inferred this behavior by the changing characteristics of the telemetry signal;

however, on seven occasions I witnessed the behavior (including attacks on prey). In

15% of foraging bouts both types of hunting were utilized. This generally occurred in

highly fragmented areas where mature forest and young, dense forest intermingle.

Medium to large birds such as Blue Grouse (*Dendragapus obscurus*), Ruffed

Grouse (*Bonasa umbellus*), and Band-tailed Pigeons (*Columba fasciata*) dominated the

diet of goshawks (Figure 2.2). Important mammal species include snowshoe hare (*Lepus

americanus*), Douglas' squirrel (*Tamiasciurus douglasii*), and northern flying squirrel

(*Glaucomys sabrinus*). Seventy-five percent of prey items were avian and 25% were

mammalian.

Breeding male goshawks returned to nests with prey every 4.8 ± 0.6 hr ($n = 126$

visits by nine birds) on average during daylight hours. Non-breeding goshawks,

however, generally consumed their prey at the site of the kill over the course of a day or

two. In general, prey were captured and returned to nests immediately, except in the case

of larger prey items, which were always prepared extensively before taken to the nest.

Grouse (500-1,000 g) were decapitated, plucked, and parceled into two pieces for

separate deliveries, while pigeons (360 g) were simply decapitated and plucked for a

single prey delivery. I never observed goshawks returning more than one prey item at a

time.

Males returned prey directly to nests, then females began feeding young (during

the early nestling stage). If females were not present at nests, males waited there with

prey until they returned (which was never more than one minute in eight video

observations). When nestlings were large enough to feed themselves males dropped prey

at the nest and left immediately. Females were generally not on the nest during this period, but would occasionally appear after the young had fed and feed on the remaining portion, if available.

There was a positive relationship between size of prey returned to the nest and the distance from nest where it was captured ($n = 12$ cases for one male; $r = 0.77$, $P = 0.003$; Figure 2.3a). The gray shaded area in Figure 2.3b shows that if goshawks traveled far from their nests (i.e. especially beyond about 4 km), they did not return with small prey. In fact, as they traveled further away larger and larger kills were required before returning to the nest ($n = 28$ cases pooled across eight hawks; $r = 0.42$, $P = 0.02$; Figure 2.3b).

HABITAT

I identified 52 kill sites of 13 individual goshawks during the four-year study. Of these 13 hawks, seven were adult males, five were adult females, and one was a juvenile male. Kills occurred in stands ranging from relatively open, 13-yr-old regeneration units (pre-canopy stage) to 200-yr-old complex, old-growth forests. Stands ranged from small (0.5 ha) and isolated to large (> 100 ha) and contiguous. All forest types and successional stages were hunted except for recent clearcuts and shrub/sapling stages. Kills were made in later stages of forest development more than expected based on availability (χ^2 test of 'Young Forest' through 'Mature', df = 3, $P < 0.001$, Figure 2.4). There was substantial variation among kill sites in vegetative attributes (Table 2.1).

Univariate Analysis

In general, overstory variables were greater at kill sites – except for small tree density and total tree density, which were greater at random sites (Table 2.1). Goshawks tended to hunt in stands with larger diameter trees and avoided areas composed primarily of small trees (sapling/pole). Kill sites also had greater overall basal area, greater total snag density and greater small snag density, though large snag density did not differ between kill and random sites. Canopy closure and percent conifer composition, which were both very high throughout the study area, did not differ between kill and random sites.

Most understory variables did not differ between kill and random sites (Table 2.1). Understory cover only differed within the 'tall' category (≥ 3 m; e.g. vine maple [*Acer circinatum*], conifer saplings, salmonberry [*Rubus spectabilis*]). Kill sites had an average of 35% less tall understory cover than random sites. Percent low understory cover ranged widely at both kill and random sites, and mean amounts of this habitat feature did not differ between sites. Extreme sites were either dense, pole stage forests devoid of a shrub layer, or mature stands with lush understories of swordfern covering $\geq$ 90% of the forest floor. Understory species richness and percent cover of both fine and coarse woody debris did not differ between kill and random sites.

Multivariate Analysis

Many of the overstory variables were highly correlated with one another as were some

overstory with understory variables (e.g. small tree density and tall understory cover).

After eliminating insignificant variables ($P > 0.25$ in univariate log likelihood ratio tests)

and further reducing the list of highly correlated variables, eight remained for

consideration (small tree density, medium tree density, large tree density, mean dbh,

basal area, canopy closure, total snag density, and total understory cover). There were

four potential models that all had similarly low AIC values (Table 2.2). Mean dbh was

the only variable found in all four models – highlighting its importance as a variable in

predicting goshawk use of a stand for hunting. Two other variables, basal area and total

snag density, also add predictive power to the model without substantially increasing the

AIC value. The model containing all three of these variables had reasonable explanatory

value with an $R^2 = 0.43$.

I calculated the average β for each of these variables over the entire possible set of

models using them ($n = 7$) based on AIC weights (Burnham and Anderson 1998). Mean

dbh was the most important variable ($\beta = 0.104$), followed by basal area ($\beta = 0.012$) and

total snag density ($\beta = 0.004$). The importance of mean dbh is further highlighted when

considering the odds ratios for the 3-variable model (Table 2.3). The odds of selection

for a given stand increased by a factor of 2.3 as the mean dbh increased from its mean at

random sites ($\bar{x}_{random} = 24$ cm) to its mean at kill sites ($\bar{x}_{kill} = 32$ cm). Using the same

model, the odds of selection increased by a factor of 1.1 for both basal area ($\overline{x}_{random}$ = 40 m^2/ha to $\overline{x}_{kill}$ = 52 m^2/ha) and total snag density ($\overline{x}_{random}$ = 45/ha to $\overline{x}_{kill}$ = 77/ha).

DISCUSSION

FORAGING BEHAVIOR

The combination of hunting techniques utilized by this population of goshawks is likely an adaptation to landscapes composed of a diversity of habitat structures where a wide variety of prey is available. The most commonly reported hunting style ('short-stay perched-hunting' [Kenward 1982]) is generally used in the "typical" goshawk foraging habitat (mature stands with large trees and sufficient flight space beneath the canopy). In managed forests of western Washington, however, where past and current forestry practices have created a mix of relatively young habitat structural stages, adoption of various hunting strategies allows goshawks to survive in landscapes with very little "typical" habitat.

The overwhelming dominance of birds in this population's diet, particularly larger birds such as grouse and Band-tailed Pigeons, is unusual compared with other goshawk populations in North America (see review in Squires and Reynolds 1997, Watson et al. 1998). Between 1986-96, Watson et al. (1998) collected 531 prey items from 38 western Washington goshawk nests. While grouse comprised a substantial portion of the diet (16.5%), pigeons were completely absent from their prey collection. Most of their nests

were in National Forests or National Parks near or above the Band-tailed Pigeons upper

altitudinal limit (pigeons are uncommon above ~ 1,000 m elevation in Washington). The

nests in my study (Figure 2.1) were mostly on State and private timberlands at lower

elevations (foothills) where this prey species is more abundant.

The positive relationship I observed between prey size and distance from nest is a

prediction of Central Place Foraging (CPF) theory (Orians and Pearson 1979) for 'single

prey loaders' such as goshawks. It appears that goshawks are non-selective with respect

to prey size within about 4 km of their nests, but beyond that distance they require

capture of relatively large prey before returning to their nests (Figure 2.3). The 'benefits'

of a given prey item must outweigh the 'costs' of traveling such great distances and

expenditure of time for it to be returned to the nest. It is likely that hunting goshawks did

capture smaller prey when far away from nests, but consumed them immediately, then

continued foraging in the area until a large prey item was captured.

HABITAT

In intensively managed forests of western Washington goshawks travel great distances to

secure prey in a wide variety of forested habitats, particularly during periods of low prey

abundance (Chapter 1). The diversity of stand conditions utilized for hunting largely

reflects the diversity of habitats available within these managed landscapes. While

goshawks hunted throughout a range of stand structural conditions, they used conditions

representative of more mature forest development more than expected based on

availability. Young (<30 yrs) forests generally do not provide the appropriate conditions (large trees with well developed canopies, adequate flight space beneath the canopy) for goshawk hunting.

This use of mature forests is similar to foraging studies on goshawks elsewhere in the western United States. Beier and Drennan (1997) found that goshawks in Arizona hunted in stands with greater densities of large trees (>40.6 cm dbh) compared with contrast plots. Good (1998) found that hunting goshawks in lodgepole pine (*Pinus contorta*) forests of Wyoming returned more often to sites with greater densities of large trees. In California, Hargis et al. (1994) detected goshawks at sites with greater densities of large trees and greater basal area relative to random points. Also in California, Austin (1993) found goshawks selecting closed-canopied mature and old-growth stands.

The association I observed with snags may be explained by providing additional perch sites while hunting an area using the 'short-stay perched-hunting' method. In structurally simple managed forests the presence of snags, even small ones, may provide strategic perch locations to a hunting goshawk that would otherwise not be available. Perhaps these small snags provide perches for hunting goshawks. Large snags are rare in managed forests so my sampling methods were probably not adequate to discern whether or not goshawks select hunting areas based on these features.

Surprisingly, I did not find goshawk hunting limited to areas of low to moderate shrub cover as expected. Finn et al. (2002a,b) found higher occupancy rates at historic goshawk nests on the Olympic Peninsula if shrub cover was relatively low in the stand ($\bar{x}$ = 19.0% at 12 occupied sites). However, I observed goshawks successfully capturing

prey in stands with up to 90% cover of a variety of shrub species. It has been

hypothesized (DeStefano and McCloskey 1997) that the reason goshawks are rare in the

Coast Ranges of Oregon is due to dense understories making capture of prey difficult.

My results for low understory (i.e., shrubs <3 m high) do not support this hypothesis for

western Washington, where understories are very similar to coastal Oregon. However,

my finding of selection for stands with lower than average tall understory (zone that

encompasses 3m to generally about 6m high) does support it. It is likely that goshawks

require an open flight corridor beneath the canopy to be successful in searching for, and

capturing, prey more than they need the ground layer to be free of shrubs. Tall

understory was highly correlated ($r = 0.74$) with small tree density so the avoidance of

areas with abundant tall understory may just be related to goshawks selecting older stands

(Figure 2.4), which have relatively few small diameter trees. In recent years, xeric forests

in eastern Washington and throughout much of the Intermountain West have become

overstocked with small diameter trees in the understory due to nearly a century of fire

suppression (Agee 1993). This condition has likely reduced the ability of goshawks to

hunt in these forests, particularly in younger stands where there is little flight space

between the overstory canopy and the shade tolerant understory conifers.

Managing young stands for hunting goshawks

In this study area, goshawks used areas containing high densities of small trees less than

expected based on availability and used areas composed of fewer, but larger, trees more

than expected based on availability. Additionally, kill sites had high canopy closures

(96% of kill sites had canopy closures ≥ 60%). Goshawks may benefit if young stands in

managed forests were thinned.

In research on goshawks in the same study area, Finn et al. (2002a,b) recommend

promoting nest stand development through moderate-level thinning to 345 – 445 trees/ha

across the range of diameter classes in stands 30-35 years of age. At 5-10 years post-

thinning, this approach begins to yield the deep forest canopies and low shrub cover

found by Finn et al. (2002a,b) as important features of nest stand habitat. Canopy cover

would also increase over this time period. Following the 5-10 year period of post-

thinning response, treated stands would serve as goshawk nest stand habitat for as long as

they were retained.

The thinning prescription recommended by Finn et al. for goshawk nest stands

would also suffice for creation of goshawk hunting habitat, however, more emphasis

should be on thinning "from below" (removal of smallest trees first) to open up the

understory without sacrificing canopy closure too much. Flight space for goshawks

would improve immediately after harvest while canopy cover would improve with time.

Heavy thinning of 30-40 year old stands, which in western Washington and Oregon is to

tree densities of 148 – 247 trees/ha (L. Raynes, pers. comm.), would likely reduce canopy

closure to levels too low to serve as goshawk habitat, even given the canopy development

that would occur post-thinning.

Employing variable density thinning (Carey and Johnson 1995, Carey et al. 1999),

as opposed to uniform prescriptions, would provide a diversity of habitat niches

supporting different prey species. Leaving some small (< 1 ha) areas unthinned would provide the dense, pole stages of forest that some key prey species thrive in (e.g. snowshoe hare, ruffed grouse). While individual goshawks often specialize on one or a few prey species (Figure 2.3a), a diverse prey assemblage may be important in maintaining goshawk populations during times of environmental stress (Chapter 1).

Commercial thinning generally reduces small snag density over the development pathway of a stand by removing trees that would otherwise die due to competitive mortality. Also, during logging snags can be inadvertently damaged or actively removed due to safety or logistical considerations (Hayes et al. 1997). These losses may be ameliorated by the effect that thinning has on the rate of snag creation from wind in stands. Because neighboring trees are removed and can no longer serve as wind buffers, trees in commercially thinned stands are more susceptible to damage to their tops and blowdown (J. Clarke, pers. comm.). Even so, it may be important to create snags in landscapes that are subject to widespread commercial thinning. Increasing snag density in young, managed forests could be achieved during commercial thinning operations through various methods (e.g., girdling, fungal inoculation, topping with mechanical harvesters; Lewis 1998).

Finally, allowing a portion of the managed forest landscape to mature beyond industrial rotation ages (currently 40-50 years on the Olympic Peninsula, L. Raynes, pers. comm.) would ensure that a wide range of goshawk hunting habitats are available within a particular area. On the Olympic Peninsula, extending rotations would be particularly useful and economically practicable (because fewer acres would be necessary) in areas

near late successional reserves of Olympic National Park or Olympic National Forest

where extant habitat can be augmented and more late successional habitat is planned

(Finn et al. 2002a, USDA, USDI 1994).

Table 2.1. Vegetative attributes at 52 goshawk kill sites and 52 randomly located sites within territories in managed forests of western Washington.

Variable	Kill sites			Random			P <
	Mean	SE	Range	Mean	SE	Range	
Overstory							
Total tree density (#/ha; all live stems $\geq$ 2.5 cm dbh)	800	84	235-4115	1308	175	248-6369	0.009
Small tree density (#/ha; <30 cm dbh)	514	90	50-4115	1107	185	54-6338	0.002
Medium tree density (#/ha; 30-50 cm dbh)	225	19	0-495	160	17	0-408	0.005
Large tree density (#/ha; >50 cm dbh)	62	7	0-235	41	7	0-223	0.035
Mean dbh (cm)	32	1	10-56	24	1	4-42	0.001
Basal area (m^2/ha)	52	2	9-90	40	2	6-70	0.001
Canopy closure (%)	77	1	35-90	75	2	36-91	0.206
Total snag density (#/ha; all snags $\geq$ 12.5 cm dbh)	77	10	0-285	45	10	0-384	0.022
Small snag density (#/ha; 12.5-30 cm dbh)	63	9	0-285	36	9	0-371	0.035
Large snag density (#/ha; >30 cm dbh)	14	3	0-74	9	3	0-124	0.201
Percent conifer (by basal area)	94	2	46-100	92	2	15-100	0.500
Understory							
Total understory cover (%)	36	4	2-90	45	4	0-97	0.109
Low understory cover (%; <3m)	25	3	0-90	26	3	0-91	0.887
Tall understory cover (%; $\geq$ 3m)	15	2	0-68	23	4	0-85	0.047
Understory species richness (spp./100 m line transect)	5	1	1-20	6	1	0-16	0.270
Slash cover (%; woody debris <30 cm diameter)	11	2	0-75	10	2	0-45	0.528
Log cover (%; woody debris $\geq$ 30 cm diameter)	4	1	0-9	3	1	0-17	0.513

Table 2.2. Akaike's Information Criterion (AIC) values for four competing goshawk
foraging habitat models.

Model	AIC
Mean dbh	55.5
Mean dbh + Snag density	55.9
Mean dbh + Basal area	57.0
Mean dbh + Basal area + Snag density	57.8

Table 2.3. Odds ratios for the single variable model and the full model containing all
three variables. Odds ratios are the factor by which the odds on selection for a given
stand increase as the variable increases from its mean at random sites to its mean at kill
sites.

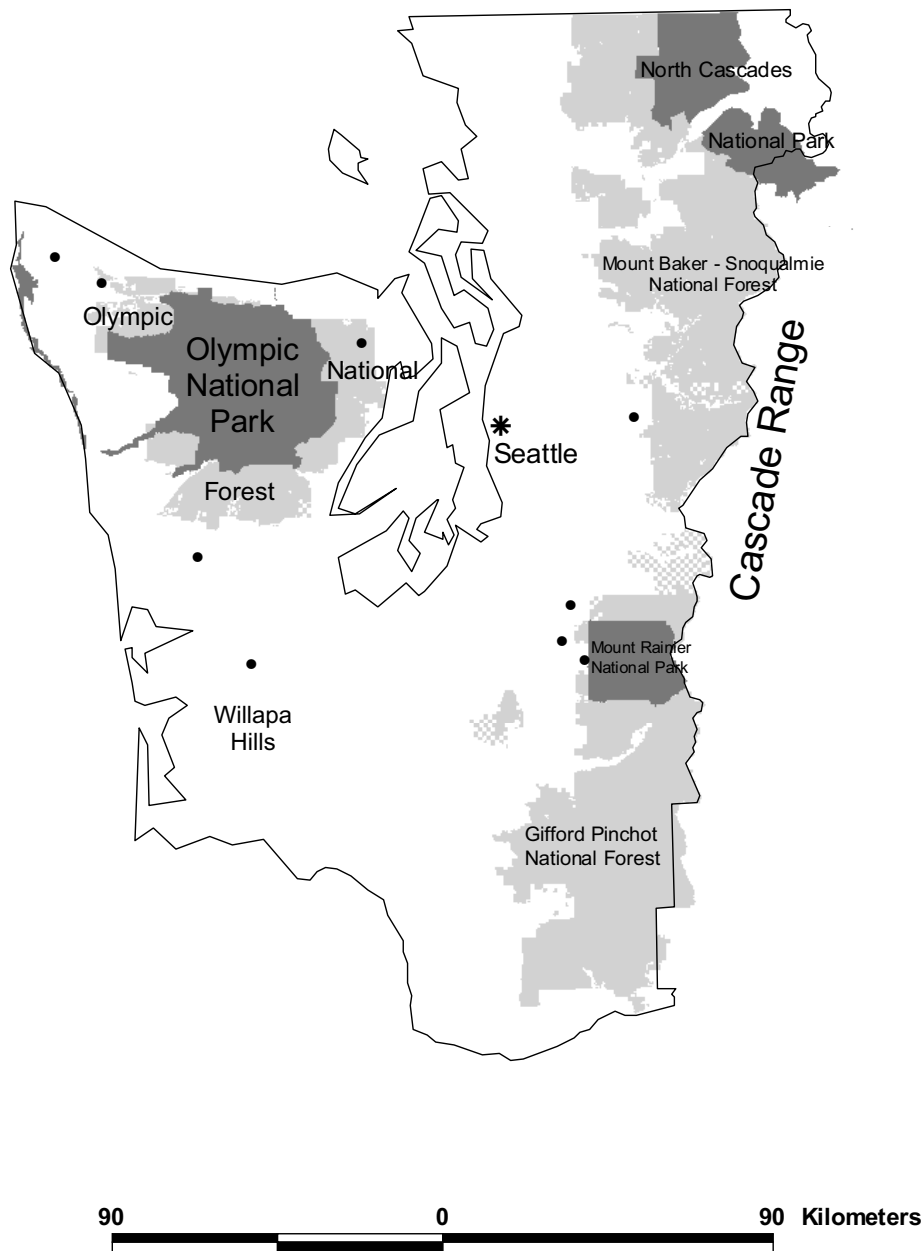|	ß	Odds ratios
Single variable model [1]		
Mean dbh	.110	2.5
Full model (3 variables) [2]		
Mean dbh	.098	2.3
Basal area	.008	1.1
Snag density	.004	1.1

[1] $R^2 = 0.40$
[2] $R^2 = 0.43$

Figure 2.1 Map of western Washington showing locations of nine goshawk territories (black dots) where foraging study took place in relation to major land ownership patterns (non-shaded areas are predominately private and state forestlands).
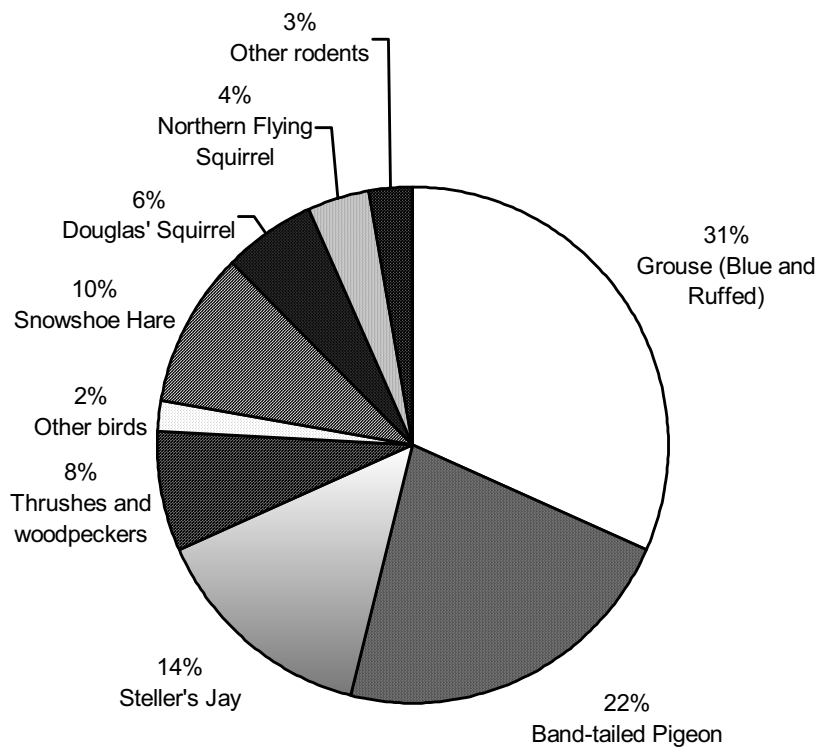
Figure 2.2. Diet of goshawks in western Washington from 1997-2000 ($n = 104$ prey items from 15 territories). Prey items were identified by collecting remains (fur, feathers, and bones) in nest stands or at kill sites, or by reviewing video footage from nest cameras.
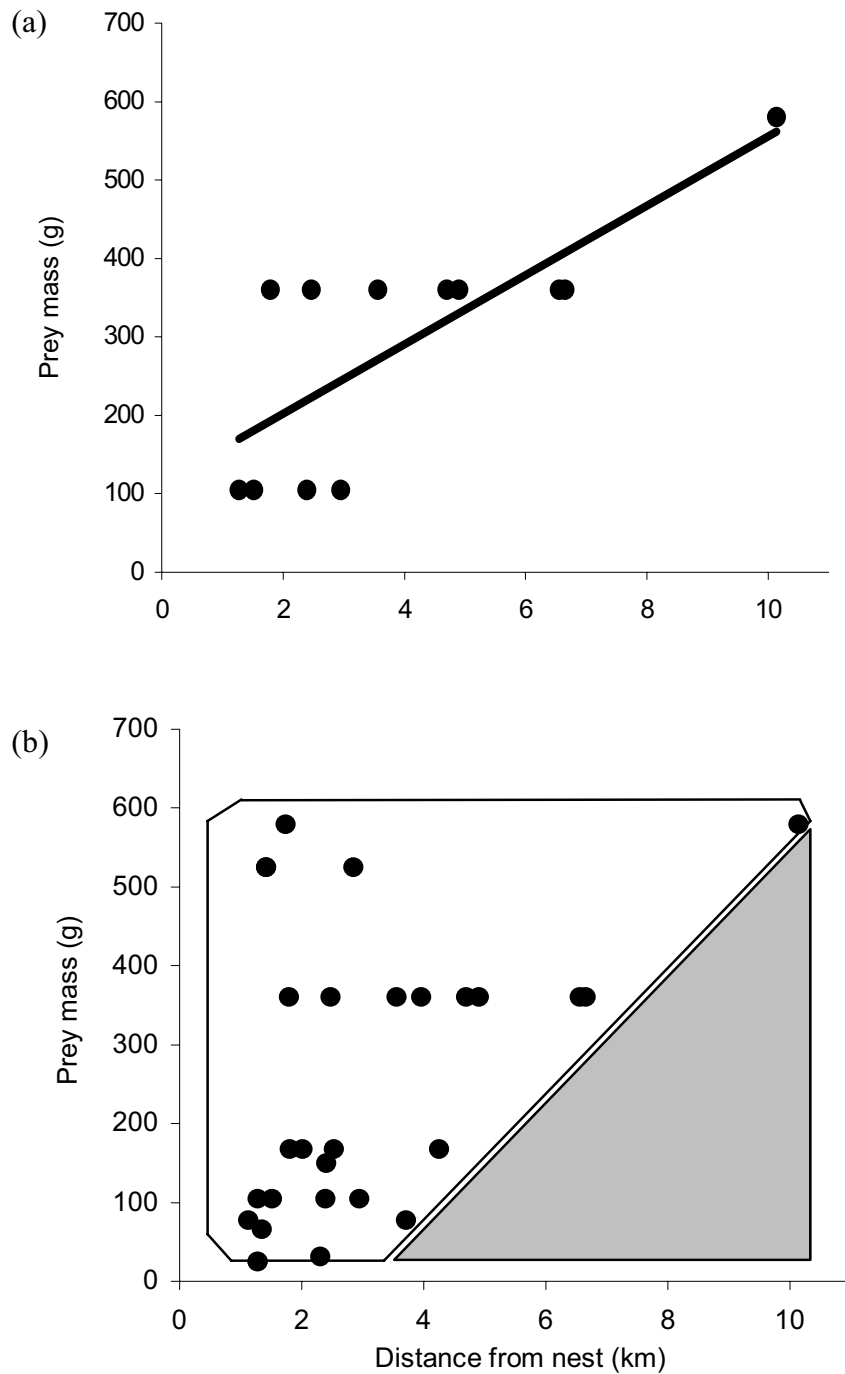
Figure 2.3. Relationship between size of prey and the distance away from the nest where it was captured for (a) a single male with 12 kills, and (b) all goshawks combined ($n = 28$ cases pooled across eight hawks). Only those prey that were returned to the nest are included.
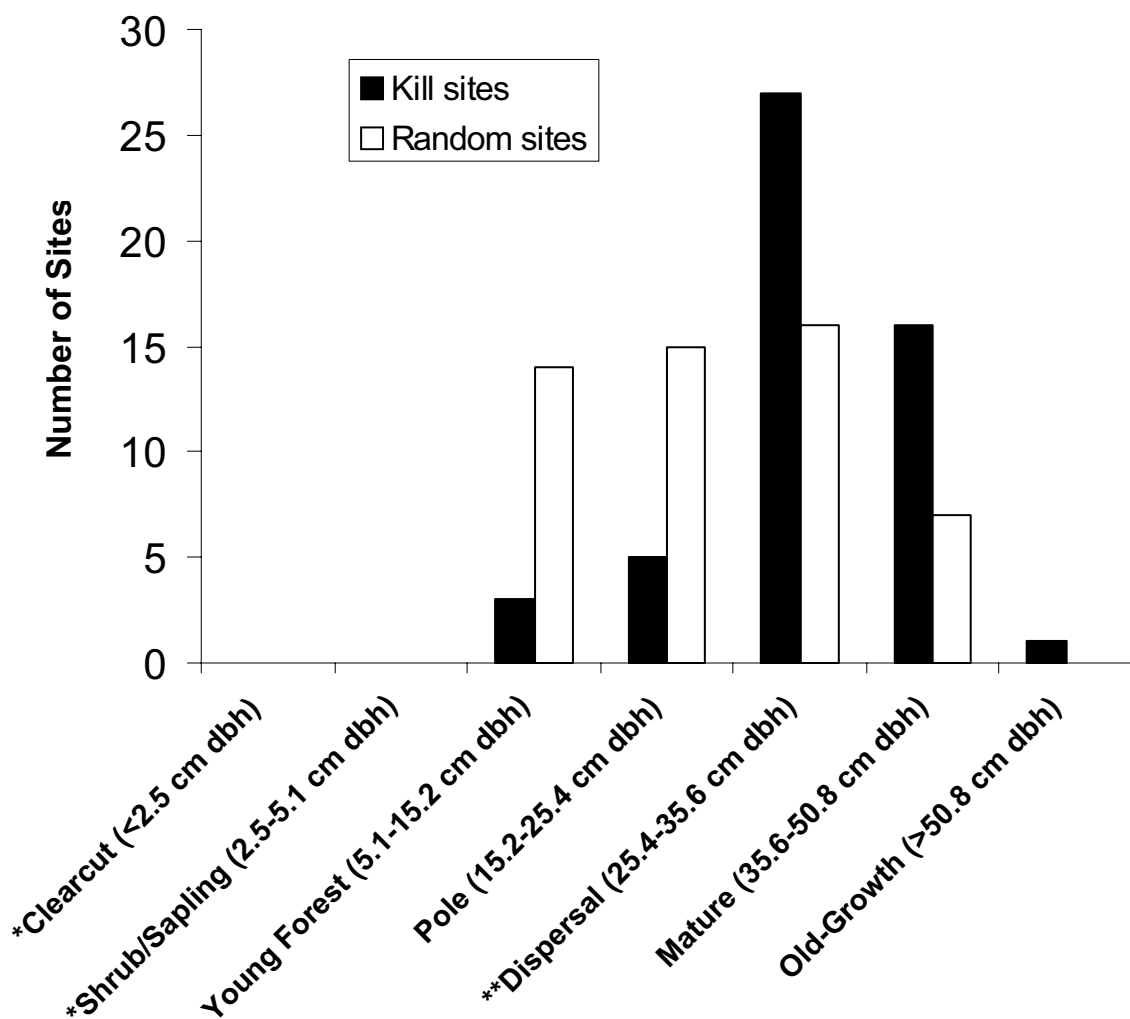
Figure 2.4 Forest structural stages at 52 goshawk kill sites and 52 randomly located sites within territories in managed forests of western Washington, 1997-2000. Structural stages are adapted from Oliver et al. (1995). *All 'Clearcut' and 'Shrub/Sapling' stage stands were excluded from the random sample because hunting goshawks did not use these stages of forest development. ** 'Dispersal' forest refers to the minimum stage required by Northern Spotted Owls for foraging and dispersal with protection from predators. Size ranges are in quadratic mean diameter (QMD).

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