HABITAT SELECTION BY CALVING CARIBOU OF THE CENTRAL ARCTIC HERD, 1980-95.

By

Scott Adrian Wolfe

RECOMMENDED:

Steph Murphy

Raymond

Advisory committee co-chair

Brad Griffith

Advisory committee co-chair

Joan Braddock

Department Head, Biology and Wildlife

APPROVED:

D Woodall

Dean, College of Science, Engineering, and Mathematics

Dean of the Graduate School

12-1-00

Date

HABITAT SELECTION BY CALVING CARIBOU OF THE CENTRAL ARCTIC HERD, 1980-95.

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

By
Scott Adrian Wolfe, B.S.

Fairbanks, Alaska

December 2000

Dedicated to:

Carrie A. Gray Wolfe

ABSTRACT

Habitat selection by calving caribou (*Rangifer tarandus granti*) of the Central Arctic Herd, Alaska, was assessed in relation to distance from roads, vegetation type, relative plant biomass (NDVI; Normalized Difference Vegetation Index), accumulation of plant biomass during early lactation (NDVIrate), snow cover, and terrain ruggedness. From 183 calving sites of 96 radio-collared females, 1980-95, calving distribution was estimated in reference (no development) and treatment (oilfields present) zones east and west of the Sagavanirktok River, respectively. In the reference zone, caribou regularly selected wet-graminoid vegetation, above-median NDVIrate, and non-rugged terrain; concentrated calving remained in habitats with zonal average NDVI on 21 June (NDVI621). In the treatment zone, selection patterns were inconsistent; concentrated calving shifted inland to rugged terrain with low NDVI621 and away from development. Repeated use of lower-quality habitats in the treatment zone could compromise nutrient intake by calving females, thereby depressing reproductive success of the western-segment of the herd.

TABLE OF CONTENTS

ABSTRACT iv

TABLE OF CONTENTS v

LIST OF FIGURES vii

LIST OF TABLES ix

ACKNOWLEDGEMENTS xi

INTRODUCTION 1

STUDY AREA 3

- Physical Description 3
- The Central Arctic Herd 5
- Petroleum Development 6

METHODS 7

- Caribou Distribution at Calving 7
  - Calving Sites 7
  - Calving Ground 7
  - Variability in Distribution of Calving Sites 9
  - Concentrated Calving Areas 9
- Habitat Characteristics 10
  - Distance from Roads 10
  - Vegetation Types 11
  - Relative Plant Biomass 11
  - Snow Cover 14

    - Terrain Ruggedness 15
  - HABITAT USE/SELECTION 16
  - TEMPORAL TRENDS IN FORAGE AVAILABILITY 17
- RESULTS 18
  - CARIBOU DISTRIBUTION AT CALVING 18
    - Calving Sites 18
    - Calving Ground 19
    - Concentrated Calving Areas 19
  - HABITAT CHARACTERISTICS OF CALVING GROUND ZONES 24
  - HABITAT USE/SELECTION 33
    - Distance from Roads 33
    - Vegetation Types 33
    - Relative Plant Biomass 37
    - Snow Cover 37
    - Terrain Ruggedness 37
  - TEMPORAL TRENDS IN FORAGE AVAILABILITY 42
- DISCUSSION 49
- LITERATURE CITED 58

LIST OF FIGURES

Figure 1. The study area, Arctic Coastal Plain, Alaska. 4

Figure 2. Boundaries of the calving ground estimated as the 99% utilization distribution contour from fixed kernel analysis of all calving sites (Seaman et al. 1998), Central Arctic caribou herd, Alaska, 1980-95.. 8

Figure 3a. Concentrated calving areas (1980-82) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. 25

Figure 3b. Concentrated calving areas (1983-86) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. 26

Figure 3c. Concentrated calving areas (1987-89) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. 27

Figure 3d. Concentrated calving areas (1990-92) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. 28

Figure 3e. Concentrated calving areas (1993-95) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. 29

Figure 4. Distance between centroids of concentrated calving areas within reference and treatment zones, between sequential periods, Central Arctic caribou herd, Alaska, 1980-95. 30

Figure 5. Percentage of concentrated calving areas in the treatment zone and in the entire calving ground within 4 km of roads that were constructed by 1981, 1987, and 1990, respectively, Central Arctic caribou herd, Alaska, 1980-95. 35

Figure 6. Percentage of area with above-median Normalized Difference Vegetation Index at calving (NDVI) within the calving ground and within

concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1981-95. 38

Figure 7. Percentage of area with above-median daily increase in Normalized Difference Vegetation Index during early lactation (NDVIrate) within the calving ground and within concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1981-95. 39

Figure 8. Relationship between Terrain Ruggedness Index (TRI, Nellemann and Thomsen 1994) calculated from 1:63,360 topographic maps and Digital Terrain Ruggedness Index (DTRI) calculated from 1:63,360 digital elevation models..41

Figure 9. Percentage of randomly selected transects with rugged terrain (above-median Digital Terrain Ruggedness Index) within concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95..43

Figure 10. Median Normalized Difference Vegetation Index on 21 June by calving ground zone and in the entire calving ground, Central Arctic caribou herd, Alaska, 1980-95. 44

Figure 11. Median Normalized Difference Vegetation Index on 21 June in used concentrated calving areas of the reference zone, Central Arctic caribou herd, Alaska, 1980-95.. 45

Figure 12. Median Normalized Difference Vegetation Index on 21 June in used concentrated calving areas of the treatment zone, Central Arctic caribou herd, Alaska, 1980-95. 46

LIST OF TABLES

Table 1. Numbers of calving sites in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1980-95. 20

Table 2. Numbers of calving sites by period in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1980-95. 21

Table 3. Sizes of concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95. 22

Table 4. Comparisons of spatial distributions of calving sites within concentrated calving areas between sequential 3-year periods, Central Arctic caribou herd, Alaska, 1980-1995. 23

Table 5. Percentages of vegetation types in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1980-95. 31

Table 6. Median Normalized Difference Vegetation Index at calving (NDVI) and median daily increase in NDVI during early lactation (NDVIrate) in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1981-95. 32

Table 7. Percentage of area by snow cover class in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1981-95. 34

Table 8. Percentage of vegetation types within concentrated calving areas (use) in reference and treatment zones, and in the calving ground (available), Central Arctic caribou herd, Alaska, 1980-95. 36

Table 9. Percentage of area by snow cover class within concentrated calving areas (use) in reference and treatment zones, and in the calving ground (available), Central Arctic caribou herd, Alaska, 1981-95. 40

Table 10. Median Normalized Difference Vegetation Index on 21 June for concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95. 47

Table 11. Median Normalized Difference Vegetation Index on 21 June, each year, for concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95. 48

ACKNOWLEDGEMENTS

I especially thank Dr. Brad Griffith of the USGS, Alaska Cooperative Fish and Wildlife Research Unit and Institute of Arctic Biology and Dr. Raymond D. Cameron of the Institute of Arctic Biology and formerly of the Alaska Department of Fish and Game for inviting me to the University of Alaska Fairbanks and co-chairing my committee. Dr. Griffith provided invaluable assistance with data analysis, creative suggestions, long discussions, and straight-up approach for objectively testing hypotheses. He also requested my involvement, which I eagerly accepted, with projects on the Bathurst caribou herd in Nunavut, Canada and the Porcupine Herd. Dr. Cameron provided direct knowledge of the Central Arctic Herd and thorough editing of papers that improved the overall style of my writing and presentation of results. These two scientists devoted countless hours reviewing and improving several drafts of proposals, posters, and this thesis. Without their assistance and dedication, I would not have been able to conduct this research project.

Dr. Robert G. White of the Institute of Arctic Biology and Stephen M. Murphy of ABR, Inc. were committee members and provided alternative views toward data interpretation and creative enthusiasm that was unparalleled. Dr. White provided enough hypotheses to test to last a lifetime. His creativity and in-depth knowledge of ruminant physiology provided alternative perspectives to landscape-level selection of habitats. Stephen Murphy and Brian Lawhead of

ABR, and Michael R. Joyce of ARCO, assisted with providing field training, transportation, and access to facilities in the Kuparuk Oilfield.

David Douglas of USGS in Anchorage accelerated the process of analyzing AVHRR imagery and my learning TERASCAN and ARC/INFO, two complex programs necessary for performing my analyses. In addition, I was able to use several images that he had processed for the Porcupine caribou herd, which expedited my analyses. Without Dave's assistance, I may have never completed some of my analyses.

Jim Greslin of the Fairbanks North Star Borough created a program (TERRAIN) for estimating terrain ruggedness from digital elevation models (DEM). In addition, Tim Hammond provided 1:63,360 DEM. Greslin's programming skills, Hammond's assistance, and Dr. Griffith's involvement were crucial to this phase of the project.

Dr. Pham Quang and Dr. Dana Thomas of the University of Alaska Fairbanks assisted with decisions regarding various statistical and habitat selection analyses.

INTRODUCTION

Calving grounds are used more consistently by barren-ground caribou (*Rangifer tarandus granti*) herds than any other area within their annual ranges (Skoog 1968). Repeated use likely reflects a survival advantage (Bergerud 1974, Cameron 1983) through greater availability of nutritious forage (de Vos 1960, Skoog 1968, White et al. 1975, Batzli et al. 1980, Batzli et al. 1981, Cameron 1983, Russell et al. 1993) and lower predation risk (Skoog 1968, Bergerud 1974, Fancy and Whitten 1991, Whitten et al. 1992).

Within calving grounds, the distribution of parturient caribou typically varies somewhat among years (Bergerud 1974, Bergerud and Page 1987, Fancy et al. 1989, Fancy and Whitten 1991, Walsh et al. 1995), apparently in response to spatial variations in forage quantity and quality (Skoog 1968, White et al. 1975, Cameron and Whitten 1980, Russell et al. 1993, Griffith et al. 2000) and predator densities (Bergerud 1974, Bergerud and Page 1987, Whitten et al. 1992). Other possible factors include habitat deterioration (Klein and Kuzyakin 1982, Couturier et al. 1990), parasite abundance (Folstad et al. 1991), snow cover (Lent 1980, Eastland et al. 1989, Russell et al. 1993), topographic features (Nellemann and Thomsen 1994, Nellemann 1997), and anthropogenic disturbance (Child 1973, Roby 1978, Jingfors et al. 1983, Smith and Cameron 1983, Fancy 1983, Whitten and Cameron 1983a, Dau and Cameron 1986, Lawhead 1988, Cameron et al. 1992, Smith et al. 1994, Nellemann and Cameron 1996, Nellemann 1997, and Nellemann and Cameron 1998).

Local shifts in calving distribution have been linked to avoidance of oilfield activities by parturient caribou of the Central Arctic Herd (CAH) (Dau and Cameron 1986, Cameron et al. 1992, Nellemann and Cameron 1998). Mean caribou density was unrelated to distance from roads before development, but decreased significantly within 1 km of roads and increased significantly 5-6 km from roads after development (Cameron et al. 1992). Redistribution occurred even with relatively low rates of vehicular traffic (100-200 vehicles/day).

These local responses may accumulate and result in a population effect. Data on calving sites of radio-collared CAH females suggested a progressive inland shift in distribution (Cameron and Ver Hoef 1996, Cameron and Griffith 1997). That shift was more apparent west of the Sagavanirktok River (oilfields present) than east of the Sagavanirktok River (no development) (Cameron and Ver Hoef 1996). In addition, concentrated calving in the west appeared to shift away from development, while concentrated calving in the east remained relatively constant in location (Cameron and Griffith 1997). However, the importance of shifts in distribution to CAH calving caribou was not quantified. In particular, potential implications of changes in habitat use were not addressed.

The goals of this study were to determine if calving distributions differed between reference (REF; no development) and treatment (TRT; oilfields present) zones of the calving ground and, if so, to evaluate the implications in terms of habitat quality. Objectives were to (1) delineate calving distribution in both zones, (2) compare habitat characteristics between zones, (3) assess habitat selection by calving caribou, and (4) compare relative availability of forage between zones and among concentrated calving areas (CCA's) within zones of the calving ground. Respective null hypotheses were: (1) changes in distribution of CCA's did not differ between zones, (2) habitats did not differ between zones, (3) caribou selected the same habitat characteristics in both zones, and (4) relative availability of forage did not change through time in either calving ground zone or in CCA's.

STUDY AREA

Physical Description

The study area lies between the Colville and Canning rivers within 150 km of the Beaufort Sea (Fig. 1). Elevation ranges from sea level to about 300 m. Snow cover is present for 8-9 months each year. Summers are short and relatively cool, with frequent coastal fog (Brown et al. 1980).

Two physiographic provinces comprise the study area (Wahrhaftig 1965, Brown et al. 1980). The Arctic Coastal Plain extends inland to about 75 m elevation (Brown et al. 1980) and is characterized by low topographic relief, poor drainage, ice-wedge polygons, scattered pingos, river terraces, and longitudinally-oriented thaw-lakes. Wet graminoid and moist graminoid prostrate-shrub (nonacidic) tundra are the dominant vegetation types (Webber and Walker 1975, Walker et al. 1985, Walker and Acevedo 1987, Muller et al. 1999). The Arctic Foothills Province to the south consists of gently rolling terrain dominated

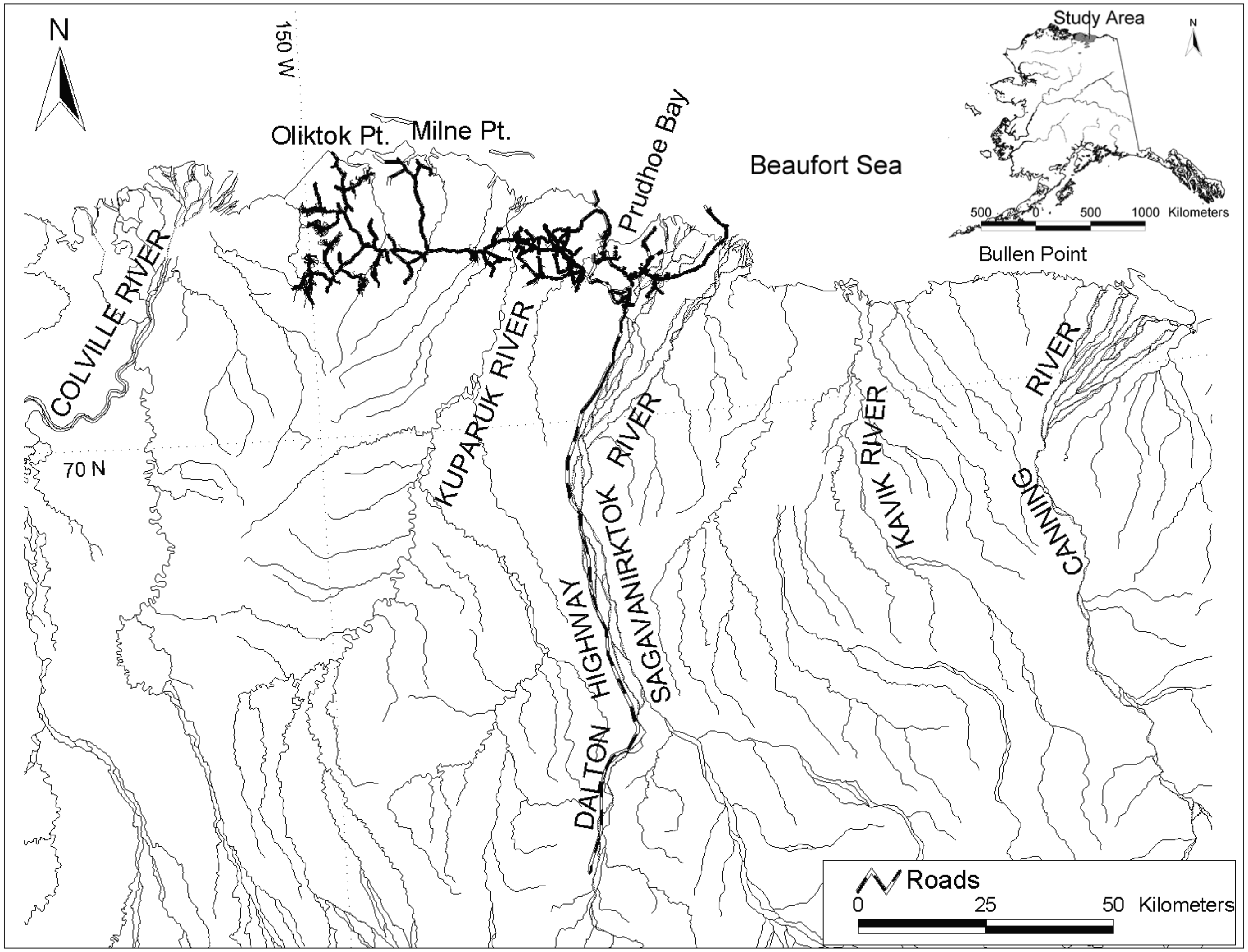

Figure 1. The study area, Arctic Coastal Plain, Alaska.

by moist dwarf-shrub tussock-graminoid (acidic) and dry prostrate-shrub vegetation types (Auerbach et al. 1992, Walker et al. 1994, Muller et al. 1999).

Muller et al. (1999) identified five vegetation types in the study area: dry prostrate-shrub and barrens, moist graminoid prostrate-shrub, moist dwarf-shrub tussock-graminoid, moist low-shrub, and wet graminoid. Moist graminoid prostrate-shrub and wet graminoid predominate in poorly drained areas. Dry prostrate-shrub and barrens, moist dwarf-shrub tussock-graminoid, and moist low-shrub are most common on rolling hills and raised areas.

The Central Arctic Herd

The annual range of the CAH is between the Canning and Colville rivers, from the Beaufort Sea south to the Brooks Range (Cameron and Whitten 1979). Winter range is primarily in the northern foothills of the Brooks Range. Calving and summer ranges are on the Arctic Coastal Plain (Cameron and Whitten 1979). Seasonal ranges often overlap (Cameron and Whitten 1979, Fancy et al. 1989). Population sizes were about 5,000 in 1978; 8,500 in 1981; 13,000 in 1983; 23,000 in 1992; 18,500 in 1995; and 19,500 in 1999 (Whitten and Cameron 1983b, ADFG unpublished).

Direct estimates of predator densities are lacking. Generally, however, wolves (*Canis lupus*) (Stephenson 1979), grizzly bears (*Ursus arctos*) (Reynolds 1979, Young and McCabe 1998, Shideler pers. comm.), and nesting golden eagles (*Aquila chrysaetos*) (Campbell 1960) are less abundant on the coastal plain than in the foothills or mountains (Young et al. 1992).

Petroleum Development

Atlantic Richfield (ARCO) and Humble Oil and Refining Companies (EXXON) discovered a major oil reserve at Prudhoe Bay in 1968. By 1970, the Prudhoe Bay and Deadhorse airports, several base camps, and a small network of drill pads and roads were constructed (Shideler 1986). Rapid expansion of the Prudhoe Bay Oilfield Complex (PBC) occurred during 1974-75 with construction of the Trans-Alaska Pipeline (TAPS), drill pads, flow lines, access roads, and support facilities (Roby 1978). By 1987, the offshore Endicott and onshore Lisburne Oilfields were operational. Thereafter, surface development within the PBC proceeded at a lower rate.

Construction of the Kuparuk Development Area (KDA), about 45 km west of Prudhoe Bay, began in 1977 with extension of the Spine Road from the PBC across the Kuparuk River. By 1981, ARCO's first central processing facility (CPF-1), a relatively small system of roads and flow lines, and the Kuparuk Pipeline were in place (Shideler 1986). Roads and flow lines were extended north to Milne and Oliktok points beginning in 1981. From 1982 to 1987, CPF-1 was enlarged; two additional processing facilities were constructed to the southwest and north (CPF-2 and CPF-3), respectively; and access roads, drill pads, and elevated pipelines were added. Most construction was completed by 1987, except for small additions near Milne and Oliktok points. By 1993, surface development, of which 75% was roads with adjacent pipelines, covered about 2% of the area comprising the PBC and KDA (Jorgenson and Joyce 1994). By

1999, more than 1,300 and 900 wells had been drilled in the PBC and KDA, respectively, and nearly all development occurred west of the Sagavanirktok River (BP Amoco Operations, unpublished).

METHODS

Caribou Distribution at Calving

Calving Sites

During 31 May - 19 June, 1980-95 (except 1984), a total of 96 different radio-collared females were located repeatedly by fixed-wing aircraft to determine parturition status (Cameron et al. 1993, Cameron and Ver Hoef 1994, Cameron and Ver Hoef 1996). One hundred eighty-three calving sites were estimated as the locations where females were first observed with a live calf at heel (Cameron and Ver Hoef 1996). For these analyses, calving sites were classified into REF and TRT zones depending on whether they were east or west of the middle of the Sagavanirktok River delta, respectively (Fig. 2).

Calving Ground

The location and size of the calving ground were estimated from fixed kernel analyses of all calving sites (version 4.27 of KERNELHR, cell size and smoothing parameter automatically selected, least squares cross validation; Seaman et al. 1998). The calving ground was defined as the contour enclosing the 99% utilization distribution (Van Winkle 1975, Worton 1989, Worton 1995,

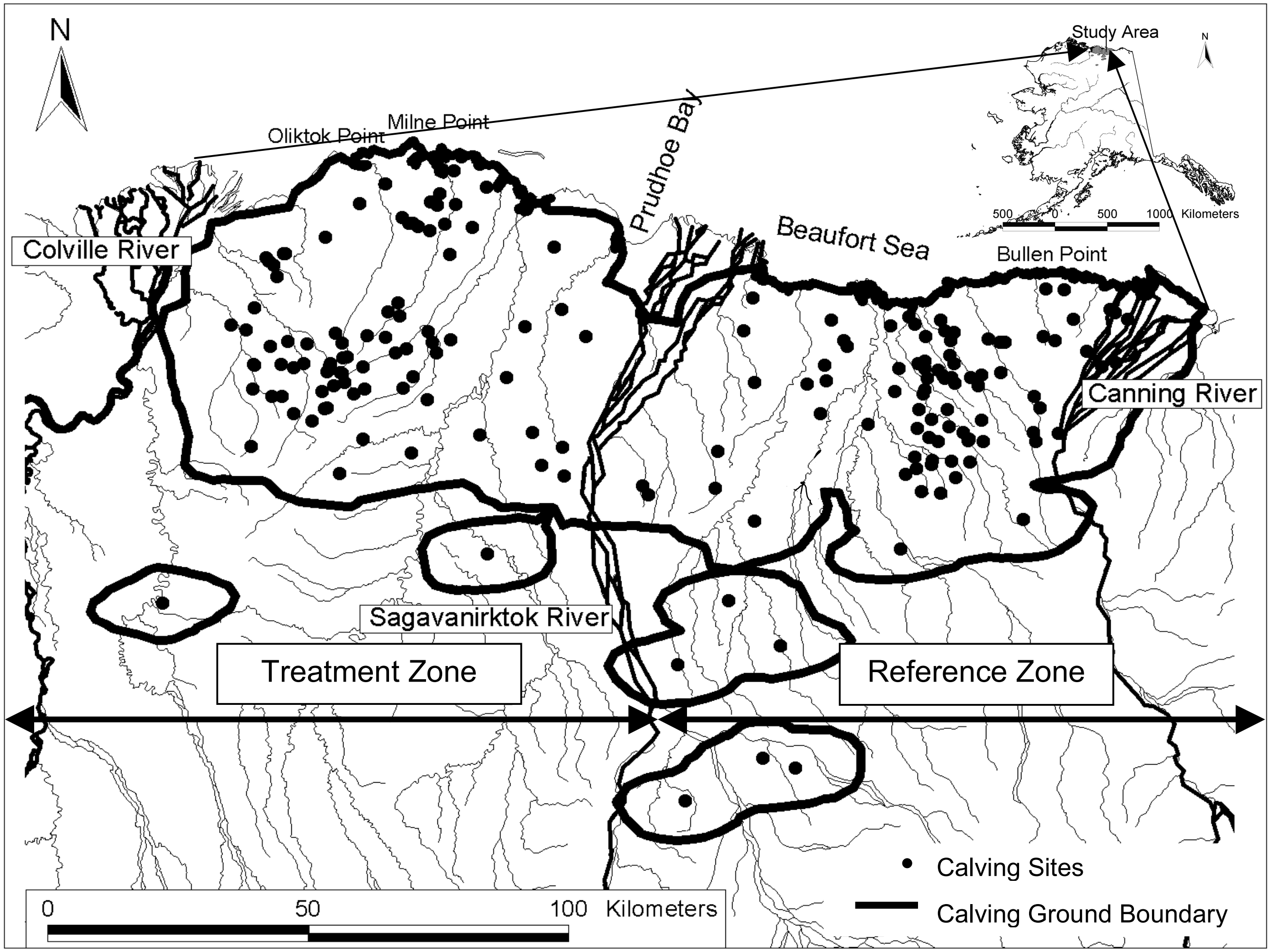

Figure 2. Boundaries of the calving ground estimated as the 99% utilization distribution contour from fixed kernel analysis of all calving sites (Seaman et al. 1998), Central Arctic caribou herd, Alaska, 1980-95. Reference and treatment zones were east and west of the middle of the Sagavanirktok River delta, respectively.

Seaman and Powell 1996). Areas that extended into the Beaufort Sea were excluded because calving has never been documented on the pack ice. Habitat characteristics were compared between REF and TRT zones of the calving ground (Fig. 2).

Variability in Distribution of Calving Sites

Multi-response permutation procedures (MRPP, Mielke and Berry 1982) were used to test for differences in the spatial distribution of calving sites between sequential years. Calculations were based on the specific MRPP function corresponding to Euclidean distance measurements (Slauson et al. 1991, Zimmerman et al. 1985).

Concentrated Calving Areas

A CCA for each zone during each period was defined as the area (kernel density contour) encompassing calving sites with greater than average observation density (Seaman et al. 1998). Because only one estimate was derived for each zone in each period, standard estimates of within-period variance were not possible (Zar 1996, Manly 1997). Thus, variance was estimated using jackknife procedures (Efron 1979, Rocke and Downs 1981, Efron 1982, Efron and Tibshirani 1993, Manly 1997), where individual sites were successively excluded, with replacement, from each set of sites. Then, each subset of sites was used to estimate a CCA. The number of estimates of a CCA was equal to the number of sites. Variance was calculated from all estimates of a CCA.

Within each zone, the spatial distribution of calving sites within CCA’s was compared between sequential periods to assess the statistical significance of shifts in concentrated calving. MRPP (Mielke and Berry 1982) was used for this test.

Directional shifts were evaluated using Rayleigh's test to determine if bearings between sequential centroids of CCA’s differed from random (Zar 1996, Batschelet 1965). The centroid of each CCA was calculated using a geometric algorithm (O'Rourke 1998). Bearings were calculated between each jackknifed centroid from the base period to the median centroid in the subsequent period.

The distance between CCA’s was assessed based on distance between sequential centroids within each zone. Distances between each jackknifed centroid from the base period to the median centroid in the subsequent period were calculated using simple geometry (Arnold and Maller 1984, Haila et al. 1996, Howery et al. 1996, Howery et al. 1998).

Habitat Characteristics

Distance from Roads

Because relative abundance of calving caribou was less than expected within 4 km of roads after development (Cameron et al. 1992, Nellemann and Cameron 1996), a zone extending 4 km from the center of all roads (4 km buffer, ESRI 1998) was generated for analysis of habitat selection. This area was assumed to represent a “response zone” to disturbance. The proportional area of the response zone within calving ground zones and CCA’s was calculated for 1981, 1987, and 1990. The additional area occupied by roads after 1990 was assumed to be negligible.

Vegetation Types

Vegetation types were obtained from a mosaic of Multi Spectral Scanner (MSS) images of arctic Alaska (Muller et al. 1999), extrapolated from a map of the Kuparuk River Region (Muller et al. 1998). Map accuracy was 85% for the Kuparuk River Region (Muller et al. 1998). Thus, accuracy of the MSS classification of arctic Alaska (Muller et al. 1999) was assumed to be 85% for the CAH calving ground. Diversity of vegetation types was calculated, based on Shannon's Diversity Index, from a census of pixels within REF and TRT zones of the calving ground (H; Shannon and Weaver 1949: P. 105).

Relative Plant Biomass

The relative biomass of green vegetation in the canopy surface was estimated using the normalized difference vegetation index (NDVI). This index, developed by Rouse (1973), was calculated as:

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED}),$$

where NIR = near-infrared light reflectance (0.7-0.9 μm wavelength), and RED = red light reflectance (~0.6 μm wavelength). As NIR (reflected by green plant chloroplasts) increased more than RED (absorbed by green plant chloroplasts), the relative biomass of green vegetation was assumed to increase (Colwell 1973). NDVI derived from satellite images has proven useful for estimating the biomass of green vegetation (Hansen 1991, Hope et al. 1993, Shippert et al. 1995), amount of plant photosynthesis (Asrar et al. 1984, Running et al. 1989), phenological progression of vegetation (Kennedy 1989, Lloyd 1989, and Markon et al. 1995), annual above-ground net primary production (Paruelo et al. 1997), snow cover (Baglio and Holroyd 1989, Harrison and Lucas 1989), crop yield (Wiegand et al. 1992), and climate-warming trends (Myneni et al. 1997, Myneni et al. 1998, Griffith et al. 2000).

Satellite images during calving (1-10 June) and post-calving (7-24 days after the first image) were obtained from Advanced Very High Resolution Radiometers (AVHRR) onboard the National Oceanic and Atmospheric Administration's (NOAA) polar orbiting satellites. Images from 1985-95 were Local Area Coverage (LAC) with 1.1 km resolution at nadir. As comparable images were not available for 1980-84, Global Area Coverage (GAC) images with 4.4 km resolution at nadir were substituted. Only two of the GAC images, both in 1981, were sufficiently cloud-free. AVHRR images were calibrated and processed following EROS guidelines (Kidwell 1997). Each image was co-registered to a 1.0 km pixel resolution in Alber's equal-area conic projection (Maling 1973). Post-launch degradation in the red and near infrared AVHRR sensors was corrected (Kaufman and Holben 1993). Clouds were identified when the difference between the temperatures of spectral channels 3 and 4 was $\geq$12 degrees Kelvin (Baglio and Holroyd 1989). When an image had substantial cloud cover, images on adjacent days were composited to obtain maximum cloud-free coverage. Pixels remaining cloud-covered were deleted from the analyses. Then, NDVI was calculated from each AVHRR pixel, and negative values were set to 0.

To estimate the daily accumulation rate of NDVI (i.e., NDVIrate), the pixel based difference between NDVI for images during calving and post-calving was divided by the number of elapsed days between images. NDVIrate was assumed to be positively related to the accumulation rate of new plant tissue during early lactation (after parturition through late June).

A correction technique was developed and applied to account for the potential negative bias in NDVI and NDVIrate caused by surface water (Lillesand and Kiefer 1994, Jensen 1996). Land cover was estimated from the MSS map of vegetation types, which included water as a type, at 100-m pixel resolution (Muller et al. 1999). Unique numbers were assigned to each AVHRR pixel by generating a fishnet grid that aligned with each pixel (ESRI 1998). The fishnet grid was superimposed on the MSS image (Muller et al. 1999) to estimate the proportion of land cover in each AVHRR pixel. To minimize registration errors, mean NDVI and mean NDVIrate were calculated from 9 km^2 blocks, centered on each 1 km^2 AVHRR pixel, and assigned to each center 1 km^2 AVHRR pixel using a 3-km$*$3-km mean filter (i.e., moving window, ESRI 1998). Then, each pixel was corrected for water bias by dividing NDVI or NDVIrate by the proportion of the pixel that was covered by land. All subsequent analyses were performed on water corrected images.

Median NDVI and median NDVIrate were calculated for the calving ground from each image. Pixels then were re-classified as $\leq$ or > the median. The subsequent biological questions posed were: 1) does relative biomass of green vegetation at calving (NDVI) or the accumulation rate of new plant tissue, post-calving (NDVIrate), differ between calving ground zones (no within-year variance occurred because of calculations from a census of pixels), 2) do calving caribou select areas with high or low NDVI at calving, and 3) do calving caribou select areas with high or low NDVIrate during early lactation.

Relative forage quantity at peak lactation was estimated as median NDVI on 21 June (NDVI621) for each year. This was calculated as NDVI from the image during calving plus the product of NDVIrate and the number of days between that image and 21 June (Griffith et al. 2000).

Snow Cover

Percentage snow cover was estimated for each pixel from AVHRR images at calving from a linear model of channel-2 reflectance (Baglio and Holroyd 1989). Estimates of snow cover were then classified into 4 categories: <25%, $\geq$25% and <50%, $\geq$50% and <75%, and $\geq$75%. Snow cover was not estimated from images during post-calving because little, if any, snow was present then.

Terrain Ruggedness

Terrain ruggedness was estimated on 4,000 random 4-km transects within the calving ground and 500 random 4-km transects within each CCA. Each random sample was generated independently (Zar 1996).

The terrain ruggedness technique developed by Nellemann and Thomsen (1994) was modified and automated. Rather than manually calculating terrain ruggedness from measurements on paper topographic maps, terrain ruggedness was calculated from digital elevation models (DEM; U.S. Geological Survey 1993) at 1:63,360 scale.

Nellemann and Thomsen (1994) calculated a "Terrain Ruggedness Index" (TRI) as:

$$TRI = (TNC * TNF) / (TNC + TNF),$$

where TNC = the number of contour lines intercepted along the transect, and TNF = the number of fluctuations in slope direction along the same transect. Slope direction fluctuations were tallied when transects appeared to cross the crest or the bottom of topographic features.

To obtain a similar index (Digital Terrain Ruggedness Index, DTRI) of terrain ruggedness from DEM, a 4-km transect was centered on random points and oriented parallel to the aspect of the 30-m pixel encompassing that point.

DTRI was calculated as:

$$\text{DTRI} = (\text{SEC} * \text{SDC}) / (\text{SEC} + \text{SDC}),$$

where SEC = the sum of absolute elevation changes, and SDC = the number of slope direction changes (i.e., the number of changes from an inclining to declining slope, and vice versa), both obtained from the 4-km transect. Four-km transects were used because they closely approximated the variable length transects (3.2 - 4.5 km) used by Nellemann and Cameron (1996, 1998). For habitat selection analyses, each DTRI was classified as non-rugged or rugged if it was $\leq$ or $>$ the median DTRI of the calving ground, respectively.

DTRI from DEM was compared to TRI from 1:63,360 topographic maps for 101 random 4-km transects, centered on each random point and oriented parallel to the aspect. The relationship between the two indices was assessed by simple linear regression (Zar 1996). Congruity of classification of terrain as non-rugged or rugged between TRI and DTRI was evaluated with contingency table analyses.

Habitat Use/Selection

Habitat selection by calving caribou was assessed for distance from roads (2 categories), NDVI at calving (2 categories), NDVIrate during early lactation (2 categories), percentage snow cover at calving (4 categories), vegetation type (5 categories), and terrain ruggedness (2 categories).

Habitat availability was defined as the proportion of each habitat attribute within the calving ground. Availability was the same for both zones because some females changed zones between years. In any year, females could have calved in either zone.

Habitat use in each zone was defined as the proportion of each habitat attribute within CCA's. Variance in habitat use was calculated from the jackknifed samples of CCA's for each period. Habitat selection was examined at the population level (Design I, sampling protocol A for each zone; Manly et al. 1993).

Selection or avoidance of a given habitat attribute was inferred when the 95% Bonferroni confidence interval (Alldredge and Ratti 1986, McDonald et al. 1991, Alldredge and Ratti 1992) of its respective proportion within a CCA did not overlap the proportion for the calving ground. Habitat attributes were considered selected when used significantly greater than availability and avoided when used significantly less than availability (Johnson 1980). Selection patterns were assessed annually for habitat characteristics that varied each year (i.e., NDVI at calving, NDVIrate during early lactation, and percentage snow cover at calving) and within 3-year periods for those that did not (i.e., distance from roads, vegetation type, and terrain ruggedness).

Temporal Trends in Forage Availability

The temporal trend in forage availability for the entire calving ground and for each calving ground zone was assessed using linear regression of NDVI621 on year. A positive trend would be expected if a climate-warming signature was present (Myneni et al. 1997).

Potential forage availability consequences of shifts in distribution were assessed with linear regression of NDVI621 within CCA's on year. The null hypothesis was that the slopes of regressions would be equivalent for REF and TRT zones. The suitability of linear regression functions was assessed by analyzing residuals for indications of systematic departure from 0, presence of outliers, and non-normality of error distributions (Neter et al. 1990). In addition, median NDVI621 each year was calculated for each CCA.

RESULTS

Caribou Distribution at Calving

Calving Sites

All 183 calving sites were within 155 km of the Beaufort Sea, and 174 (>95%) were within 50 km of the coast (Fig. 2). Ten (18%) of 55 radio-collared females, for which calving was recorded in >1 year, switched between REF and TRT zones. In the TRT zone, 7 (<8%) of the sites were within 4 km of existing roads.

Distributions of annual calving sites did not differ ($P > 0.05$) between sequential years. Thus, calving sites for each zone were combined into five 3-year periods because annual sample sizes were too small for kernel estimates of annual distributions (Seaman and Powell 1996). Three-year periods were chosen to minimize the likelihood of overestimating calving distributions (i.e., small sample sizes overestimate animal distribution; Silverman 1985, Worton 1995, Seaman and Powell 1996) and of masking among year changes in distribution and habitat selection (i.e., the number of years that data are pooled is positively related to the likelihood of masking patterns in habitat selection; Schooley 1994). On average, 11 and 37 sites were recorded for each year (Table 1) and for each 3-year period (Table 2), respectively.

Calving Ground

The calving ground (Fig. 2) encompassed 12,410 km^2. The REF and TRT zones were similar in size, 6,493 km^2 and 5,917 km^2, respectively.

Concentrated Calving Areas

Sizes of CCA's ranged from 156 to 1,182 km^2, with both extremes occurring in the TRT zone (Table 3). Size differed ($P < 0.01$) between zones, except during 1993-1995. On average, CCA's comprised only 9% (range 6 - 14%) of the calving ground area, but included 52% (range 45 - 59%) of the calving sites.

Concentrated calving varied in location between 3-year periods in both zones. Calving sites within CCA's shifted ($P < 0.05$) between sequential periods for 3 of the 4 comparisons in both zones (Table 4).

Table 1. Numbers of calving sites in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1980-95.

	Number of calving sites		
Year	Reference	Treatment	Both
1980	4	3	7
1981	8	8	16
1982	4	6	10
1983	6	3	9
1985	11	6	17
1986	7	0	7
1987	13	10	23
1988	12	9	21
1989	5	6	11
1990	6	7	13
1991	1	10	11
1992	4	10	14
1993	5	5	10
1994	6	3	9
1995	2	3	5
Total	94	89	183

Table 2. Numbers of calving sites by period in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1980-95.

	Number of Calving Sites		
Period	Reference	Treatment	Both
1980-82	16	17	33
1983-86	24	9	33
1987-89	30	25	55
1990-92	11	27	38
1993-95	13	11	24
Total	94	89	183

Table 3. Sizes of concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95.

	Concentrated calving area, km^2 (% of calving ground)	
Period	Reference	Treatment
1980-82	724 (5.8) A[a]	363 (2.9) B
1983-86	591 (4.8) A	1182 (9.5) B
1987-89	317 (2.6) A	596 (4.8) B
1990-92	893 (7.2) A	156 (1.3) B
1993-95	384 (3.1) A	345 (2.8) B

[a] Different letters indicate that area was significantly different ($P < 0.01$) between zones based on ANOVA of jackknifed area estimates for that period.

Table 4. Comparisons of spatial distributions of calving sites within concentrated calving areas between sequential 3-year periods, Central Arctic caribou herd, Alaska, 1980-1995.

	Probability that calving sites came from the same distribution[a] (respective sample sizes)	
Comparison Periods	Reference	Treatment
1980-82 vs. 1983-86	P < 0.001 (14,9)	P = 0.013 (7,5)
1983-86 vs. 1987-89	P = 0.759 (9,15)	P < 0.001 (5,14)
1987-89 vs. 1990-92	P < 0.001 (15,6)	P = 0.028 (14,11)
1990-92 vs. 1993-95	P = 0.005 (6,7)	P = 0.174 (11,5)

[a] Probabilities evaluated with Multi-response Permutation Procedures (Slauson et al. 1991).

The character of spatial shifts in CCA's differed between the two zones (Figs. 3a - 3e). In the REF zone, shift direction did not differ from random ($P = 0.14$). In the TRT zone, however, CCA's shifted southwestward ($P < 0.002$), away from oilfields. Distance between sequential centroids of CCA's was greatest in the TRT zone in the 1980's (Fig. 4), during development of areas near Milne and Oliktok points. Thereafter, TRT zone CCA's remained inland, well beyond 4 km of roads.

Habitat Characteristics of Calving Ground Zones

Only 2.3% of the REF zone was within 4 km of roads (i.e., short segments of the Dalton Highway; Figs. 1, 3a - 3e). Corresponding areas in the TRT zone were 17.8%, 28.6%, and 28.8% by 1981, 1987, and 1990, respectively.

Slightly less dry-prostrate shrub tundra, moist graminoid tundra, and wet graminoid tundra were present in the REF zone than in the TRT zone (Table 5). Moist dwarf-shrub tundra and other shrub-land, however, were more common in the REF zone. Shannon's Diversity Index (Shannon and Weaver 1949) was higher in the REF zone ($H = 1.25$) than in the TRT zone ($H = 0.90$).

NDVI and NDVIrate varied among years and between zones (Table 6). Median NDVI differed between zones, except in 1993, although the direction of differences was not consistent. In contrast, NDVIrate was higher in the REF zone than in the TRT zone, except in 1981 and 1985. Across all years, median NDVI did not differ ($P = 0.85$) between zones, but median NDVIrate was higher ($P = 0.04$) in the REF zone than in the TRT zone.

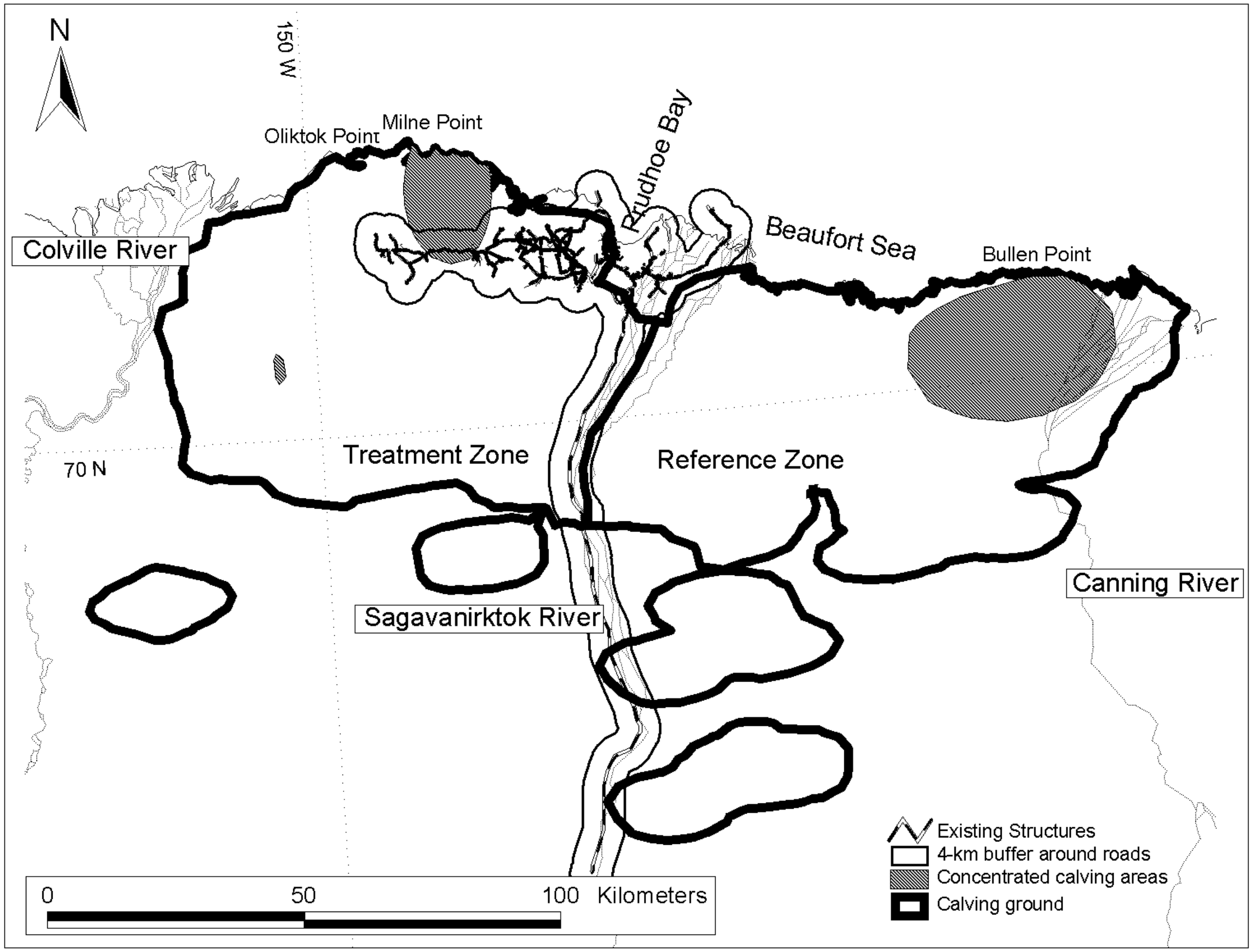

Figure 3a. Concentrated calving areas (1980-82) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. Roads were constructed by 1981.

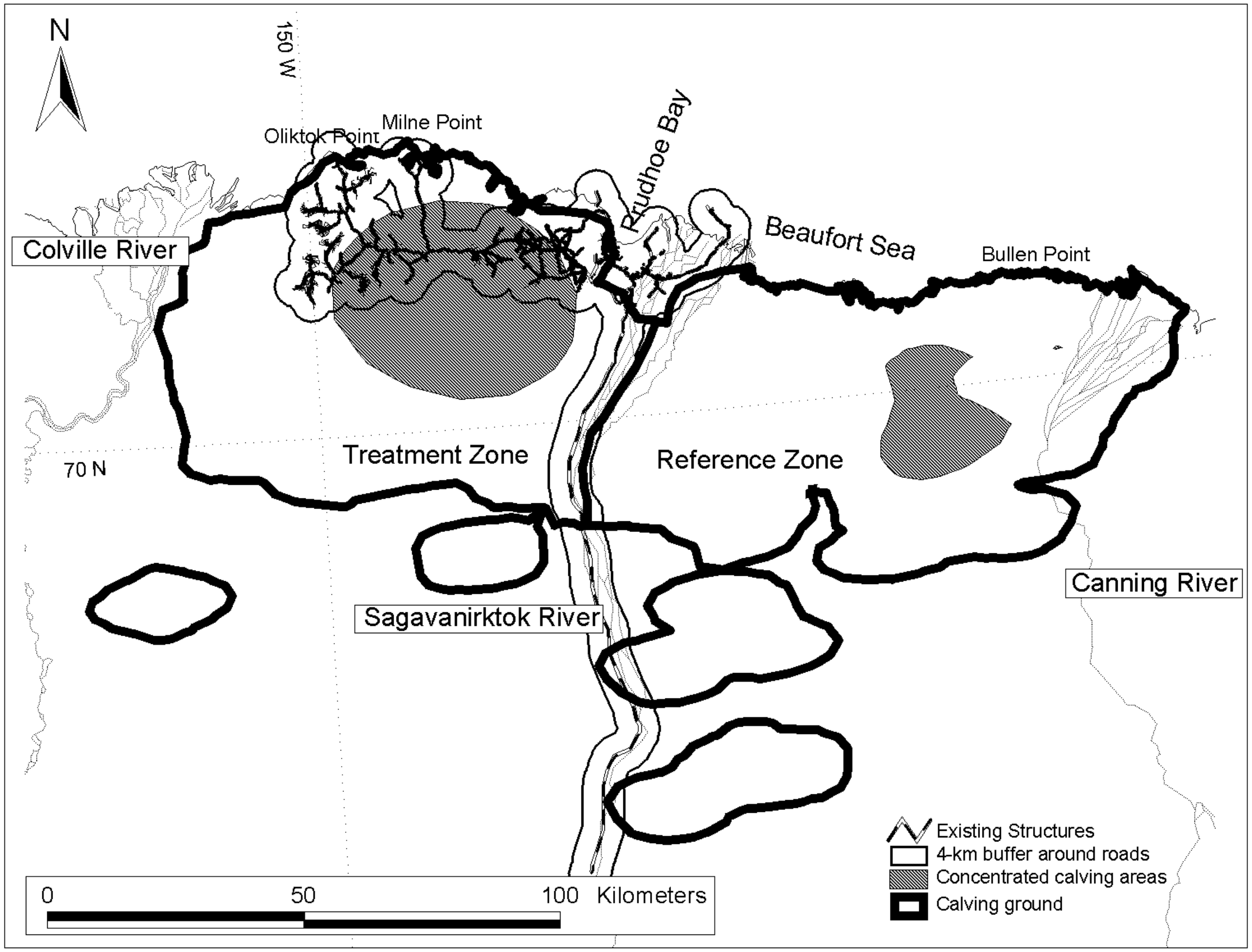

Figure 3b. Concentrated calving areas (1983-86) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. Roads were constructed by 1987.

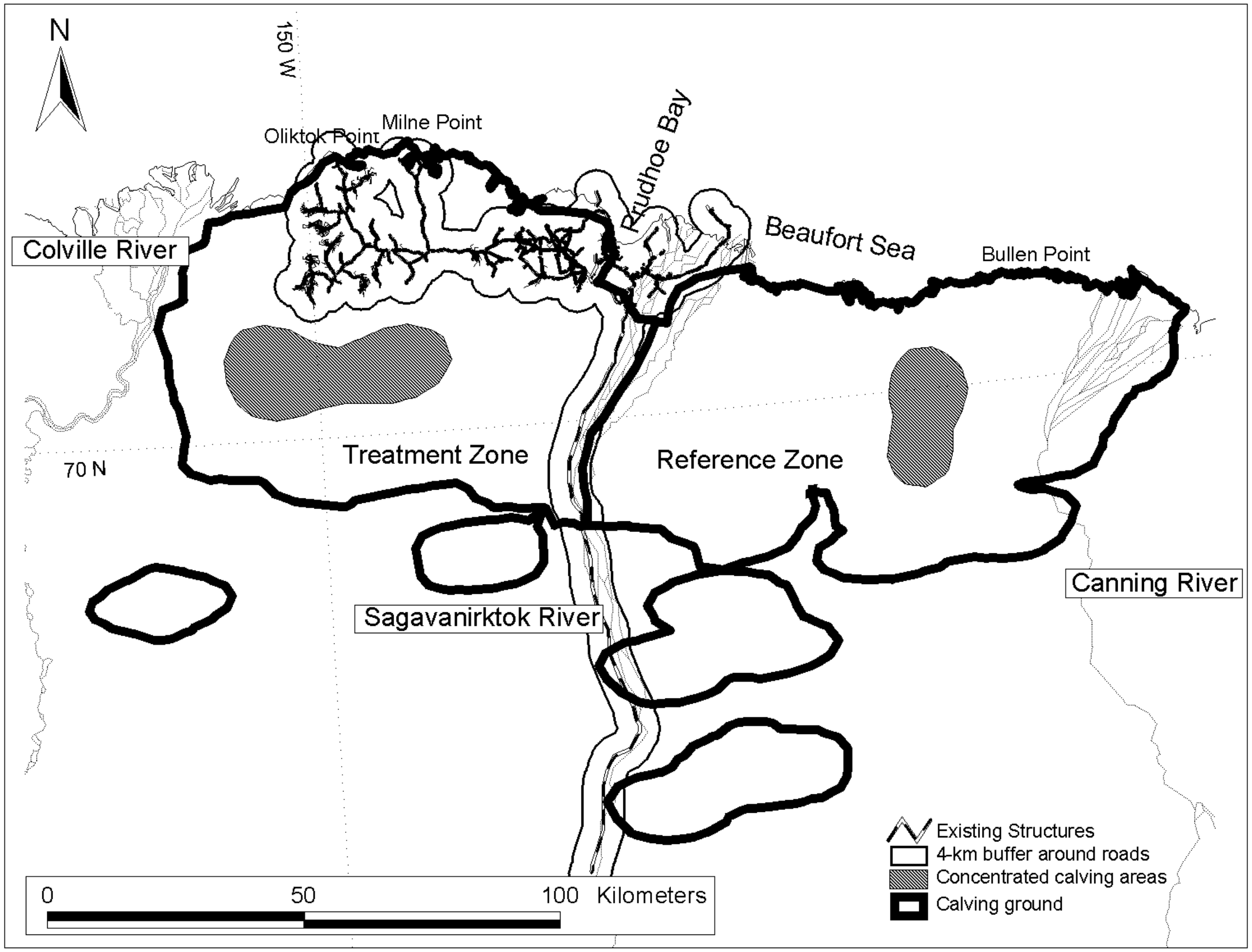

Figure 3c. Concentrated calving areas (1987-89) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. Roads were constructed by 1987.

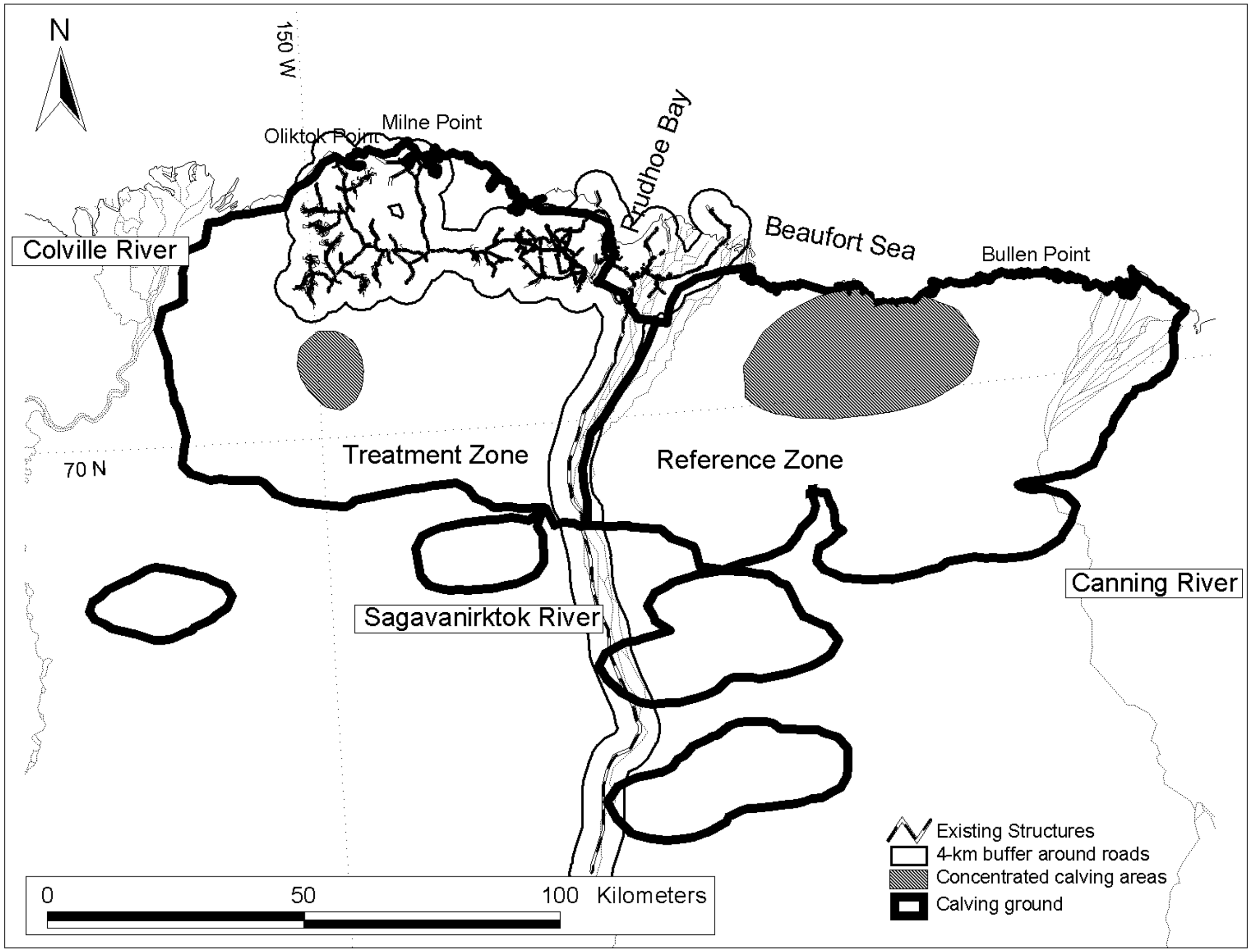

Figure 3d. Concentrated calving areas (1990-92) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. Roads were constructed by 1990.

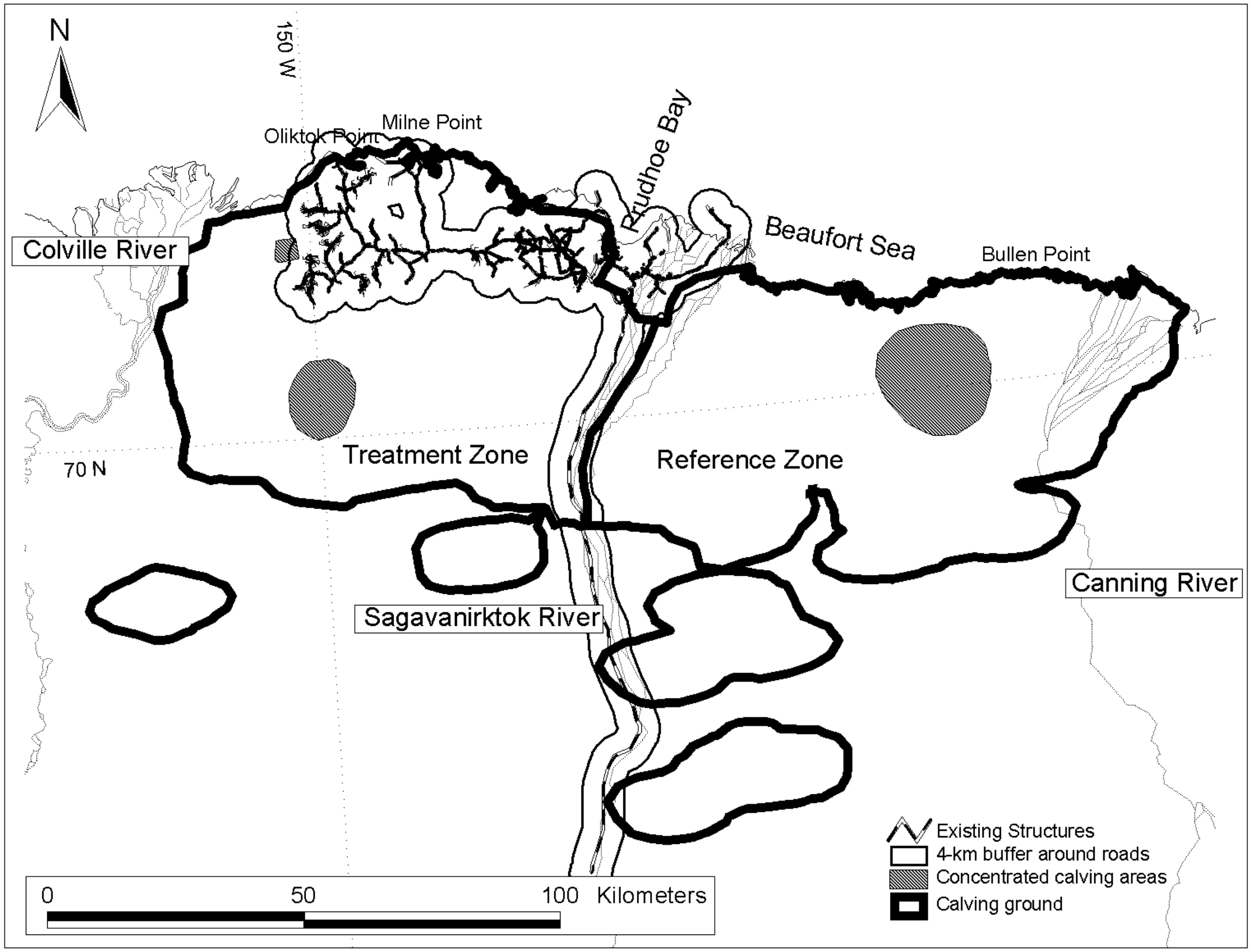

Figure 3e. Concentrated calving areas (1993-95) within the calving ground (1980-95), Central Arctic caribou herd, Alaska. Roads were constructed by 1990.

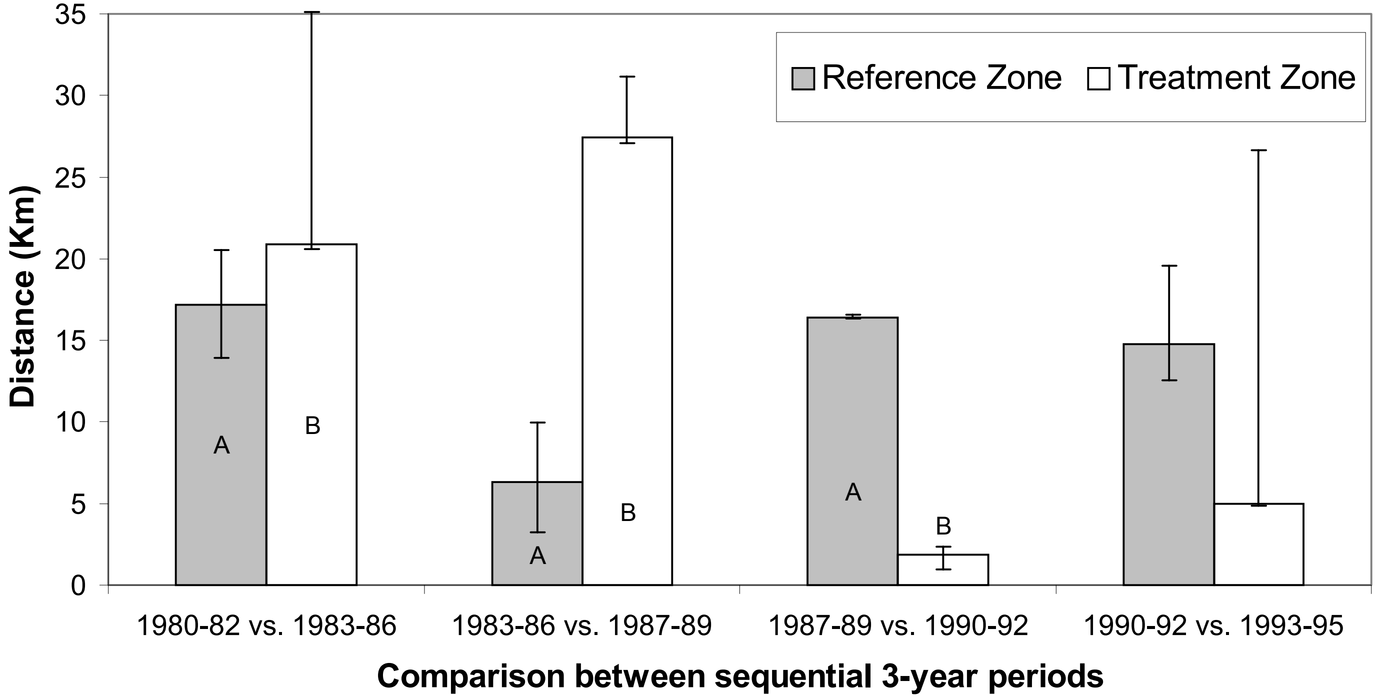

Figure 4. Distance between centroids of concentrated calving areas within reference and treatment zones, between sequential periods, Central Arctic caribou herd, Alaska, 1980-95. Values are medians; error bars are upper and lower quartiles. Different letters indicate that distance was significantly different between zones ($P < 0.01$) based on Kruskal-Wallis ANOVA for that comparison period.

Table 5. Percentages of vegetation types in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1980-95.

	% of Area	
Types	Reference	Treatment
Dry Prostrate-shrub tundra and barrens	4	6
Moist Graminoid, Prostrate-shrub [a]	54	59
Moist Dwarf-shrub, Tussock-graminoid [b]	13	1
Moist Low-shrub Tundra [c]	10	1
Wet Graminoid Tundra	19	33

[a] Nonacidic tundra
[b] Typical tussock tundra
[c] Includes other shrublands

Table 6. Median Normalized Difference Vegetation Index at calving (NDVI) and median daily increase in NDVI during early lactation (NDVIrate) in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1981-95.

	Median NDVI		**Median NDVIrate**	
Year	Reference	Treatment	Reference	Treatment
1981	0.15	0.10	0.013	0.013
1985	0.17	0.13	0.002	0.002
1986	0.01	0.08	0.003	0
1987	0.03	0.02	0.011	0.008
1988	0.04	0.06	0.010	0.006
1989	0.02	0.08	0.010	0.001
1990	0.26	0.19	0.002	0
1991	0.02	0.07	0.010	0.007
1992	0.07	0.08	[a]	[a]
1993	0	0	0.011	0.006
1994	0.04	0.02	0.019	0.009
1995	0.03	0.07	0.012	0

[a] No data due to complete cloud cover

Percentage snow cover at calving also varied among years (Table 7). In 1985, 1990, 1992, and 1994, little snow was present (i.e., mostly <25%) in either zone. In 1986, 1988, and 1989, however, snow cover was extensive (i.e., mostly >75%) in both zones. Snow cover was correlated between zones across years ($r^2 = 0.803$, $P < 0.01$).

Percentages of rugged terrain were similar in REF (48.1%) and TRT (46.2%) zones. Most rugged terrain was located in southern sections of the calving ground.

Habitat Use/Selection

Distance from Roads

Caribou in the REF zone avoided ($P < 0.05$) the area within 4 km of roads during all periods. Caribou in the TRT zone selected ($P < 0.05$) the area within 4 km of roads during 1980-86, but avoided ($P < 0.05$) that area thereafter (Fig. 5).

Vegetation Types

In the REF zone, caribou selected ($P < 0.05$) wet graminoid vegetation during all periods and selected moist graminoid vegetation during 1983-92 (Table 8). In the TRT zone, caribou selected ($P < 0.05$) wet graminoid vegetation only in the first 2 periods and, thereafter, selected ($P < 0.05$) moist graminoid vegetation exclusively. Dry and moist shrub types were generally avoided in both zones.

Table 7. Percentage of area by snow cover class in reference and treatment zones of the calving ground, Central Arctic caribou herd, Alaska, 1981-95.

	% of Area by Snow Cover Class							
	0-24		**25-49**		**50-74**		**75-100**	
Year	Reference	Treatment	Reference	Treatment	Reference	Treatment	Reference	Treatment
1981	27.4	9.8	55.4	74.9	16.5	5.4	0.7	9.9
1985	100.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
1986	0.7	0.4	1.0	0.4	3.5	1.4	94.7	97.8
1987	42.0	13.8	18.8	13.0	21.2	44.9	18.0	28.4
1988	12.4	5.6	14.4	5.9	10.8	13.9	62.3	74.5
1989	2.0	2.8	3.4	4.4	9.3	8.4	85.3	84.5
1990	99.7	97.5	0.1	2.2	0.2	0.2	0.0	0.0
1991	16.1	0.2	21.1	5.3	38.9	31.3	24.0	63.2
1992	84.5	81.6	8.9	15.0	4.9	3.4	1.8	0.0
1993	20.9	22.4	17.1	15.3	32.1	34.0	29.9	28.3
1994	99.3	54.9	0.5	27.4	0.1	17.5	0.1	0.2
1995	27.8	15.1	24.7	11.1	27.0	22.9	20.5	50.9

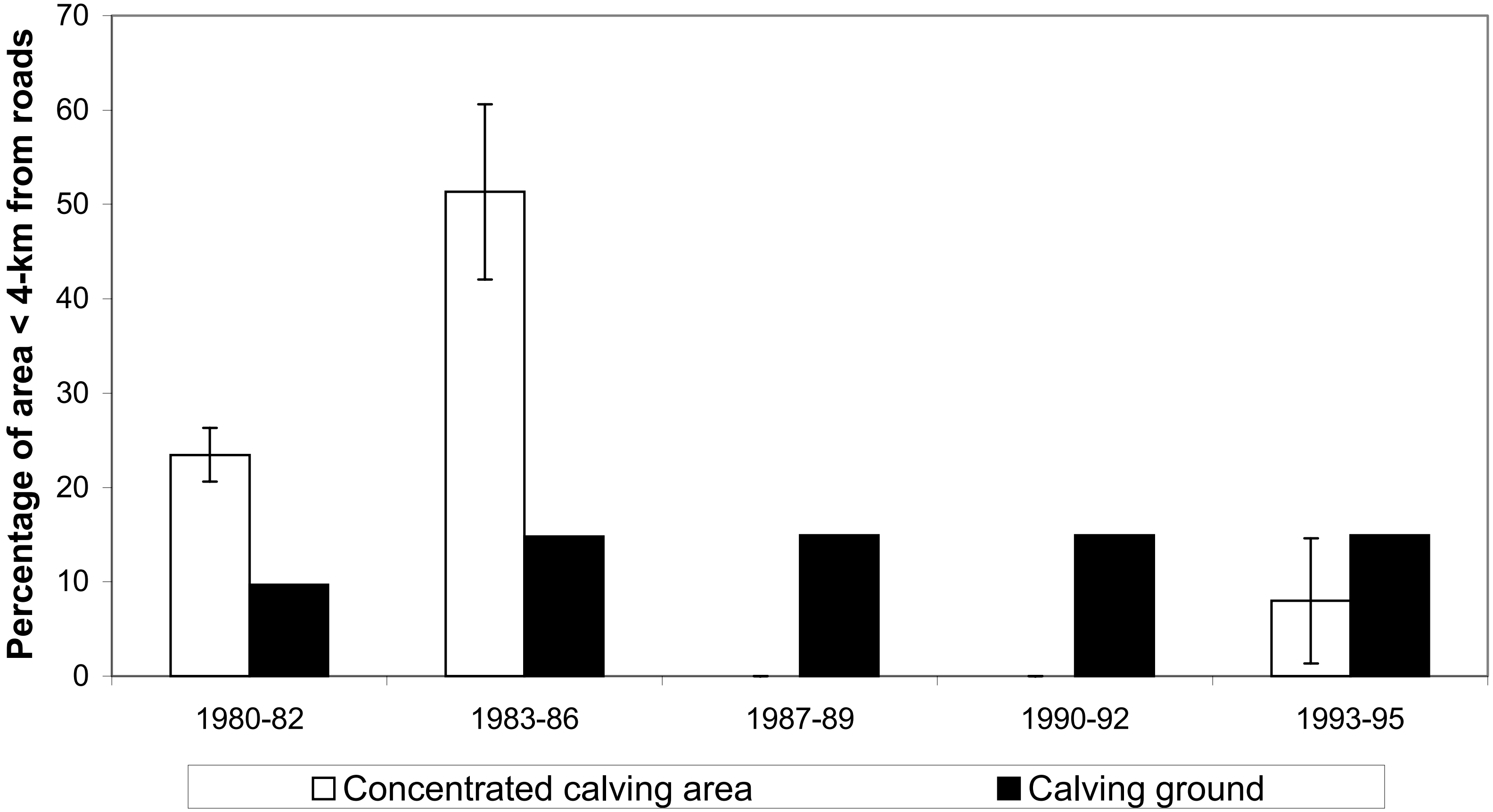

Figure 5. Percentage of concentrated calving areas in the treatment zone and in the entire calving ground within 4 km of roads that were constructed by 1981, 1987, and 1990, respectively, Central Arctic caribou herd, Alaska, 1980-95. Error bars depict 95% confidence intervals.

Table 8. Percentage of vegetation types within concentrated calving areas (use) in reference and treatment zones, and in the calving ground (available), Central Arctic caribou herd, Alaska, 1980-95.

			% Area				
Class	Period	Zone	Dshrub[a]	Mgram[b]	MShrub[c]	Lshrub[d]	Wgram[e]
Use	1980-82	Reference	3.2^{-}	35.3^{-}	0.1^{-}	0.0^{-}	61.4^{+}
		Treatment	6.7^{+}	51.5^{-}	0.5^{-}	0.5^{-}	40.8^{+}
Use	1983-86	Reference	1.3^{-}	59.7^{+}	0.9^{-}	0.8^{-}	37.3^{+}
		Treatment	7.8^{+}	43.7^{-}	0.2^{-}	0.1^{-}	48.2^{+}
Use	1987-89	Reference	1.6^{-}	65.5^{+}	1.4^{-}	1.4^{-}	30.1^{+}
		Treatment	1.1^{-}	75.0^{+}	0.1^{-}	0.0^{-}	23.8^{-}
Use	1990-92	Reference	4.0^{-}	61.1^{+}	0.9^{-}	1.8^{-}	32.2^{+}
		Treatment	0.6^{-}	73.9^{+}	0.1^{-}	0.0^{-}	25.4^{NS}
Use	1993-95	Reference	1.9^{-}	55.4^{NS}	0.3^{-}	0.2^{-}	42.2^{+}
		Treatment	1.0^{-}	77.4^{+}	0.1^{-}	0.0^{-}	21.5^{NS}
Available	1980-95	Calving Ground	4.6	55.6	6.0	8.8	25.0

[a] Dry Prostrate-shrub tundra and barrens

[b] Moist Graminoid, Prostrate-shrub Tundra (nonacidic)

[c] Moist Dwarf-shrub, Tussock-graminoid Tundra (typical tussock tundra)

[d] Moist Low-shrub Tundra and Other Shrublands

[e] Wet Graminoid Tundra

\+ Selection. Significantly greater than availability, $P < 0.05$.

\- Avoidance. Significantly less than availability, $P < 0.05$.

NS Not significantly different than availability, $P > 0.05$.

Relative Plant Biomass

Caribou in the REF zone avoided ($P < 0.05$) above-median NDVI slightly more than half of the time and selected it slightly less than half of the time (Fig. 6). In the TRT zone, above-median NDVI was avoided ($P < 0.05$) in all but two years (Fig. 6).

Caribou in the REF zone selected above-median NDVIrate more often ($P < 0.05$) than those in the TRT zone. Caribou selected ($P < 0.05$) above-median NDVIrate in 9 of 11 years in the REF zone, but in only 3 of 9 years in the TRT zone (Fig. 7).

Snow Cover

Snow cover was highly variable across the landscape among years. Caribou did not consistently select ($P < 0.05$) any particular class of snow cover in either zone, but there was a tendency to avoid snow cover classes <75% (Table 9).

Terrain Ruggedness

DTRI and TRI were correlated ($P < 0.0001$) (Fig. 8). The slope of the relationship did not differ from 1 ($P < 0.05$), nor did the intercept differ from 0 ($P < 0.05$). There was 86% agreement on classification of the 101 points as non-rugged or rugged. Incongruous classifications were equitably distributed on the off diagonal. Thus, DTRI and TRI were assumed to be equivalent.

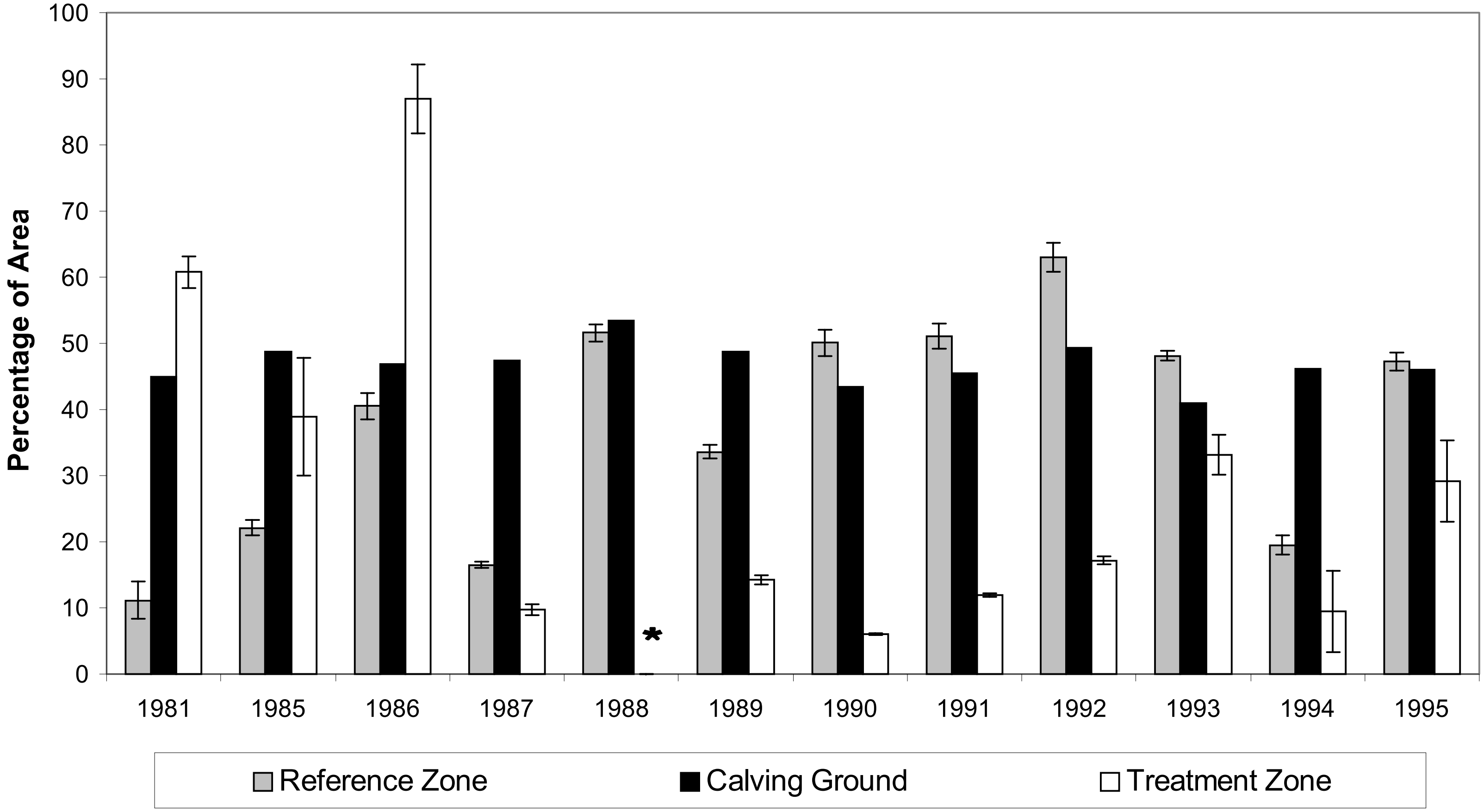

Figure 6. Percentage of area with above-median Normalized Difference Vegetation Index at calving (NDVI) within the calving ground and within concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1981-95. Error bars depict 95% confidence intervals. * denotes no data due to complete cloud cover.

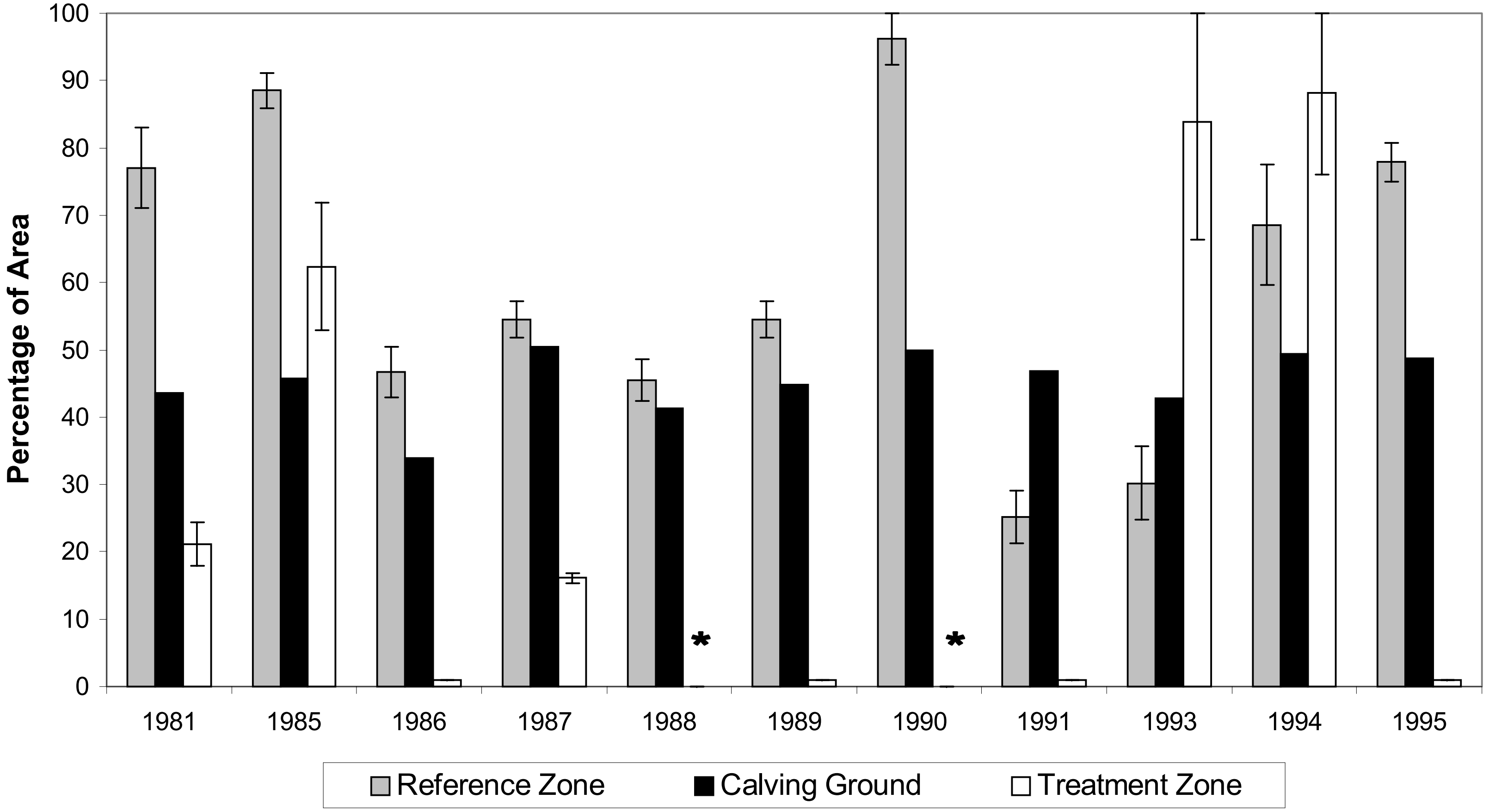

Figure 7. Percentage of area with above-median daily increase in Normalized Difference Vegetation Index during early lactation (NDVIrate) within the calving ground and within concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1981-95. Error bars depict 95% confidence intervals.
* denotes no data due to complete cloud cover.

Table 9. Percentage of area by snow cover class within concentrated calving areas (use) in reference and treatment zones, and in the calving ground (available), Central Arctic caribou herd, Alaska, 1981-95.

Snow		**Percentage of area**												#Years	#Years
Class	Zone	1981	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Selected	Avoided
0-24%	Reference	95+	100	0	4-	0-	0-	100	1-	95+	0-	100+	2-	3	6
	Treatment	46+	100	0	0-	[a]	[a]	100	0-	48-	6-	24-	0-	1	6
	Available	19	100	1	30	19	4	99	11	81	23	76	25		
25-49%	Reference	4-	0	0	43+	0-	0-	0	13	5-	0-	0-	4-	1	7
	Treatment	54	0	0	2-	[a]	[a]	0	0-	52+	7-	23+	0-	2	4
	Available	65	0	1	16	12	5	1	13	11	16	12	19		
50-74%	Reference	1-	0	0	32	0-	0-	0	50+	0-	5-	0-	31	1	6
	Treatment	0-	0	1	34+	[a]	[a]	0	0-	0-	12-	51+	2-	2	5
	Available	11	0	3	32	10	9	0	35	5	33	8	25		
75-100%	Reference	0-	0	100	22	100+	100+	0	36-	0-	95+	0-	63+	4	4
	Treatment	0-	0	99	64+	[a]	[a]	0	100+	0-	75+	2-	98+	4	3
	Available	5	0	96	22	59	83	0	41	3	28	4	31		

\+ Selection; use significantly greater than availability, $P < 0.05$.

\- Avoidance; use significantly less than availability, $P < 0.05$.

[a] Data missing, complete cloud cover.

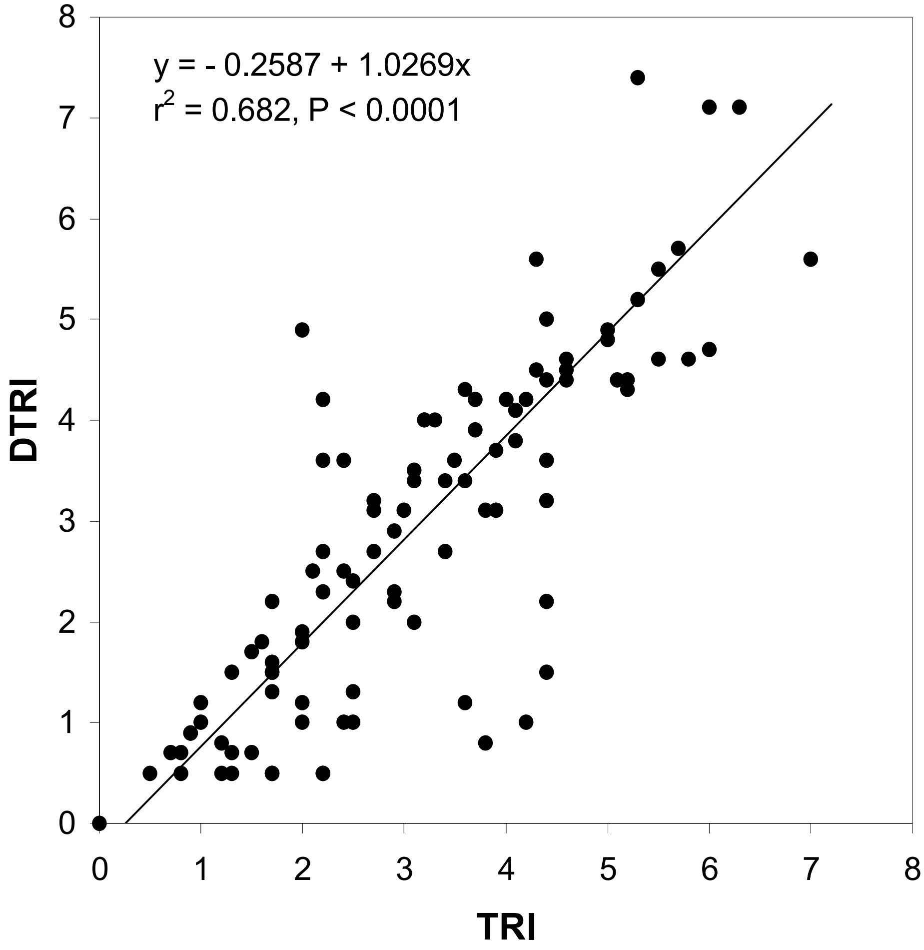

Figure 8. Relationship between Terrain Ruggedness Index (TRI, Nellemann and Thomsen 1994) calculated from 1:63,360 topographic maps and Digital Terrain Ruggedness Index (DTRI) calculated from 1:63,360 digital elevation models.

Patterns of selection of DTRI classes by caribou were nearly opposite in the two zones (Fig. 9). In the REF zone, rugged terrain was avoided ($P < 0.05$) during all periods. In the TRT zone, however, rugged terrain was selected ($P < 0.05$) except during the 1983-86 period.

Temporal Trends in Forage Availability

There was no relationship between NDVI621 and time for the REF zone ($r^2 = 0.047$, $P = 0.52$), TRT zone ($r^2 = 0.059$, $P = 0.47$), or entire calving ground ($r^2 = 0.032$, $P = 0.60$) (Fig. 10).

For the CCA’s within the REF zone, NDVI621 was relatively constant through time ($P = 0.23$, $r^2 = 0.007$) (Fig. 11). For the CCA’s within the TRT zone, however, NDVI621 declined significantly ($P < 0.0001$, $r^2 = 0.299$) (Fig. 12).

In the REF zone, NDVI621 in CCA's used during 1983-95 was substantially higher than in the CCA used during 1980-82 (Tables 10, 11). Differences in NDVI621 among REF zone CCA's, 1983-95, were relatively small. In contrast, in the TRT zone, NDVI621 in CCA's, 1980-86, was substantially higher than in CCA’s, 1987-95 (Table 10). Throughout the entire study period, NDVI621 for the 1980-82 CCA in the TRT zone was higher than that for any other CCA in the TRT zone (Table 11).

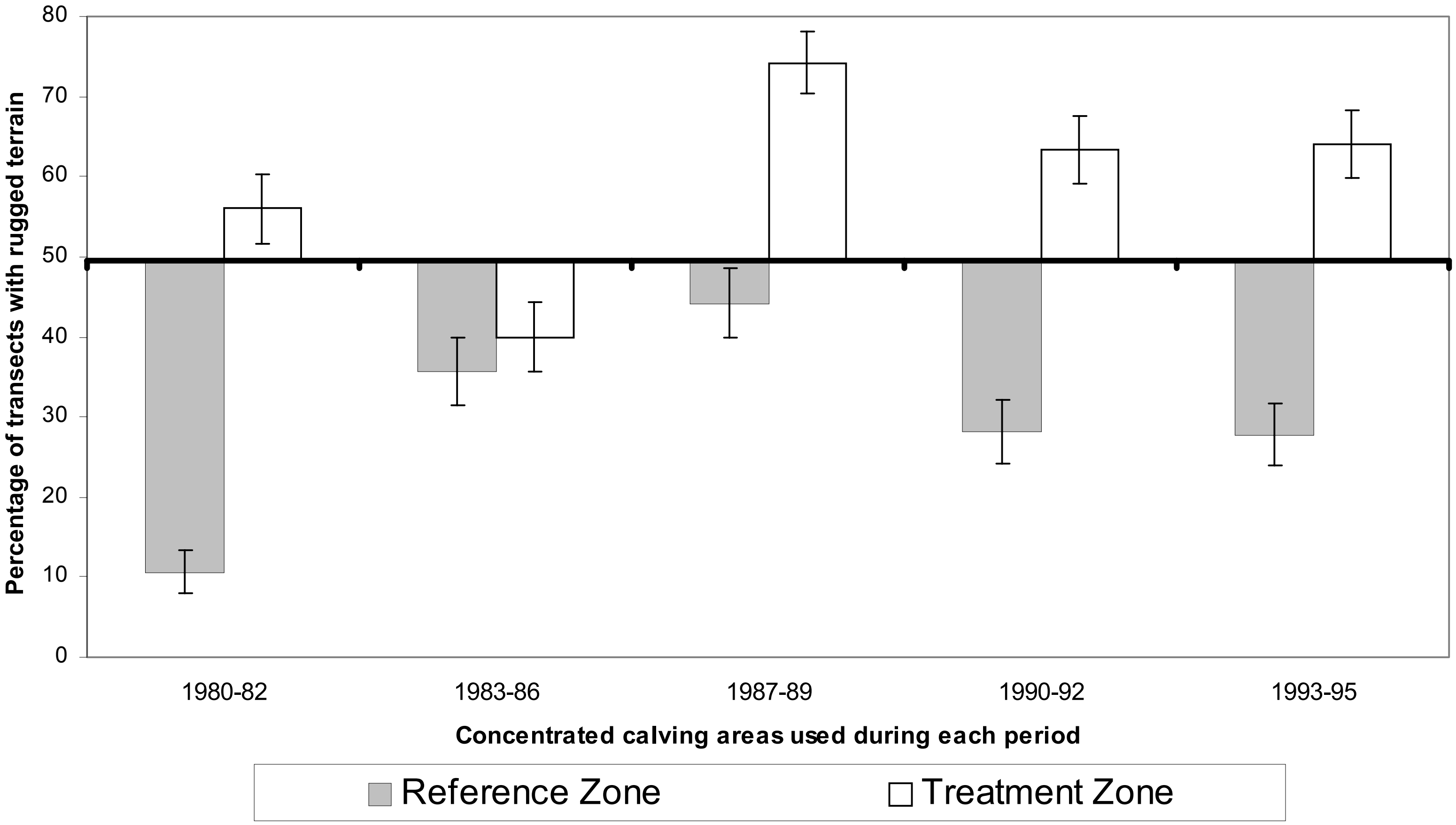

Figure 9. Percentage of randomly selected transects with rugged terrain (above-median Digital Terrain Ruggedness Index) within concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95. The horizontal line at 49.4% is the proportion of the calving ground with above-median DTRI. Error bars depict 95% confidence intervals.

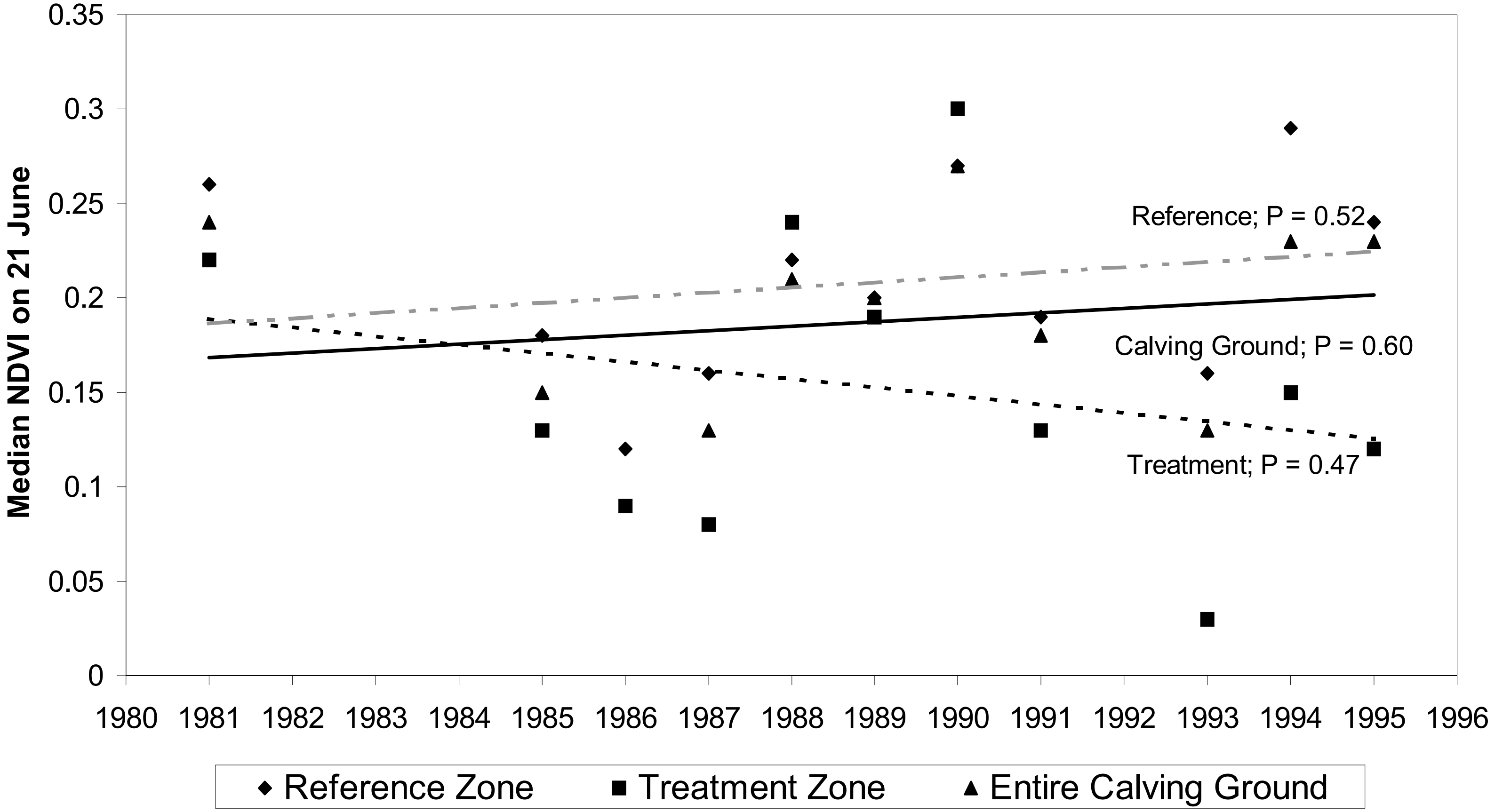

Figure 10. Median Normalized Difference Vegetation Index on 21 June by calving ground zone and in the entire calving ground, Central Arctic caribou herd, Alaska, 1980-95.

Figure 11. Median Normalized Difference Vegetation Index on 21 June in used concentrated calving areas of the reference zone, Central Arctic caribou herd, Alaska, 1980-95. Some data points represent several identical estimates derived from jackknife analyses.

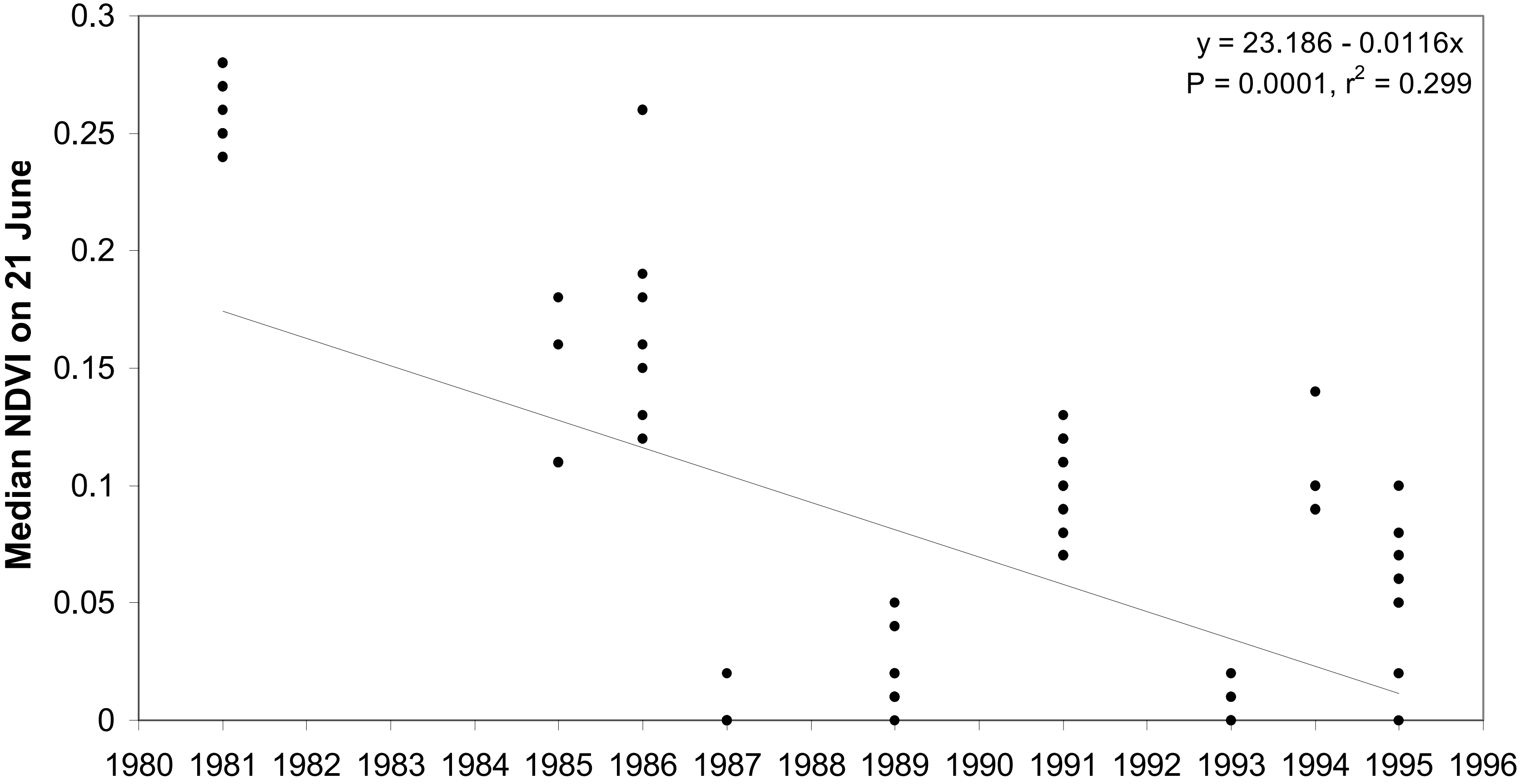

Figure 12. Median Normalized Difference Vegetation Index on 21 June in used concentrated calving areas of the treatment zone, Central Arctic caribou herd, Alaska, 1980-95. Some data points represent several identical estimates derived from jackknife analyses.

Table 10. Median Normalized Difference Vegetation Index on 21 June for concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95.

	Concentrated Calving Area				
	1980-82	1983-86	1987-89	1990-92	1993-95
	Median NDVI on 21 June				
Reference Zone	0.05	0.14	0.15	0.12	0.11
Treatment Zone	0.20	0.16	0.01	0.05	0.06

Median was calculated from jackknifed samples, pooled across years, 1981-95.

Table 11. Median Normalized Difference Vegetation Index on 21 June, each year, for concentrated calving areas in reference and treatment zones, Central Arctic caribou herd, Alaska, 1980-95.

		Concentrated Calving Area				
		1980-82	1983-86	1987-89	1990-92	1993-95
Year	Zone	Median NDVI on 21 June				
1981	Reference	0.17	0.22	0.22	0.25	0.20
1985	Reference	0.08	0.12	0.13	0.14	0.11
1986	Reference	0.03	0.04	0.04	0.10	0.05
1987	Reference	0.01	0.12	0.11	0.07	0.08
1988	Reference	0.04	0.06	0.13	0.11	0.13
1989	Reference	0.04	0.05	0.07	0.11	0.05
1990	Reference	0.17	0.21	0.22	0.25	0.20
1991	Reference	0.04	0.18	0.20	0.10	0.07
1992	Reference	[a]	[a]	[a]	[a]	[a]
1993	Reference	0.00	0.14	0.15	0.04	0.01
1994	Reference	0.09	0.24	0.23	0.16	0.12
1995	Reference	0.23	0.24	0.24	0.18	0.24
1981	Treatment	0.27	0.24	0.18	0.16	0.17
1985	Treatment	0.13	0.11	0.12	0.12	0.13
1986	Treatment	0.25	0.16	0.00	0.00	0.01
1987	Treatment	0.01	0.00	0.00	0.00	0.00
1988	Treatment	[a]	0.08	[a]	[a]	[a]
1989	Treatment	0.25	0.20	0.01	0.05	0.12
1990	Treatment	0.34	0.30	[a]	[a]	0.13
1991	Treatment	0.19	0.17	0.10	0.11	0.03
1992	Treatment	[a]	[a]	[a]	[a]	[a]
1993	Treatment	0.11	0.05	0.00	0.00	0.01
1994	Treatment	0.15	0.14	0.12	0.09	0.10
1995	Treatment	0.25	0.14	0.01	0.00	0.06

Median was calculated from jackknifed samples.

[a] No data due to complete cloud coverage

DISCUSSION

The calving sites of radio-collared female caribou used in this study were assumed to be an unbiased sample of the calving population. Rather than arbitrarily delineating the available area for habitat selection analyses, the distribution of this entire sample defined overall availability (Manly et al. 1993, McClean et al. 1998).

Forage availability, estimated as NDVI621, did not change through time in the calving ground or in either calving ground zone (Fig. 10), indicating the absence of a climate-warming signature. Using similar methods, however, Griffith et al. (1999, 2000) did detect such a signature in calving ground habitat of the Porcupine caribou herd. These and other results clearly show that plant growth is highly variable in arctic regions (Myneni et al. 1997, Myneni et al. 1998).

The two techniques used to evaluate terrain ruggedness in this study (DTRI, TRI) yielded equivalent point estimates. Computerized DTRI estimates and hand-calculated TRI's were highly correlated (Fig. 8), classification as rugged or non-rugged concurred in nearly all cases, and misclassifications were skewed in neither direction.

However, there were differences in sampling design between previous work using TRI and this study emphasizing DTRI. Nellemann and Cameron (1996), in an analysis of a portion of the calving ground > 10 km from surface development, obtained a positive relationship between caribou abundance and terrain ruggedness (TRI) during 1987-92, after concentrated calving in the TRT zone had shifted away from development. In the present study, the analysis was extended to include the entire calving ground during 1980-95, and that area was stratified into the two zones. As a result of these temporal and spatial modifications, the pattern of caribou use of rugged terrain became more refined: caribou in REF zone CCA's avoided rugged terrain, while those in TRT zone CCA's primarily selected rugged terrain (Fig. 9).

What remains uncertain is the value of rugged terrain to caribou. Nellemann and Thomsen (1994) regarded rugged terrain as superior foraging habitat based on prolonged availability of green plant tissue and increased cover of graminoids for study sites in the KDA (i.e., within the northern TRT zone); whereas in this study, selection of rugged terrain by caribou in the TRT zone CCA (Fig. 9) was associated with declining NDVI621 (Fig. 12), particularly from 1987 onward. However, the 1980-82 TRT zone CCA (Fig. 3a) was relatively rugged (Fig. 9), continually had high NDVI621 (Tables 10, 11), and overlapped the study area used by Nellemann and Thomsen (1994). Most importantly, Nellemann and Thomsen's sample (1994) did not include inland rugged terrain that was within the TRT zone CCA during 1987-92. At this point the relationship between DTRI and NDVI621 is unclear. However, NDVI621 does appear to be a good indicator of habitat quality owing to a strong correlation between June calf survival and NDVI621 in the calving ground of the adjacent, undisturbed, Porcupine caribou herd (Griffith unpublished). More work remains to be done on relationships between forage quantity, forage quality, NDVI621, and DTRI.

The location of concentrated calving varied in both REF and TRT zones (Figs. 3a - 3e). Moreover, sequential shifts in CCA's were detected at the same frequency in both zones (Table 4). These results emphasize that calving distributions are not static on a local scale, even though caribou consistently calve in the same general area (Skoog 1968).

The spatial patterns of these shifts, however, differed between the two zones. In the REF zone, direction of shifts was random, whereas in the TRT zone, shifts were significantly directional (south, southwest) (Figs. 3a - 3e). When roads were extended to Milne and Oliktok points during the 1980-82 and 1983-86 periods (Figs. 3a - 3b), CCA's shifted farther than during any other period in either zone (Fig. 4). Thereafter, CCA's in the TRT zone remained inland (Fig. 3c - 3e).

These data are consistent with other authors' suggestions that calving CAH caribou avoided areas beyond the physical presence of surface development (Whitten and Cameron 1983a, Whitten and Cameron 1985, Dau and Cameron 1986, Lawhead 1988, Cameron et al. 1992, Nellemann and Cameron 1998). Although roads, pipelines, and other facilities comprised <2% of the area in the PBC and KDA (Jorgenson and Joyce 1994), the 4-km avoidance zone eventually encompassed 29% of the TRT zone. Thus, observed shifts in calving distribution were ostensibly occurring in response to increasing surface development, even though caribou did not entirely abandon the KDA (Lawhead 1988, Cameron et al. 1992).

Consistent selection of high NDVIrate by caribou in the REF zone suggests that the non-directional shifts in concentrated calving were in response to spatial variation of high-quality forage. Similarly, calving caribou of the nearby Porcupine herd selected high NDVIrate in 9 of 10 years (Griffith et al. 2000). Areas with high NDVIrate should contain rapid-growing forage, which is readily digestible and high in nutrients (Chapin et al. 1980, Kuropat and Bryant 1982, Van Soest 1983). In fact, the distribution of caribou has been correlated with availability of easily digestible forage (White et al. 1975, Kuropat 1984, White et al. 1989), which is directly related to body condition and, hence, reproductive performance (Reimers 1983, Rognmo et al. 1983, White 1983, Skogland 1984, White 1992, Cameron et al. 1993, Crete and Huot 1993, Cameron 1994, Cameron and Ver Hoef 1994, Chan-Mcleod et al. 1994, Gerhart 1995, Griffith et al. 2000, Russell et al. 1998).

Use of areas with high-quality forage is also consistent with nutritional requirements after calving. During early lactation, body fat and protein reserves are lowest (Adamczewski et al. 1987, Allaye-Chan 1991, Gerhart 1995, Gerhart et al. 1996) and metabolic demands are highest (White et al. 1975, Robbins et al. 1981, White et al. 1981, Sadlier 1984, Robbins 1993, Russell et al. 1993). By selecting areas with an abundance of easily digestible forage, maternal caribou likely maximize nutrient intake (White and Trudell 1980, Trudell and White 1981, Kuropat 1984, White 1992), thereby minimizing use of body reserves (Cameron and Luick 1972, Skogland 1984, Allaye-Chan 1991, Gerhart 1995, Gerhart et al. 1996) while sustaining milk production (Loudon and Milne 1985, White and Luick 1984, Parker et al. 1990, Chan-Mcleod et al. 1994, Russell et al. 1998, Russell and White 1998). Milk intake by calves is directly related to their growth and survival (Haukioja and Salovaara 1978, Rognmo et al. 1983, Loudon and Kay 1984, White and Luick 1984, Loudon and Milne 1985, Parker et al. 1990, White 1992, Crete and Huot 1993).

In contrast, shifts in CCA's within the TRT zone could not be attributed to selection of more favorable habitats. During all periods, inland CCA's (i.e., those used during 1987-95) contained less green plant biomass at peak lactation than the coastal CCA's (i.e., those used during 1980-86), even after caribou had shifted inland (Tables 10, 11). Although NDVI621 in the REF zone CCA showed no temporal trend (Fig. 11), matching the zonal pattern (Fig. 10), NDVI621 in the TRT zone CCA's declined through time (Fig. 12). Thus, concentrated calving in the TRT zone progressively shifted to habitats with less green plant biomass at peak lactation. In addition, predation risk may have been higher in the inland habitats because of closer proximity to foothills where wolf and bear densities are purportedly higher than in the coastal habitats (Campbell 1960, Stephenson 1979, Reynolds 1979, Young et al. 1992, Young and McCabe 1998, Shideler pers. comm.).

Repeated use of the inland habitats in the TRT zone could have had nutritional and reproductive consequences if nutritional requirements of calving females were not met. Lower availability of easily digestible forage might have reduced forage intake (White et al. 1975, Trudell and White 1981, Robbins 1993), overall diet quality (White 1983, Robbins 1993), summer weight gain (White 1992, Cameron et al. 1993, Russell et al. 1998), body condition (Gerhart 1995, Gerhart et al. 1996), parturition rate (Cameron 1994, Cameron and Ver Hoef 1994), milk production (White and Luick 1984, Loudon and Milne 1985, Parker et al. 1990, Chan-McLeod 1994), and calf growth and survival (Rognmo et al. 1983, Skogland 1984, Cameron et al. 1988, Lenvik et al. 1988, Griffith et al. 2000). Other possible effects include early weaning and mortality (Clutton-Brock et al. 1983, White 1992, Russell et al. 1998), prolonged lactation (Trivers 1974, White and Luick 1984, Gerhart 1995, Russell et al. 1998), and delayed sexual maturity (Leader-Williams and Rosser 1983, Tyler 1987, Langvatn 1994, Langvatn et al. 1996). Early hypotheses on the nutritional ecology of CAH caribou suggested that use of inland ranges adjacent to the coastal plain were necessary to balance annual energy budgets and ensure consistent reproduction (White et al. 1975).

Nevertheless, the actual consequences of shifts to inland areas are somewhat uncertain. Long-term datasets of nutritional status of individual caribou are lacking for REF and TRT zones. Cameron (1995) reported lower parturition rates among females west of the Sagavanirktok River after 1986 when

CCA's in the TRT zone had shifted inland, suggesting that inland habitats may not have met the nutritional requirements of calving females. Parturition and calf:cow ratios, 1994-99 (ADFG, unpublished), did not differ ($P > 0.05$) between REF and TRT zones. However, estimates of calving distribution were not made after 1995, making interpretation of these data, 1996-99, ambiguous.

Arctic caribou herds commonly fluctuate in size over long-periods, but the causes of population fluctuations are difficult to measure. Population trajectories can be influenced by variations in forage (Russell et al. 1993, Crete and Hout 1993, Ouellet et al. 1996, Griffith et al. 1999), weather (Gates et al. 1986, Crete and Payette 1990, Caughley and Gunn 1993), population density (Skogland 1990, Ouellet et al. 1996, Crete et al. 1996), predator abundance (Bergerud 1980, Bergerud and Elliot 1986, Bergerud 1996), human harvest (Williams and Heard 1986, Ouellet et al. 1996), accident rates (Klein 1991), disease (Whitten 1996) and parasite prevalence. Unfortunately, much of these long-term data for the CAH region are incomplete.

The probabilities of detecting effects of industrial development on population trajectories and demographic parameters are perhaps lower for the CAH than for other arctic caribou herds if exposed to similar intensities of development. Compared to other arctic caribou herds in North America (e.g., Porcupine, Bathurst), population size of the CAH is small in relation to calving ground size and, hence, absolute caribou density is considerably lower (Bergerud 1996, Griffith pers. comm.). Thus, intraspecific competition for forage during calving may be lower for CAH caribou, making expression and detection of density dependent resource-limitation less likely (McCullough 1979, Clutton-Brock et al. 1982, Skogland 1985, Skogland 1989, Skogland 1990). Thus, the CAH, if below carrying capacity, may be less affected by shifts to areas with less forage than other herds near carrying capacity.

These results suggest that concentrated calving in the TRT zone shifted well beyond the spatial extent of surface development, resulting in use of lower-quality habitats and variability in habitat selection patterns. Disturbance associated effects at the population-level could have been obscured by the rapid growth rate of the herd, low proportion of the herd that was exposed to disturbance (i.e., only about 25% of the calving population shifted to areas with less green plant biomass during lactation), relatively low animal density, favorable environmental conditions, low adult mortality rates, high inter-annual variability in forage quality, and nutritional influences during other times of the year. Thus, future research should attempt to separate cumulative effects of disturbance from natural influences on demographic parameters. Specifically, studies that quantify the annual summation of energetic costs/benefits of exposure to human disturbance will be particularly valuable for developing models to predict cumulative effects of disturbance on survival, weight gain, and parturition rate.

Our ability to predict nutritional consequences of shifts to inland habitats is limited by an unknown relationship between habitat quality and the nutritional requirements of calving caribou. Thorough investigations should be conducted to estimate whether forage in inland habitats meets nutritional requirements. In addition, NDVI621 should be field validated in relation to the quantity and quality of important plant species in the coastal versus inland habitats during multiple years. Studies that relate NDVI621 to forage intake rates, weight gain, body condition, parturition rate, and calf growth and survival would increase our ability to predict nutritional, reproductive, and population-level consequences.

In summary, although these data suggest that CAH caribou in the TRT zone shifted to areas with less green plant biomass during lactation, more research is needed before possible population consequences can be identified, understood, and predicted.

LITERATURE CITED

Adamczewski, J. Z., C. C. Gates, R. J. Hudson, and M. A. Price. 1987. Seasonal changes in body condition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an Arctic island with limited winter resources. Canadian Journal of Zoology 65:1149-1157.

Allaye-Chan, A. C. 1991. Physiological and ecological determinants of nutrient partitioning in caribou and reindeer. Ph. D. Dissertation. University of Alaska Fairbanks. 135 pp.

Alldredge, J. R. and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157-165.

_____ and _____. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1-9.

Arnold, G. W. and R. A. Maller. 1984. An analysis of factors influencing spatial distribution in flocks of grazing sheep. Applied Animal Behaviour Science 14:173-189.

Asrar, G., M. Fuchs, E. T. Kanemasu, and J. L. Hatfield. 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. Agron Journal 76:300-306.

Auerbach, N., D. A. Walker, M. D. Walker, A. Hope, and D. Stow. 1992. Landscape-scale vegetation production on glaciated surfaces of different ages in the Arctic Foothills, Alaska. Bulletin of the Ecological Society of America 73:100.

Baglio, J. V., and E. W. Holroyd, III. 1989. Methods for operational snow cover area mapping using the advanced very high resolution radiometer - San Juan Mountain test study. Research Technical Report, United States Geological Survey, EROS Data Center, Sioux Falls, South Dakota. 81 pp.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Washington D. C.

Batzli, G. O., R. G. White, S. F. MacLean, Jr., F. A. Pitelka and B. D. Collier. 1980. The herbivore-based trophic system. Pages 335-410 *in* J. Brown, P. C. Miller, L. L. Tieszen and F. L. Bunnell, editors. An Arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania. 571 pp.

_____, _____, and F. L. Bunnell. 1981. Herbivory: a strategy of tundra consumers. Pages *in* L. C. Bliss, O. W. Heal and J. J. Moore, editors. Tundra ecosystems: a comparative analysis. IBP Vol. 25, Cambridge University Press, Cambridge. 813 pp.

Bergerud, A. T. 1974. The role of the environment in the aggregation, movement, and disturbance behaviour of caribou. Pages 552-582 *in* V. Geist and F. Walther, editors. The Behaviour of ungulates and its relation to management, IUCN New Series 24, Vol. 2.

_____. 1980. A review of the population dynamics of caribou and wild reindeer in North America. Pages 556-581 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second Reindeer/Caribou Symposium, Roros, Norway, September 17-21, 1979.

_____ and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology 64:1515-1529.

_____ and R. E. Page. 1987. Displacement and dispersion of parturient caribou as antipredator tactics. Canadian Journal of Zoology 65:1597-1606.

_____. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer Special Issue 9:95-115.

Brown, J., K. R. Everett, P. J. Webber, S. F. MacLean Jr., and D. F. Murray. 1980. The Coastal Tundra at Barrow. Pages 1-29 *in* J. Brown, P. C. Miller, L. L. Tieszen and F. L. Bunnell, editors. An Arctic ecosystem: the coastal tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania. 571 pp.

Cameron, R. D. and J. R. Luick. 1972. Seasonal changes in total body water, extracellular fluids, and blood volume in grazing reindeer. Canadian Journal of Zoology 50:107-116.

_____ and K. R. Whitten. 1979. Seasonal movements and sexual segregation of caribou determined by aerial survey. Journal of Wildlife Management 43:626-633.

_____ and _____. 1980. Nutrient dynamics of caribou forage on Alaska's Arctic Slope. Pages 159-166 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/Caribou Symposium, Roros, Norway, September 17-21, 1979.

_____. 1983. Issue: caribou and petroleum development in Arctic Alaska. Arctic 36:227-231.

_____, W. T. Smith, and R. T. Shideler. 1988. Variations in initial calf production of the Central Arctic caribou herd. Pages 1-7 *in* R. D. Cameron and J. L. Davis, editors. Reproduction and Calf Survival. Proceedings of the Third North American Caribou Workshop, Chena Hot Springs, Alaska, 4-6 November 1987. Alaska Department Fish and Game, Wildlife Technical Bulletin 8. 229 pp.

_____, D. J. Reed, J. R. Dau, and W. T. Smith. 1992. Redistribution of caribou in response to oil field developments on the Arctic Slope of Alaska. Arctic 45:338-342.

_____, W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480-486.

_____. 1994. Reproductive pauses by female caribou. Journal of Mammalogy 75:10-13.

_____ and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58:674-679.

_____. 1995. Can petroleum development depress the productivity of arctic caribou? Second International Arctic Ungulate Conference, 13-17 August 1995, Fairbanks, Alaska. (Abstract).

_____ and J. Ver Hoef. 1996. Declining abundance of calving caribou in an Arctic oil-field complex. Paper presented at the Northwest Section Meeting, The Wildlife Society, Banff, Alberta, 29-31 March, 1996. (Abstract).

_____ and B. Griffith. 1997. Detecting shifts in the distribution of calving caribou. Paper presented at the Fourth Annual Conference of the Wildlife Society, Snowmass, Colorado, 22-27 September 1997. (Abstract).

Campbell, J. M. 1960. Nesting of the golden eagle in the central Brooks Range of Arctic Alaska. Condor 62:298.

Caughley, G. and A. Gunn. 1993. Dynamics of large herbivores in deserts: kangaroos and caribou. Oikos 67:47-55.

Chan-McLeod, A. C. A., R. G. White and D. F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Canadian Journal of Zoology 72:938-947.

Chapin, F. S., III, D. A. Johnson, and J. D. McKendrick. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. Journal of Ecology 68:189-209.

Child, K. N. 1973. The reactions of barren-ground caribou (*Rangifer tarandus granti)* to simulated pipeline and pipeline crossing structures at Prudhoe Bay, Alaska. Completion Report to Alyeska Pipeline Service Company, Alaska Cooperative Wildlife Research Unit, University of Alaska Fairbanks. 50pp.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University Chicago Press, Chicago. 378 pp.

_____, _____, and _____. 1983. The costs of reproduction to Red deer hinds. Journal of Animal Ecology 52:367-383.

Colwell, J. E. 1973. Bidirectional spectral reflectance of grass canopies for determination of above ground standing biomass. Ph. D. Dissertation, University of Michigan, Ann Arbor.

Couturier, S., J. Brunelle, D. Vandal, and G. St-Martin. 1990. Changes in the population dynamics of the George River Caribou Herd 1976-87. Arctic 43:9-20.

Crete, M. and S. Payette. 1990. Climatic changes and caribou abundance in northern Quebec over the last century. Rangifer Special Issue 3:159-165.

_____ and J. Hout. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 71:2291-2296.

_____, S. Couturier, B. J. Hearn, and T. E. Chubbs. 1996. Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Riviere George Caribou Herd. Rangifer Special Issue 9:27-36.

Dau, J. R. and R. D. Cameron. 1986. Effects of a road system on caribou distribution during calving. Rangifer Special Issue 1:95-101.

De Vos, A. 1960. Behavior of barren-ground caribou on their calving grounds. Journal of Wildlife Management 24:250-258.

Eastland, W. G., R. T. Bowyer, and S. G. Fancy. 1989. Effects of snow cover on selection of calving sites by caribou. Journal of Mammalogy 70:824-828.

Efron, B. 1979. Bootstrap methods: another look at the jackknife. The Annals of Statistics 7:1-26.

_____. 1982. The jackknife, the bootstrap and other resampling plans. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania.

_____ and R. J. Tibshirani. 1993. An introduction to the bootstrap. Monographs on Statistics and Applied Probability. Chapman & Hall, New York.

ESRI. 1998. Understanding GIS: the ARC/INFO method (for UNIX and Windows NT). Environmental Systems Research Institute, Incorporated, Redlands, CA. 525 pp.

Fancy, S. G. 1983. Movements and activity budgets of caribou near oil drilling sites in the Sagavanirktok River floodplain, Alaska. Arctic 36:193-197.

_____, L. F. Pank, K. R. Whitten, and W. L. Regelin. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology 67:644-650.

_____ and K. R. Whitten. 1991. Selection of calving sites by the Porcupine caribou herd. Canadian Journal of Zoology 69:1736-1743.

Folstad, I., A. C. Nilssen, O. Halvorsen, and J. Andersen. 1991. Parasite avoidance: the cause of post-calving migrations in Rangifer? Canadian Journal of Zoology 69:2423-2429.

Gates, C. C., J. Adamczewski, and R. Mulders. 1986. Population dynamics, winter ecology and social organization of Coats Island caribou. Arctic 39:216-222.

Gerhart, K. L. 1995. Nutritional and ecological determinants of growth and reproduction in caribou. Ph. D. Dissertation. University of Alaska Fairbanks. 147 pp.

_____, R. G. White, R. D. Cameron, and D. E. Russell. 1996. Body composition and nutrient reserves of arctic caribou. Canadian Journal of Zoology 74:136-146.

Griffith, B., and D. E. Russell. 1999. Herd-specific predictive models that integrate effects of climate and development on caribou as a subsistence resource for Arctic communities. Poster presented at the Tenth Arctic Ungulate Conference, Tromso, Norway, 9-12 August 1999.

_____, D. C. Douglas, D. E. Russell, R. G. White, T. R. McCabe, and K. R. Whitten. 2000. Effects of recent climate warming on caribou habitat and calf survival: implications for management. Rangifer Special Issue 12:3. (abstract).

Haila, Y., Nicholls, A. O., Hanski, I. K., and Raivio, S. 1996. Stochasticity in bird habitat selection: year-to-year changes in territory locations in a boreal forest bird assemblage. Oikos 76:536-552.

Hansen, B. U. 1991. Monitoring natural vegetation in southern Greenland using NOAA AVHRR and field measurements. Arctic 44:94-101.

Harrison, A. R. and R. M. Lucas. 1989. Multi-spectral classification of snow using NOAA AVHRR imagery. International Journal of Remote Sensing 10:907-916.

Haukioja, E. and R. Salovaara. 1978. Summer weight of reindeer (*Rangifer tarandus*) calves and its importance for their future survival. Republic Kevo Subarctic Research Station 14:1-4.

Hope, A. S., J. S. Kimball, and D. A. Stow. 1993. The relationship between tussock tundra spectral reflectance properties and biomass and vegetation composition. International Journal of Remote Sensing 14:1861-1874.

Howery, L. D., Provenza, F. D., Banner, R. E., and Scott, C. B. 1996. Differences in home range and habitat use among individuals in a cattle herd. Applied Animal Behaviour Science 49:305-320.

_____, _____, _____, _____. 1998. Social and environmental factors influence cattle distribution on rangeland. Applied Animal Behaviour Science 55:231-244.

Jensen, J. R. 1996. Introductory digital image processing: a remote sensing perspective. Prentice Hall, Englewood Cliffs, New Jersey. 316 pp.

Jingfors, K, A. Gunn, and F. L. Miller. 1983. Caribou disturbance research on the Beverly calving grounds, Northwest Territories, Canada. Acta Zoologica Fennica 175:127-128.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Jorgenson, M. T. and M. R. Joyce. 1994. Six strategies for rehabilitating land disturbed by oil development in arctic Alaska. Arctic 47:374-390.

Kaufman, Y. J. and B. N. Holben. 1993. Calibration of the AVHRR visible and near-IR bands by atmospheric scattering, ocean glint, and desert reflection. International Journal of Remote Sensing 14:21-52.

Kennedy, P. J. 1989. Monitoring the phenology of Tunisian grazing lands. International Journal of Remote Sensing 10:835-845.

Kidwell, K. B. 1997. NOAA polar orbiter data users guide. National Climatic Data Center, Data Service Division, Washington D. C.

Klein, D. R. and Kuzyakin, V. 1982. Distribution and Status of Wild Reindeer in the Soviet Union. Journal of Wildlife Management 46:728-733.

Klein, D. R. 1991. Caribou in the changing north. Applied Animal Behaviour Science 29:279-291.

Kuropat, P. and Bryant, J. P. 1982. Digestibility of caribou summer forage in Arctic Alaska in relation to nutrient, fiber, and phenolic constituents. Acta Zoological Fennica 175:51-52.

_____. 1984. Foraging behavior of caribou on a calving ground in northwestern Alaska. M. S. thesis. University of Alaska Fairbanks. 95 pp.

Langvatn, R. 1994. Climate-associated variation in the resource base for red deer (*Cervus elaphus*), - relationships to body size and reproductive performance within and between cohorts. Ph. D. Dissertation. University of Norway, Oslo.

_____, S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653-670.

Lawhead, B.E. 1988. Distribution and movements of Central Arctic Herd caribou during the calving and insect seasons. Proceedings of the Third North American Caribou Workshop. Alaska Department of Fish and Game. Wildlife Technical Bulletin 8:8-13.

Leader-Williams, N., and A. M. Rosser. 1983. Ovarian characteristics and reproductive performance of reindeer, *Rangifer tarandus*. Journal of Reproductive Fertility 67:247-256.

Lent, P.C. 1980. Synoptic snowmelt patterns in Arctic Alaska in relation to caribou habitat use. Pages 71-77 in Reimers, E., E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/Caribou Symposium, Roros, Norway, September 17-21, 1979.

Lenvik, D., E. Bo, A. Fjellheim. 1988. Relationship between the weight of reindeer calves in autumn and their mother's age and weight in the previous spring. Rangifer 8:20-24.

Lillesand, T. M. and R. W. Kiefer. 1994. Remote sensing and image interpretation. Wiley and Sons, New York. 750 pp.

Loudon, A. S. I. and R. N. B. Kay. 1984. Lactational constraints on a seasonally breeding mammal: the red deer. Symposium Zoological Society London 51:233-252.

_____ and J. A. Milne. 1985. Nutrition and growth of young red deer. Biology of deer production, Royal Society New Zealand, Bulletin 22:423-427.

Lloyd, D. 1989. A phenological description of Iberian vegetation using short wave vegetation index imagery. International Journal of Remote Sensing 10:827-833.

Maling, D. H. 1973. Coordinate systems and map projections. George Philip and Son, Ltd. London. 255 pp.

Manly, B. F., L. L. McDonald, D. L. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London, New York. 163 pp.

_____. 1997. Randomization, bootstrap and monte carlo methods in biology. Chapman & Hall, London, New York. 399 pp.

Markon, C. J, M. D. Fleming, and E. F. Binnian. 1995. Characteristics of vegetation phenology over the Alaskan landscape using AVHRR time-series data. Polar Record 31:179-190.

McClean, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62:793-801.

McCullough, D. R. 1979. George reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor. 271 pp.

McDonald, L. L., D. J. Reed, and W. Erickson. 1991. Analysis procedures for habitat and food selection studies. Pages 429-474 *in* C. E. Butler and S.P. Mahoney, editors. Proceedings of the Fourth North American Caribou Workshop. St. Johns, Newfoundland.

Mielke, P. W. and K. J. Berry. 1982. An extended class of permutation techniques for matched pairs. Communications in Statistics. A. Theory and Methods 11:1197-1207.

Muller, S. V., D. A. Walker, F. E. Nelson, N. A. Auerbach, J. G. Bockheim, S. Guyer, and D. Sherba, 1998. Accuracy assessment of a land-cover map of the Kuparuk River basin, Alaska: considerations for remote regions. Photogrammetric Engineering and Remote Sensing 64:619-628.

_____, A. E. Racoviteanu, and D. A. Walker. 1999. Landsat-MSS derived land-cover map of northern Alaska: extrapolation methods and a comparison with photo-interpreted and AVHRR-derived maps. International Journal of Remote Sensing 20:2921-2946.

Myneni, R. B., C. D. Keeling, C. J. Tucker, A. Asrar, and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698-702.

_____, C.J. Tucker, G. Asrar, and D.S. Kimes. 1998. Interannual variations in satellite-based vegetation index data from 1981 to 1991. Journal of Geophysical Research 103:6145-6160.

Nellemann, C. and M. G. Thomsen. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the Arctic Coastal Plain, Alaska. Arctic 47:361-367.

_____ and R.D. Cameron. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49:23-28.

_____. 1997. Range ecology of the Arctic ungulates during winter and spring: relations to terrain structure and anthropogenic disturbance. Ph. D. Thesis. University of Norway, Oslo.

_____and _____. 1998. Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. Canadian Journal of Zoology 76:1425-1430.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. R. R. Donnelley and Sons Company, Boston, Massachusetts. 1,181 pp.

O'Rourke, J. 1998. Computational geometry in C. Second Edition, Cambridge University Press, New York. 392 pp.

Ouellet, J-P., D. C. Heard, and R. Mulders. 1996. Population ecology of caribou populations without predators: Southampton and Coats Island herds. Rangifer Special Issue 9:17-25.

Parker, K. L., R. G. White, M. P. Gillingham, and D. F. Holleman. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. Canadian Journal of Zoology 68:106-114.

Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, and I. C. Burke. 1997. ANPP estimates from NDVI for the central grassland region of the United States. Ecology 78:953-958.

Reimers, E. 1983. Reproduction in wild reindeer in Norway. Canadian Journal of Zoology 61:211-217.

Reynolds, H. V. 1979. Population biology, movements, distribution, and habitat utilization of a grizzly bear population in NPR-A. Pages 129-182 *in* P. C. Lent, editor. Studies of selected wildlife and fish and their use of habitats on and adjacent to NPR-A, Vol. 1, 1977-1978. U.S. Department Interior, Anchorage.

Robbins, C. T., R. S. Podbielancik-Norman, D. L. Wilson, and E. D. Mould. 1981. Growth and nutrient composition of elk calves compared to other ungulate species. Journal of Wildlife Management 45:172-186.

_____. 1993. Wildlife feeding and nutrition. Second edition, Academic Press, San Diego, California. 352 pp.

Roby, D. D. 1978. Behavioral patterns of barren-ground caribou of the Central Arctic herd adjacent to the Trans-Alaska Oil Pipeline. M.S. Thesis, University Alaska, Fairbanks. 200 pp.

Rocke, D. M. and G. W. Downs. 1981. Estimating the variances of robust estimators of location: influence curve, jackknife and bootstrap. Communications in Statistics. B. Simulation and Computation 10:221-248.

Rognmo, A., K. A. Markussen, E. Jacobsen, H. J. Grav, and A. S. Blix. 1983. Effects of improved nutrition in pregnant reindeer on milk quality, calf birth weight, growth, and mortality. Rangifer 3:10-18.

Rouse, J. W., R. H. Haas, J. A. Schell, and D. W. Deering. 1973. Monitoring vegetation systems in the great plains with ERTS. NASA (SP-351) 1:309-317. Third ERTS Symposium, Greenbelt, Maryland.

Running, S. W., R. R. Nemani, D. L. Peterson, L. E. Band, D. F. Potts, L. L. Pierce, and M. A. Spanner. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation. Ecology 70:1090-1101.

Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993. Range ecology of the Porcupine Caribou Herd in Canada. Rangifer Special Issue 8. 167pp.

_____, R. D. Cameron, R. G. White and K. L.Gerhart. 1998. Mechanisms of summer weight gain in northern caribou herds. Proceedings of the Eighth North American Caribou Workshop, 23-25 April 1998. Whitehorse, Canada.

_____ and R.G. White. 1998. Surviving in the north - a conceptual model of reproductive strategies in arctic caribou. Proceedings of the Eighth North American Caribou Workshop, 23-25 April 1998. Whitehorse, Canada.

Sadlier, R.M.F.S. 1984. Ecological consequences of lactation. Acta Zoological Fennica 171:179-182.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26:95-100.

Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. Journal of Wildlife Management 58:367-374.

Shannon, C. E. and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana. 117 pp.

Shideler, R. T. 1986. Impacts of human developments and land use on caribou: a literature review. Vol. II. Impacts of oil and gas development on the Central Arctic Herd. Alaska Department Fish & Game, Habitat Division Technical Report 86-3.

Shippert, M. M, D. A. Walker, N. A. Auerbach, B. E. Lewis. 1995. Biomass and leaf-area index maps derived from SPOT images for Toolik Lake and Imnavait Creek areas, Alaska. Polar Record 31:147-154.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman & Hall, Ltd. London. 175 pp.

Skogland, T. 1984. The effects of food and maternal condition on fetal growth and size in wild reindeer. Rangifer 4:39-46.

____. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54:359-374.

_____. 1989. Natural selection of wild reindeer life history traits by food limitation and predation. Oikos 55:101-110.

_____. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. Oecologia 84:442-450.

Skoog, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph. D. Dissertation, University of California, Berkeley. 699 pp.

Slauson, W. L., B. S. Cade, and J. D. Richards. 1991. User manual for BLOSSOM statistical software. Midcontinent Ecological Science Center, National Biological Survey. Fort Collins, Colorado.

Smith, W. T. and R. D. Cameron. 1983. Responses of caribou to industrial development on Alaska's Arctic slope. Acta Zoological Fennica 175:43-45.

_____, _____, and D. J. Reed. 1994. Distribution and movements of caribou in relation to roads and pipelines, Kuparuk Development Area, 1978-90. Alaska Department of Fish and Game, Wildlife Technical Bulletin No. 12.

Stephenson, R.O. 1979. Abundance, movements, and food habits of wolves in and adjacent to NPR-A. Pages 53-87 *in* P. C. Lent, editor. Studies of selected wildlife and fish and their use of habitats on and adjacent to NPR-A, Vol. 1, 1977-1978. U.S. Department Interior, Anchorage.

Trivers, R. L. 1974. Parent-offspring conflict. American Zoologist 14:249-264.

Trudell, J. and R. G. White. 1981. The effect of forage structure and availability on food intake, biting rate, bite size, and daily eating time of reindeer. Journal of Applied Ecology 18:63-81.

Tyler, N.J.C. 1987. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. Symposium Zoological Society London 57:203-229.

U.S. Geological Survey. 1993. Digital elevation models: data users guide 5. Reston, Virginia. 48 pp.

Van Soest, P. J. 1983. Nutritional ecology of the ruminant. Second edition, O and B Books, Corvallis, Oregon.

Van Winkle, W. 1975. Comparison of several probabilistic home-range models. Journal of Wildlife Management 39:118-123.

Wahrhaftig, C. 1965. Physiographic divisions of Alaska. U.S. Geological Survey Professional Paper 482. 52 pp.

Walker, D. A., M. D. Walker, N. D. Lederer, and P. J. Webber. 1985. Pingos of the Prudhoe Bay regions, Alaska. Arctic and Alpine Research 17:321-336.

_____ and W. Acevedo. 1987. Vegetation and a Landsat-derived land cover map of the Beechey Point Quadrangle, Arctic Coastal Plain, Alaska. U.S. Army Cold Regions Research and Engineering Laboratory. CRREL Report 87-5. 63 pp.

Walker, M. D., D. A. Walker, and N. A. Auerbach, 1994. Plant communities of a tussock tundra landscape, Brooks Range foothills, Alaska. Journal of Vegetation Science 5:843-866.

Walsh, N. E., B. Griffith, and T. R. McCabe. 1995. Evaluating growth of the Porcupine caribou herd using a stochastic model. Journal of Wildlife Management 59:262-272.

Webber, P. J., and D. A. Walker. 1975. Vegetation and landscape analysis at Prudhoe Bay, Alaska: a vegetation map of the tundra biome study area. Pages 80-91 *in* J. Brown, editor. Ecological Investigations of the Tundra Biome at Prudhoe Bay, Alaska. Biological Papers of the University of Alaska, Special Report 2.

White, R. G., B. R. Thomsen, T. Skogland, S. J. Person, D. E. Russell, D. F. Holleman, and J. R. Luick. 1975. Ecology of caribou at Prudhoe Bay, Alaska. Pages 151-201 *in* J. Brown, editor. Ecological investigations of the Tundra Biome in the Prudhoe Bay region, Alaska. Alaska Biological Papers of the University of Alaska, Special Report 2.

_____ and J. Trudell. 1980. Habitat preferences and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research 12:511-529.

_____, F. L. Bunnell, E. Gaare, T. Skogland, and B. Hubert. 1981. Ungulates on arctic ranges. Pages 397-484 *in* L. C. Bliss, O. W. Heal, and J. J. Moore, editors. Tundra ecosystems: a comparative analysis. Cambridge University Press, Cambridge.

_____. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377-384.

_____ and J. R. Luick. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. Pages 215-232 *in* M. Peaker, R. G. Vernon, C. H. Knight, editors. Physiological Strategies in Lactation, Symposium Zoological Society London 51, Academic Press.

_____, N. A. Felix, and J. Milne. 1989. Regional variation in the digestibility of caribou forage in the calving ranges of the Porcupine and Central Arctic herds. Pages 151-168 *in* T. R. McCabe, editor. Terrestrial research: 1002 Area - Arctic National Wildlife Refuge, Annual Progress Report, 1988. Anchorage, U.S. Fish and Wildlife Service.

_____. 1992. Nutrition in relation to season, lactation, and growth of north temperate deer. Pages 407-414 *in* R. D. Brown, editor. The Biology of Deer. Springer-Verlag, New York.

Whitten, K. R. and R. D. Cameron. 1983a. Movements of collared caribou in relation to petroleum development on the Arctic Slope of Alaska. Canadian Field-Naturalist 97:143-146.

_____ and _____. 1983b. Population dynamics of the Central Arctic Herd, 1975-1981. Acta Zoological Fennica 175:158-161.

_____ and _____. 1985. Distribution of calving caribou in relation to the Prudhoe Bay oil field. Pages 35-39 *in* A.M Martell and D.E. Russell, editors. Proceedings of the First North American Workshop, Whitehorse, Yukon, Canadian Wildlife Service, Ottawa.

_____, G.W. Garner, F.J. Mauer, and R.B. Harris. 1992. Productivity and early calf survival of the Porcupine caribou herd. Journal of Wildlife Management 56:201-212.

_____. 1996. Ecology of the Porcupine caribou herd. Rangifer Special Issue 9:45-52.

Wiegand, C. L., S. J. Maas, J. K. Aase, J. L. Hatfield, P. J. Pinter, R. D. Jackson, E. T. Kanemasu, and R. L. Lapitan. 1992. Multisite analyses of spectral-biophysical data for wheat. Remote Sensing of the Environment 42:1-21.

Williams, M. T. and D. C. Heard. 1986. World status of wild *Rangifer tarandus* populations. Rangifer Special Issue 1:19-28.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

_____. 1995. Using Monte Carlo simulation to evaluate Kernel-based home range estimators. Journal of Wildlife Management 59:794-800.

Young. D. D., G. Garner, R. Ambrose, G. Weiler, H. Reynolds, M. Udevitz, and D. Reed. 1992. Differential impacts of predators (brown bears, wolves, golden eagles) on caribou calving in the 1002 area and potential displacement areas: an assessment of predation risks. Pages 37-66 *in* T. R. McCabe, B. Griffith, N. E. Walsh, D. D. Young, editors. Terrestrial research: 1002 area - Arctic National Wildlife Refuge, Interim Report, 1988-1990. U. S. Fish and Wildlife Service, Anchorage, Alaska. 432 pp.

_____ and T. R. McCabe. 1998. Grizzly bears and calving caribou: what is the relation with river corridors? Journal of Wildlife Management 62:255-261.

Zar, J. H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey. 929 pp.

Zimmerman, G. M., H. Goetz,, and P. Mielke. 1985. Use of an improved statistical method for group comparisons to study the effects of prairie fire. Ecology 66:606-611.