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Arctic Refuge Coastal Plain Terrestrial Wildlife Research Summaries

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Arctic Refuge Coastal Plain Terrestrial Wildlife Research Summaries

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Preface

In 1980, when the U.S. Congress enacted the Alaska National Interest Lands Conservation Act (ANILCA), it also mandated a study of the coastal plain of the Arctic National Wildlife Refuge. Section 1002 of ANILCA stated that a comprehensive inventory of fish and wildlife resources would be conducted on 1.5 million acres of the Arctic Refuge coastal plain (1002 Area). Potential petroleum reserves in the 1002 Area were also to be evaluated from surface geological studies and seismic exploration surveys. Results of these studies and recommendations for future management of the Arctic Refuge coastal plain were to be prepared in a report to Congress.

In 1987, the Department of Interior published the Arctic National Wildlife Refuge, Alaska, Coastal Plain Resource Assessment - Report and Recommendation to the Congress of the United States and Final Environmental Impact Statement. This report to Congress identified the potential for oil and gas production (updated* most recently by the U.S. Geological Survey in 2001), described the biological resources, and evaluated the potential adverse effects to fish and wildlife resources. The 1987 report analyzed the potential environmental consequences of five management alternatives for the coastal plain, ranging from wilderness designation to opening the entire area to lease for oil and gas development. The report's summary recommended opening the 1002 Area to an orderly oil and gas leasing program, but cautioned that adverse effects to some wildlife populations were possible.

Congress did not act on this recommendation nor any other alternative for the 1002 Area, and scientists continued studies of key wildlife species and habitats on the coastal plain of the Arctic Refuge and surrounding areas. This report contains updated summaries of those scientific investigations of caribou, muskoxen, predators (grizzly bears, wolves, golden eagles), polar bears, snow geese, and their wildlife habitats.

Contributions to this report were made by scientists affiliated with the U.S. Geological Survey; U.S. Fish and Wildlife Service; Alaska Department of Fish and Game; University of Alaska-Fairbanks; Canadian Wildlife Service; Yukon Department of Renewable Resources; and the Northwest Territories Department of Resources, Wildlife, and Economic Development.

Sections of the report presenting new information on caribou and forage plants were peer-reviewed by three independent, non-affiliated scientists. The remaining sections summarize previously published peer-reviewed scientific papers and were reviewed by a single independent scientist. The U.S. Geological Survey and the U.S. Fish and Wildlife Service collaborated in the publication of this report.

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Section 1: Introduction

Background

The Arctic National Wildlife Refuge in northeastern Alaska is one of 16 refuges in Alaska and 539 refuges nationwide within the National Wildlife Refuge System administered by the U.S. Fish and Wildlife Service. First established as the Arctic National Wildlife Range in 1960 by Public Land Order 2214, it initially had a three-fold purpose to preserve unique wildlife, wilderness, and recreation values on 8.9 million acres.

In 1980, the Arctic National Wildlife Range was expanded to the southwest and renamed the Arctic National Wildlife Refuge (also called the Arctic Refuge in this report) when the U.S. Congress passed the Alaska National Interest Lands Conservation Act (ANILCA), Public Law 96-487 (94 Stat. 2371). This legislation also designated almost all of the original Arctic National Wildlife Range as wilderness, and it directed the Secretary of the Interior to conduct studies evaluating both the biological resources and the potential petroleum reserves of 1.5 million acres (titled the 1002 Area) on the coastal plain of the Arctic Refuge.

In April 1982, the Arctic Refuge staff completed a report summarizing the then current state of knowledge on the fish, wildlife, and their habitats present on the coastal plain of the Arctic Refuge (U.S. Fish and Wildlife Service 1982). From 1982 to 1985, field investigations of biological resources of the 1002 Area were carried out by a number of investigators, and annual reports summarized the results (Garner and Reynolds 1983, 1984, 1985, 1986, 1987). These reports and other resources were used to prepare a Department of the Interior report to Congress: *Arctic National Wildlife Refuge, Alaska, Coastal Plain Resource Assessment - Report and Recommendation to the Congress of the United States and Final Environmental Impact Statement* (Clough et al. 1987).

Biological investigations continued from 1988 through 1994 in and near the 1002 Area coordinated by research scientists from the U.S. Fish and Wildlife Service who are now part of the U.S. Geological Survey (McCabe et al. 1992). Collaborators included specialists from the Arctic National Wildlife Refuge; Alaska Department of Fish and



Figure 1.1. Geographic map of the Arctic National Wildlife Refuge, Alaska, USA, and surrounding areas.

Game; University of Alaska-Fairbanks; Canadian Wildlife Service; Yukon Department of Renewable Resources; and the Northwest Territories Department of Resources, Wildlife, and Economic Development. Additional information continued to be collected from 1995 until the present (2001) as part of monitoring caribou (*Rangifer tarandus*), polar bear (*Ursus maritimus*), and muskox (*Ovibos moschatus*) populations and their habitats.

This current report is a summary of these recent investigations, building upon the information of past studies. It includes updated information about population dynamics, distribution, energetics, and habitat use of the key wildlife species as well as discussions about potential effects and mitigation of petroleum development on wildlife and habitats in the 1002 Area.

Study Area

The studies summarized in this report focused on the 1002 Area of the Arctic National Wildlife Refuge but also extended into adjacent regions of the Arctic Refuge, eastward into Canada, and as far west as the Prudhoe Bay and Kuparuk petroleum development areas in north central Alaska (Fig. 1.1).

The Arctic National Wildlife Refuge is the largest and most northern national wildlife refuge in the United States, encompassing 19.6 million acres (30,000 square miles). A variety of arctic and subarctic habitats exist in the Arctic Refuge, including near shore marine habitats along the coast, arctic tundra on the coastal plain, alpine habitats in the foothills and mountains of the Brooks Range, and taiga and boreal forests south of the mountains (Fig. 1.1).

The coastal plain of the Arctic Refuge contains calving grounds of the international Porcupine caribou herd, year-round habitats for muskoxen, fall staging areas for lesser snow geese (*Chen caerulescens caerulescens*), denning habitat for pregnant polar bears, and summer nesting areas for numerous species of migratory birds.

The 1002 Area is a region on the coastal plain in the northern part of the Arctic Refuge (Fig. 1.2). It lies between the mountains of the Brooks Range (69° 35' N) and the Beaufort Sea (70° 10' N) and is bounded on the east by the Aichilik River (142° 10' W) and on the west by the Canning River (146° 15' W).

Numerous northward-flowing rivers and streams bisect the 1002 Area. Only a few large lakes are present and most freeze to the bottom by late winter. The climate is characterized by extremely low winter temperatures, persistent winds, and short cool summers. Temperatures at Kaktovik on the coast of the Beaufort Sea (Fig. 1.2), averaged -25°C (-13°F) in February and +6°C (+43°F) in June during 1986-1995.

Precipitation occurs frequently as drizzle in summer and light snow in winter. The ground surface is frozen from September until June. A permanently frozen substrate called permafrost lies below the surface of the soil. Winter conditions with below freezing temperatures and snow exist for 8 to 9 months each year. Easterly winds predominate most of the year, although storms usually arrive on westerly winds. At Kaktovik, the sun is continuously above the horizon from May 15 to July 27 and below the horizon from November 24 to January 17.

The mountains of the Brooks Range converge with the Beaufort Sea in this northeastern corner of Alaska. The result is a unique juxtaposition of landscape features in the Arctic Refuge compared with surrounding areas (Fig. 1.1). The steeper elevation gradient between mountains and ocean on the coastal plain condenses a diversity of habitats and ecological niches into a narrow area.

Vegetation in the study area is predominantly tundra with a groundcover of low-growing plants (<1 foot high) that includes dwarf shrubs, sedges, small herbs, lichens, and mosses. Taller shrubs are restricted to drainages and south facing slopes. Almost the entire coastal plain is classified as wetland.

Five terrain types predominate across the study area. *Mountain terrain*, with its complex and often sparsely distributed vegetation communities, occurs along the southern periphery. Sedges, tussock-forming sedges, and low willow and birch shrubs dominate the *foothill terrain*. *Hilly coastal plains* of gently rolling topography have large areas of patterned ground formed by ice-wedge polygons and frost boils and support tussock tundra, low shrubs, and graminoid-dominated tundra. *River flood plains* support localized habitats of willow thickets as well as a rich diversity of other plant species and communities. *Flat thaw-lake plains* near the seacoast have wet and moist graminoid tundra and abundant shallow lakes formed by thawing of permafrost.

More extensive descriptions of the study area can be found in Clough et al. (1987) and U.S Fish and Wildlife Service (1982, 1988).

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Figure 1.2. Geographic map of the 1002 Area of the coastal plain of the Arctic National Wildlife Refuge, Alaska.

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Section 2: Land Cover

Janet C. Jorgenson, Peter C. Joria, and David C. Douglas

Vegetation Mapping of the Arctic Refuge Coastal Plain

Documenting the distribution of land-cover types on the Arctic National Wildlife Refuge coastal plain is the foundation for impact assessment and mitigation of potential oil exploration and development. Vegetation maps facilitate wildlife studies by allowing biologists to quantify the availability of important wildlife habitats, investigate the relationships between animal locations and the distribution or juxtaposition of habitat types, and assess or extrapolate habitat characteristics across regional areas.

To meet the needs of refuge managers and biologists, satellite imagery was chosen as the most cost-effective method for mapping the large, remote landscape of the 1002 Area.

Objectives of our study were the following: 1) evaluate a vegetation classification scheme for use in mapping; 2) determine optimal methods for producing a satellite-based vegetation map that adequately met the needs of the wildlife research and management objectives; 3) produce a digital vegetation map for the Arctic Refuge coastal plain using Landsat-Thematic Mapper (TM) satellite imagery, existing geobotanical classifications, ground data, and aerial photographs; and 4) perform an accuracy assessment of the map.

The land-cover classification scheme developed for the mapping project was based on Walker's hierarchical vegetation classification system for northern Alaska (Walker 1983). During the development of the map, the scheme was altered slightly to provide a group of landcover classes that were more compatible with the information content of the Landsat-TM spectral data and ancillary data. Wildlife biologists were consulted to ensure that the system included land-cover types relevant to wildlife habitat studies.

We conducted a preliminary assessment of mapping tundra habitats with Landsat-TM and SPOT satellite image data. We used an integration of the 2 data sources for one study area and used Landsat-TM exclusively for another. Results indicated that the expense (at the time of the study) of integrating SPOT data would not be cost effective for the entire mapping project. Landsat-TM methods, however, could improve existing maps made previously with Landsat-MSS data due to TM's finer spatial resolution and additional spectral bands. Therefore, further studies focused on using the Landsat-TM data. We evaluated 3 methods for producing a land-cover map from Landsat-TM data: 1) a supervised classification approach where spectral categories were defined by reference to field data; 2) an unsupervised approach where spectral categories were defined by a statistical clustering algorithm without reference to field data; and 3) a modeling approach where the unsupervised classification was combined with ancillary data about the landscape, such as terrain types, slope, and elevation (Joria and Jorgenson 1996). Accuracy assessments indicated that modeling was the best approach due to limited spectral differences among several tundra vegetation types.

Spatial data used to produce the land-cover map included 2 Landsat-TM multispectral images, digital elevation data (including derived slope and sunillumination themes), and maps of riparian zones and terrain types (including hilly coastal plains, foothills, mountains, thaw-lake plains, and floodplains). Each of these data sources comprised a thematic layer in a geographic information system (GIS).

Field data were collected at 102 sites in the Arctic Refuge, with 5 to 20 plots established in different landcover types at each site over 4 years. The sampling locations were digitized and a GIS theme of field-verified land-cover types was produced.

Field data were cross-referenced with the statistically generated spectral classes to determine the most common land-cover type associated with each of the spectral classes. Because many spectral classes represented more than one land-cover type, the ancillary, non-spectral data layers were used to improve the classification (Hutchison 1982). Each spectral class was cross-tabulated with the field land-cover, terrain type, elevation, sun-illumination, and slope layers. These tables were used to guide the modeling of decision rules for splitting confounded spectral classes into separate land-cover types.

The land-cover class assigned to each unit area on the map (30-m² pixel) depended on its spectral class and associated ancillary data, most commonly slope and terrain type. Preliminary land-cover maps were produced, and then the distribution of each land-cover class was viewed in conjunction with color-infrared aerial photographs showing vegetation to judge the map accuracy. Additional field data were gathered for problem areas, and the decision rules were modified as necessary. The process was repeated through several iterations before the final map was produced.

The mapping methods, data, summary statistics, and an accuracy assessment were presented in a map user's guide (Jorgenson et al. 1994). The image processing methods were presented in more detail in Joria and Jorgenson 1996. Sixteen land-cover classes were mapped (Fig. 2.1). They included: 1) wet graminoid tundra, 2) wet graminoid tundra with 10-50% moist inclusions, 3) moist



Figure 2.1. Land-cover map of the 1002 Area with corresponding vegetation class names, descriptions, and class codes, Arctic National Wildlife Refuge, Alaska.

sedge-willow tundra with 10-50% wet inclusions, 4)
moist sedge-willow tundra, 5) moist sedge-Dryas tundra,
6) moist sedge-tussock tundra, 7) moist shrub-tussock
tundra, 8) moist low-shrub tundra, 9) moist shrub tundra

on high-centered polygons, 10) Dryas-graminoid alpine tundra, 11) riparian shrub, 12) Dryas river terrace, 13) partially vegetated, 14) barren, 15) ice, and 16) water. 5

The land-cover classes are described in detail in the map user's guide, which includes quantitative vegetation cover data, species lists of typical plant communities occurring in each land-cover class, photographs, and cross-reference to 7 other classification systems used in northern Alaska.

An accuracy assessment was performed with an independent data set of 318 vegetation plots that were not used to make the map. The plots were systematically located across the coastal plain and foothills but not across the mountains. Point-by-point overall agreement between the mapped land-cover classes and the fieldassigned classes was 50% (Table 2.1).

Although land-cover types in the classification system were distinct, land-cover types in the field occurred across a continuum. Almost all of the vegetation in the mapped area was less than 0.5 meters tall and the structural and floristic differences among related types were not great. Subtle transition zones between landcover types are characteristic of the vegetation of low arctic tundra. Most errors reported in the accuracy assessment were between closely related types that were typically adjacent and interspersed in the field.

Approximately 86% of the assessment points were classified as the correct type or one of the most closely related other types. Agreement is higher when similar classes are combined into the fewer, more general classes typically used in wildlife studies. For example, when the map was combined into 6 or 7 more generalized classes for ungulate habitat studies, over 70% agreement was obtained. The greater initial detail of the 16-class map was preserved, however, because it allows adaptability to a wider range of studies.

Proportional occurrences of the vegetation classes across the entire coastal plain and within various terrain types were roughly similar between the mapped classes and the independent ground-truth data set (Table 2.2), again with the majority of discrepancy arising between closely-related vegetation communities.

The final land-cover map is available to the public in digital format at http://agdc.usgs.gov. The ancillary GIS data layers (topographic data, digitized field data, accuracy assessment point locations, terrain types, and riparian zones) are archived at the Arctic National Wildlife Refuge headquarters in Fairbanks, Alaska.

Because the land-cover map and its associated landscape themes have compatible digital formats, they can easily be applied to a variety of future GIS applications. Additional themes can easily be incorporated as more resource information becomes available, or as new management or mitigation needs are identified.

Table 2.1. Contingency table used to assess the accuracy of the land-cover map of the coastal plain of the Arctic Na	tional Wildlife Re	efuge,
Alaska. Table compares the map's coastal plain and foothill land-cover classes (rows, ordered by ecological continue	m) with field-ass	igned
classes (columns) from an independent systematically-sampled data set of 318 points. Land-cover class codes are d	efined in Fig. 2.1	

Land	W	W	М	М	М	T	S	S	S	A	R	D	Р	В	w	T	%
Cover Class	G	G M	s W	S	S D	Т	T T	Р	Т	Т	S	Т	V	A	A	О Т	Agree
WG	2	1	1									1				5	40
WGM	7	19	4	4	6			1			1	2				44	43
MSW	4	9	12	8				2								35	34
MS	I		4	15	4	5										28	54
MSD	1	5	4	11	18	14	1			2		1				56	32
Π	Ī	1	6	2	8	51	3	6								77	66
STT	l	1		1	1	5	13		2	2						25	52
SP		1				1		6								8	75
ST				1			1		2							4	50
AT	l –								1	1						2	50
RS	l										2	3			1	6	33
DT	1										1	6				7	86
PV		2								1		1	1	1		6	17
BA		1												8		9	89
WA	Ì										1			1	4	6	67
TOTAL	13	40	31	42	37	76	18	15	5	6	5	14	1	10	5	318	
%Agree	15	47	39	36	49	67	72	40	40	17	40	43	100	80	80		50

Land Cover Class	Entire Map	Entire Coastal Plain ^a	Mountain	Foothill	Hilly Coastal Plain	Thaw Lake Plain	Flood- plain	Riparian Zone ^b
WG	1	2 (4) ^C	<1	<1 (0)	4 (5)	18	3 (5)	1
WGM	9	13 (9)	<1	1 (0)	21 (9)	23	39 (20)	
MSW	6	9 (10)	<1	4 (7)	10 (10)	23	17 (13)	2
MS	6	9 (20)	1	8 (17)	16 (36)	6	9 (16)	2
MSD	10	13 (12)	3	17 (12)	20 (5)	8	6 (14)	
Π	14	21 (22)	<1	32 (33)	23 (29)	<1	4 (2)	1
STT	9	12 (6)	2	24 (11)	<1 (0)	0	<1 (0)	2
ST	5	3 (1)	8	6 (2)	0 (0)	0	<1 (0)	
SP	1	1 (4)	<1	1 (5)	1 (0)	<1	1 (0)	
AT	1	2 (1)	20	3 (4)	0 (0)	0	<1 (0)	
RS	1	1 (2)	<1	1 (0)	<1 (0)	<1	4 (4)	18
DT	1	2 (3)	<1	<1 (0)	<1 (0)	<1	5 (10)	14
PV	6	2 (2)	14	1 (1)	<1 (0)	<1	2 (6)	8
BA	15	7 (2)	32	1 (0)	<1 (0)	2	9 (6)	33
IC			3	<1 (0)	<1 (0)	4	1 (0)	3
WA			<1	<1 (0)	2 (1)	16	5 (5)	13
SH	6	<1 (0)	16	<1 (0)	<1 (0)	<1	<1 (0)	
Sq-km ^d	18501	12145	7073	6397	1810	271	3523	1038

Table 2.2. Percent of each land-cover class in the land-cover map of the coastal plain of the Arctic National Wildlife Refuge, Alaska, and the percent partitioned among various terrain types. Land-cover class codes are defined in Fig. 2.1.

a Entire map excluding the mountain terrain type.

b Riparian zone is included within the floodplain terrain type.

c Number in parentheses is the percent cover for each land-cover type as estimated by an *independent* systematic field sample of 756 points.

d Number of square-kilometers in each terrain type.

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Section 3: The Porcupine Caribou Herd

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Documentation of the natural range of variation in ecological, life history, and physiological characteristics of caribou (*Rangifer tarandus*) of the Porcupine caribou herd is a necessary base for detecting or predicting any potential effects of industrial development on the performance (e.g., distribution, demography, weight-gain of individuals) of the herd. To demonstrate an effect of development, post-development performance must differ from pre-development performance while accounting for any natural environmental trends.

We had 2 working hypotheses for our investigations: 1) performance of the Porcupine caribou herd was associated with environmental patterns and habitat quality, and 2) access to important habitats was a key influence on demography.

We sought to document the range of natural variation in habitat conditions, herd size, *demography* (defined here as survival and reproduction), sources and magnitude of mortality, distribution, habitat use, and weight gain and loss; and to develop an understanding of the interactions among these characteristics of the herd.

In addition, we investigated ways that we could use this background information, combined with auxiliary information from the adjacent Central Arctic caribou herd, to predict the direction and magnitude of any potential effects of industrial oil development in the 1002 Area of the Arctic National Wildlife Refuge on Porcupine caribou herd calf survival on the herd's calving grounds during June.

Data, Methods and Assumptions

This work focused on the calving and post-calving seasons of the Porcupine caribou herd. The *calving season* was defined as the 3-week period that began with the birth of calves (spring). *Post-calving* was defined as the 3-week period that followed the calving season (early summer).

Porcupine caribou herd size was estimated by the Alaska Department of Fish and Game (ADF&G) from aerial photo-censuses during post-calving aggregations. Only censuses considered reliable by ADF&G were used. Variance in annual censuses due to multiple observers counting portions of the photo sets was relatively small when compared with each census ($\pm 2\%$) and was ignored in the display of annual censuses to the nearest 1,000 animals.

Demography and calf weight-gain were estimated from repeated locations and/or recaptures of radio-

collared animals. Calving distributions were estimated from 767 calving sites of adult (\geq 3 year old) radiocollared female caribou obtained during 1983-2001 [average of 40 sites per year; fixed-kernel analyses using Least Squares Cross Validation (Silverman 1986, Seaman et al. 1996, 1998, 1999)]. Concentrated calving areas were defined as the annual kernel contour that included calving sites with greater than average density (Seaman et al. 1998). Annual calving grounds were defined as the 99% kernel utilization distributions obtained from annual calving sites. Extent of calving was defined as the aggregate extent of all annual calving grounds.

Vegetation types were mapped from Landsat-Thematic Mapper satellite imagery (Fig. 2.1; Jorgensen et al. 1994) and reduced from 17 to 7 classes for caribou habitat analyses (Fig. 3.1). We estimated the Normalized Difference Vegetation Index (NDVI) (Tucker 1979, Tucker et al. 1986) and snowcover from Advanced Very High Resolution Radiometer (AVHRR) data from National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites. Snowcover was estimated using a linear regression that we derived by correlating AVHRR infrared reflectance with estimates of snowcover extracted from aerial photographs collected in the 1002 Area during the snowmelt periods of 1987 and 1988 ($r^2 = 0.87$, n = 80). Cloud contaminated areas in the AVHRR images were identified (Baglio and Holroyd 1989) and excluded from analyses, as were large water bodies. AVHRR and Thematic Mapper images were transformed to an Albers Equal Area projection and resampled to 1-km² pixel size.

NDVI indexes the disproportionate reflectance of nearinfrared radiation from green vegetation (Tucker and Sellars 1986) in the canopy of plant communities. Thus, relationships between NDVI and *total green plant biomass* or leaf area index (LAI) would be expected to be strongest for plant communities with reduced vertical distribution of green biomass and leaf area (e.g., communities dominated by sedges, grasses, or short shrubs that are common in the Arctic). Due to the size of the pixels (~1 km²) AVHRR data are linked more to landscape processes than to individual plant communities (Malingreau and Belward 1992).

Relatively good correlations have been obtained between above ground net primary productivity (ANPP) and seasonally integrated NDVI ($r^2 = 0.89$; Paruelo et al. 1997), LAI and NDVI when integrated across physiognomic categories ($r^2 = 0.97$; Shippert et al. 1995), and photosynthetic biomass and NDVI in small plots ($r^2 =$ 0.51; Hope et al. 1993). Because NDVI indexed total green biomass and caribou are selective feeders (White 1983), we assumed that the biomass of forages eaten by caribou was positively correlated with total green biomass at the landscape scale.



Figure 3.1. Land-cover classes on the coastal plain of the Arctic National Wildlife Refuge, Alaska, and eastward into the Yukon Territory, Canada, as generalized for studies of the Porcupine caribou herd. Classes are based on Jorgensen et al. (1994) as depicted in Fig. 2.1 and are expanded to include Canada using a Canadian Wildlife Service Landsat-derived vegetation map of the Northern Yukon. Classes on this map and their corresponding classes in Jorgensen et al. (1994) include: Wet Graminoid (WG, WGM, some PV), Moist Sedge (MSW, MS, MSD), Herbaceous Tussock Tundra (TT, SP), Shrub Tussock Tundra (STT), Alpine (ST, AT, some PV), Riparian (RS, DT, some PV), and Non-vegetated (BA, IC, WA, SH).

We directly estimated NDVI at 3 times:

 NDVI_calving - composite (Holben 1986) images obtained as close as possible to median calving date each year (mean image date of 2 June, SE = 2.0 days). Snowcover was also estimated from these images. Negative NDVI values (areas with snowcover) were converted to zero NDVI.
 NDVI_mid-June - approximately 2 weeks after

calving (mean image date of 16 June, SE = 2.6 days). 3) $NDVI_early_July$ - during the first week of July (mean image date of 3 July, SE = 2.4 days).

From these images we derived 2 additional estimates:
1) NDVI_rate - the pixel-based daily rate of increase in NDVI from calving to mid-June.
2) NDVI_621 - NDVI on the fixed date of 21 June each year (approximately 3 weeks after calving, linearly interpolated from mid-June and early-July images).

In years when snowcover was substantial (i.e., 1986, 1988, 1989, 1992, 1997) and NDVI_calving was near zero, there may have been a small overestimate of NDVI_rate. In addition, cloud cover made it impossible to obtain a complete image on any fixed date. Thus,

NDVI_621 was the most robust NDVI estimate because it was interpolated to a fixed date from 2 snow-free images.

We assumed that NDVI_calving and NDVI_621 represented relative green forage quantity while NDVI_rate reflected forage quality because it estimated the daily accumulation of new plant tissue which is highly digestible (Cameron and Whitten 1980). The quality implication of NDVI_rate was based on the assumption that caribou forage selectively for the most digestible food items (White 1983). Because energy and protein intake from milk by caribou calves remains high during the first 3 weeks of life and then declines as calves increase their intake of vegetation (White and Luick 1984, Parker et al. 1990), we assumed that NDVI_621 estimated forage availability to lactating females during the 3-week period of peak lactation demand immediately after calving.

Predator distributions and relative densities were estimated from annual relocations of radio-collared grizzly bears (*Ursus arctos*), 1983-1994, and from aerial survey locations of golden eagle (*Aquila chrysaetos*) nest structures and wolf (*Canis lupus*) dens (Fig. 6.1).

Satellite-collared caribou provided supplemental information on distribution throughout the herd's annual range. Estimates of minimum daily movement rates were obtained from satellite-collared animals, 1985-1995, and from near-daily relocations of conventional radio-collared calves on the calving ground, 1992-1994.

Data were analyzed with contingency tables, linear and stepwise logistic regression, multi-response permutation procedures (MRPP, Mielke and Berry 1982), and analysis of variance. Akaike's Information Criteria (AIC; Akaike 1973, Sakamoto et al. 1986) were used for final model selection. Bonferroni procedures were used to provide overall experiment error protection as appropriate. GIS technology, remotely-sensed habitat data-layers, habitat-demography relationships, and simulation modeling were used to assess potential effects of displacement of calving grounds on calf survival each June.

Not all types of data were available throughout the entire primary study period of 1983-2001. Calf weights near birth were estimated from captured 1- and 2-day-old animals in 1983-1985, and again in 1992-1994. Calf weight-gains on the calving ground and cow weights in June and September were estimated in 1992-1994.

Caribou food habits were estimated during 1973 (Thompson and McCourt 1981), 1979-1981 (Russell et al. 1993), and for this study during 1993-94 from microhistological analyses of fecal pellets (Sparks and Malechek 1968) corrected for forage digestibility (Duquette 1984).

Annual adult caribou survival was estimated in 1983-1992 (Fancy et al. 1994, Walsh et al. 1995). Over-winter calf survival was estimated in 1983-1985 and 1988 (Fancy et al. 1994, Walsh et al. 1995). *June calf survival* (the proportion of parturient radio-collared females retaining live calves during the last week of June) was estimated in 1983-1992 (Fancy et al. 1994, Walsh et al. 1995) and for this study in 1993-2001.

Calving distributions and vegetation types on the calving grounds were available for all years 1983-2001, but satellite-based estimates of NDVI and snowcover were only available for the years 1985-2001.

The study area covered the annual range of the Porcupine caribou herd (Fig. 3.2), emphasizing the calving ground, and was described in the introduction to



Figure 3.2. For the Porcupine caribou herd: annual range (wide white solid line), calving sites (yellow points), and aggregate extent of calving (thin solid yellow line), 1983-2001. For the Central Arctic caribou herd: aggregate extent of calving (thin solid white line) and calving sites (white points), 1980-1995. (Adapted *from* Wolfe 2000).

this report and in the 1987 Final Legislative Environmental Impact Statement (Clough et al. 1987).

Nutritional Importance of the Calving Ground

Spring arrival on the calving ground is the time of minimum body reserves for *parturient females* (those about to give birth or accompanied by very young calves) (Chan-McLeod et al. 1999). Thereafter, their energy and protein requirements reach the highest level of the year during peak lactation in the first 3 weeks of June (White and Luick 1984, Parker et al. 1990). The females' appetites are high and forage intake rates can match lactation demand only where primary production is high (White et al. 1975, 1981). Small changes in nutritional content and digestibility of forage, however, can have substantial multiplier effects on digestible energy and protein intake (White 1983), and thus may influence nutritional performance of Porcupine caribou herd females on the calving ground.

Recent advances in identifying the basis of selection of food by ungulates demonstrate that forage intake is a function of ungulate morphology, plant architecture, and biomass of acceptable forage (White et al. 1975, Trudell and White 1981, Spalinger et al. 1988, Shipley and Spalinger 1992, Gross et al. 1993, Langvatn and Hanley 1993, Wilmshurst and Fryxell 1995). Because ungulates select forage with high digestible energy and high digestible protein (Langvatn and Hanley 1993, Wilmshurst and Fryxell 1995), these properties are the relevant measure of forage value of habitats at any spatial scale (White et al. 1975, White and Trudell 1980a,b). Thus, the forage currency for ungulates is primarily a function of digestibility of acceptable foods and is not simply plant biomass or gross energy (Fryxell 1991).

The source of protein for fetal growth comes almost exclusively from body protein of female caribou entering winter (Gerhart et al. 1996). Females with high body protein in late winter produce the largest calves (Allaye-Chan 1991). Early weaning of calves occurs when habitat conditions do not support a protein intake sufficient to meet a minimal rate of body protein deposition; milk synthesis then ceases (Russell and White 1998). The protein:energy ratio of forage consumed during lactation increases the milk protein intake by calves (Chan-McLeod et al. 1994), the most important milk nutrient affecting calf growth rate at all calf ages (White 1992).

When forage biomass is low at calving, Porcupine caribou herd females might be expected to use microhabitats of highest biomass of acceptable foods and to select the most digestible forages from within them, as has been documented for caribou of the Central Arctic herd (White et al. 1975) and the Western Arctic herd (White and Trudell 1980b). This change in the basis of selection, from forage biomass to forage digestibility, constitutes scale-dependent selection (cf. Wiens 1989, O'Neil and King 1998). We pursued this issue of scale dependency in habitat selection by the Porcupine caribou herd at the larger scales of the annual calving grounds and concentrated calving areas.

Because the inability to meet lactation demands may lower the *performance* (i.e., weight-gain, survival) of calves, calving ground habitats may be important. They may be important because they can contribute substantially to the female and calf protein budgets during the calving season, when maternal protein reserves can be low (Gerhart et al. 1996, Chan-McLeod et al. 1999).

Habitat Trends During the Study Period

The climate of the Arctic has been warming in both summer and winter during recent decades (Chapman and Walsh 1993, Groisman et al. 1994, Houghton et al. 1995). Temperature increases have been greatest in winter. The warming has been heterogeneous across the Arctic (Chapman and Walsh 1993, Serreze 2000), but was evident in spring (Fig. 3.3a) and winter (Fig. 3.3b) temperatures within the northern part of the annual range of the Porcupine caribou herd.

An earlier greening and later senescence of green plant biomass in areas north of 40°N (Myneni et al. 1997, 1998; Zhou et al. 2001) have been detected with NDVI and associated with the warming trend. The earlier greening was evident locally within the extent of calving (Fig. 3.2) of the Porcupine caribou herd in the form of an increasing relative amount of green plant biomass on 21 June (NDVI_621, $r^2 = 0.50$, P = 0.002) during 1985-1999 (Fig. 3.4).

A very low value for NDVI_621 was observed in 1992, the year that stratospheric aerosols from the 1991 eruption of Mount Pinatubo in the Philippines reached the Arctic in spring (Minnis et al. 1993). Both 2001 and 2000 were substantial outliers (RStudent = -2.49, -2.86, respectively) from the relationship between NDVI_621 and year, 1985-1999 (Fig. 3.4). Both 2001 and 2000 had exceptionally late springs with high snowcover at calving. We do not yet know if these outliers indicate a change in the trend observed during 1985-1999.

The Arctic Oscillation (Fig. 3.5) is centered over the high Arctic and is one of a number of correlated indices of large-scale atmospheric pressure differentials (e.g., North Atlantic Oscillation, Northern Hemispheric Annular Mode) (Thompson and Wallace 1998, 2001). The Arctic Oscillation is the height of the level of one-half atmosphere of pressure above the surface of the earth and is weakly correlated with surface temperatures (Thompson and Wallace 1998). The Arctic Oscillation has a warm positive phase when surface pressures are low and warm North Atlantic water enters the Arctic Ocean,



Figure 3.3. Mean temperatures for 2 stations within the Porcupine caribou herd's aggregate extent of calving (Komakuk Beach and Shingle Point, Yukon Territory, Canada) and 1 station within its winter range (Old Crow, Yukon Territory) for *a*) June, and *b*) winter (January, February, March), 1950-1995.



Figure 3.4. Median Normalized Difference Vegetation Index (NDVI) on 21 June within the aggregate extent of calving for the Porcupine caribou herd, 1983-2001. Values for 2000 and 2001 were outliers (RStudent = -2.49, -2.86, respectively) and excluded from the displayed regression line, $r^2 = 0.496$, P = 0.002.



Figure 3.5. Standardized values of the Arctic Oscillation (AO) for winter (January, February, March) and population size of the Porcupine caribou herd, 1958-2001. Mean value indicated by solid horizontal line. ^a PDO is the Pacific Decadal Oscillation (Hare and Matuna, 2000).

and a cool negative phase when surface pressures are relatively high.

Initiation of increasing and decreasing trends in the Arctic Oscillation has been coincident with phase shifts in the Pacific Decadal Oscillation in 1977 and 1989 (Hare and Matuna, 2000) (Fig. 3.5). Correlations between the closely related North Atlantic Oscillation and a number of vegetative and ungulate population characteristics have been reported for Northern Europe (Post et al. 1997, Post and Stenseth 1999).

Median annual NDVI at calving (NDVI_calving) within the extent of calving of the Porcupine caribou herd was positively correlated with the Arctic Oscillation from the winter (January, February, March) of the previous calendar year (~15 month lag, $r^2 = 0.32$, P = 0.011) (Fig. 3.6). This suggested that early forage availability for lactating females was influenced by weather patterns on a hemispheric scale.

Further, the suspected phase shift in the Arctic Oscillation at the end of the 1980s (Fig. 3.5) was coincident with an increase in the frequency of daily temperature excursions above freezing in both the spring (Fig. 3.7a) and fall (Fig. 3.7b) on the transitional ranges of the Porcupine caribou herd during the 1990s. There has been a decrease in the depth and extent of snowcover in Northwestern Canada near the wintering grounds of the Porcupine caribou herd during this latter period as well (Brown and Braaten 1998).

Thus, forage biomass during peak lactation demand (NDVI_621) increased during the period of study, 1985-1999 (Fig. 3.4), and this positive trend was coincident with summer warming on the calving ground (Fig. 3.3*a*). In addition, forage availability at calving (NDVI_calving) has been positively correlated with hemispheric-scale



Figure 3.6. Median Normalized Difference Vegetation Index at calving (NDVI_calving) within the aggregate extent of calving (EC) of the Porcupine caribou herd for the current year, and winter Arctic Oscillation index (AO, January, February, March) for the previous calendar year, 1985-2001.

atmospheric conditions (Fig. 3.6). Counteracting the positive trend in forage abundance during peak lactation has been a tendency toward more freeze-thaw cycles on spring and fall transitional ranges of the Porcupine caribou herd (Fig. 3.7a,b) coincident with a suspected phase shift in the Arctic Oscillation.

These freeze-thaw cycles on transitional and winter ranges may have influenced snow properties, reduced access to forage, increased travel costs, and/or decreased the ability of caribou to escape their predators. These climateinfluenced conditions on transitional/winter ranges may have contributed to the decline in size of the Porcupine caribou herd (Fig. 3.5) in spite of favorable conditions on the calving ground. Local and large-scale climate patterns as well as catastrophic events in the Southern Hemisphere (e.g., eruption of Mount Pinatubo) apparently have had major influences on Porcupine caribou herd habitats during the period of study and have set the stage for all observations of Porcupine caribou herd distribution and demographic processes during the past 2 decades.

Herd Dynamics and Demography

The growth curve of the Porcupine caribou herd suggested an approximate 30- to 40-year cycle of increase and decrease in abundance (Fig. 3.8). The herd numbered ~100,000 in 1972, increased at about 4.9% per year from 1979 through 1989 when it reached ~178,000 animals, then declined at about 3.6% per year from 1989 to 1998 (Fig. 3.8). The decline from 1998 to 2001 was only about 1.5% per year, and the herd now totals ~123,00 animals. If the current decline continues, the herd would be expected to again reach the lowest levels ever recorded during 2005-2010. If the herd continues to decline below ~100,000 animals, then the length of a complete herd cycle may exceed 30 years.



Figure 3.7. Frequency of days with daytime temperatures above freezing in *a*) spring (21 March - 30 April) and *b*) fall (21 September - 20 October) on transitional ranges of the Porcupine caribou herd during the herd increase phase, 1970-1988, and the herd decrease phase, 1989-1998. Brackets indicate 95% confidence intervals on mean values.



Figure 3.8. Population size of the Porcupine caribou herd, 1972-2001, estimated from aerial photo-censuses by the Alaska Department of Fish and Game.

Porcupine caribou herd size appeared correlated with Arctic Oscillation although there were too few data to conduct a proper time series analysis (Fig. 3.5). In contrast to the Porcupine caribou herd, other Alaska barren-ground caribou herds (Western Arctic, Teshekpuk Lake, Central Arctic), generally continued to increase during the downward trend in the Arctic Oscillation that was evident during the 1990s (Fig. 3.5).

Capacity for growth (defined as the maximum realized long-term growth rate) of the Porcupine caribou herd appeared substantially less than for other Alaska herds. Capacity for growth among herds of dramatically different sizes is best visualized by plotting relative herd sizes (Fig. 3.9). Maximum long-term growth rate (~4.9%, assumed linear, 1979-1989) (Fig. 3.8) of the Porcupine caribou herd was never more than about half the rate observed for other Alaska barren-ground caribou herds [Western Arctic herd (1976-1996, ~9.5%), Teshekpuk Lake herd (1978-1993, ~13%), Central Arctic herd (1978-1992, ~10.3%)] (Fig. 3.9).

The Porcupine caribou herd was the first Alaska barren-ground caribou herd to begin and maintain a prolonged decline in the last 2 decades (Fig. 3.9). Annual survival of Porcupine caribou herd adult females was only about 84% (Fancy et al. 1994, Walsh et al. 1995), which was lower than that generally observed in other caribou herds (Bergerud 1980); and adult female survival may have been responsible for the relatively low growth rate of the Porcupine caribou herd.

Annual calf survival averaged about 48% with about half (56%) of the annual mortality occurring on the calving ground (Whitten et al. 1992, Fancy et al. 1994, Walsh et al. 1995).



Figure 3.9. Relative post-calving herd sizes (minimum observed = 1.0) of the 4 Alaska barren-ground caribou herds (PCH = Porcupine caribou herd; WAH = Western Arctic herd; CAH = Central Arctic herd; TLH = Teshekpuk Lake herd), 1976-2001. Maximum observed population size for each herd is noted in the legend.

There were no significant differences in mean parturition, calf survival during June, or *net calf production* (defined as the product of parturition rate and June calf survival) (Fig. 3.10a-c) between the increase and decrease phases of the herd (Fig. 3.8). Parturition rate averaged 0.81 (range 0.71-0.92) during 1983-2001 (Fig.



Figure 3.10. Reproductive estimates for the Porcupine caribou herd, 1983-2001: *a*) parturition rate of adult females, *b*) calf survival from birth through the last week of June, and *c*) *net calf production* [the product of parturition rate and calf survival].

3.10*a*) and did not differ between the increase phase (0.80, SE = 0.04, 1983-1989) and the decrease phase (0.82, SE = 0.08, 1990-2001).

Calf survival during June was quite high and averaged 0.75 (range 0.57-0.94) during 1983-2001 (Fig. 3.10*b*) but did not differ between the increase phase (0.71, SE = 0.07, 1983-1989) and the decrease phase (0.79, SE = 0.13, 1990-2001). Net calf production averaged 0.62 during 1983-2001 (range 0.50-0.82) (Fig. 3.10*c*) and did not differ between the increase phase (0.58, SE = 0.06, 1983-1989) and the decrease phase (0.63, SE = 0.13, 1990-2001). For all these demographic characteristics, variance tended to be greater during the decrease than during the increase phase of the herd.

Because average parturition, calf survival during June, and net calf production did not differ between the increase and decrease phases of the Porcupine caribou herd, 1983-2001, a reduction in adult, sub-adult, and/or calf survival while animals were off the calving ground in late-summer through winter must have accompanied the herd decline. Emigration to the adjacent Central Arctic herd was an unlikely cause of the Porcupine caribou herd decline because satellite-collared animals that occasionally (4 out of 167 collar-years) wintered with the Central Arctic herd, returned to the Porcupine caribou herd the following summer.

Periodic lows in net calf production and calf survival during June (1992, 1993, 1997; Figs. 3.10*b*, *c*) were not sufficient to maintain the herd decline (S. A. Arthur, Alaska Department of Fish and Game, personal communication). Unfortunately, a complete record of adult, sub-adult, and calf survival estimates was not available for late-summer through winter during the decrease phase of the herd, 1989-2001.

Seasonal Distribution and Movements

The Porcupine caribou herd caribou wintered (15 November – 14 April) in Alaska south of the Brooks Range and in Canada in the Richardson and Ogilvie Mountains in the Yukon Territory (Fig. 3.11). Their annual range encompassed ~290,000 km² (Fig. 3.2). The extent of calving encompassed ~36,000 km². Spring migration to the annual calving grounds began in mid-April and continued through April and May (Fig. 3.11). Return to fall/winter ranges began with departure from the annual calving grounds in late-June and early-July (Fig. 3.11). In fall (15 September – 14 November), the Porcupine caribou herd was distributed widely.

Minimum daily travel rates of parturient females were variable throughout the year (Fig. 3.12). Non-parturient females had similar movement rates. Minimum movement occurred during winter. Movement began increasing in mid-April with initiation of migration to the annual calving ground and was directional toward the annual calving ground.

After their calves were born, the direction of movement of satellite-collared parturient females was random for 20 days (Fancy and Whitten 1991). Calf movement rate (minimum, straight line, estimated from conventional radio-collars) in the years 1992-1994 was about 2.5 km/day during the first week after birth. The rate increased gradually during the next week to about 5 km/day and then increased through the end of June to approximately 15-20 km/day. As females and calves departed the calving ground in late June and early July, some individual calves traveled as much as 90 km/day. Relatively high rate of movement continued throughout July. Because movement rates were low during the calving season and direction of movement was random for 20 days after birth (Fancy and Whitten 1991), the distribution of calving sites was assumed to be representative of habitat use by caribou through 21 June.

Movement declined during August perhaps in response to harassment by Oestrid flies or to localized forage abundance. Movement increased during the pre-rut period in late-September and October and then reached a minimum again by mid-November. The average female of the Porcupine caribou herd traveled approximately 4,355 km annually (Fancy et al. 1989).

During 1985-1992, median arrival of satellite-collared parturient females on the annual calving ground ranged from 17 May-4 June and median date of departure ranged from 3-26 July. Non-parturient females tended to lag slightly behind and south of the parturient females from early-May through calving (Whitten et al. 1992), but within 1 week after calving, parturient and non-parturient female distributions were essentially coincident.

Length of stay on the annual calving ground ranged from 34-67 days. Caribou have tended to depart the annual calving grounds earlier since 1995 (F. J. Mauer, U.S. Fish and Wildlife Service, personal communication). This trend may have been related to more advanced plant phenology within the extent of calving in late June during the late 1990s (Fig. 3.4).

Median calving date, 1983-1996, was 1 June (range 30 May-6 June) with 50% of annual calving occurring within 2 days of the annual median calving date. No temporal trends were evident in median calving date, and annual calf survival was not related to median calving date (P > 0.05).

Sizes and locations of annual calving distributions were quite variable. Annual calving grounds encompassed 3,672-16,667 km² during 1983-2001 (Fig. 3.13, Table 3.1). Similar distributions were observed during aerial surveys, 1972-1982 (Figs. II-5 *in* Clough et al. 1987). On average, concentrated calving areas occupied 12.3% (range 0.7-25%) of the annual calving grounds (255-



Figure 3.11. Distribution of satellite-collared female caribou of the Porcupine caribou herd during 7 time periods, 1985-1995. An average of 10 animals (range 4-17) were collared each year yielding 14,447 observations; 87% of these observations were obtained 1985-1990. Not included were the locations of 3 females that each spent one winter with the adjacent Central Arctic herd.

2,548 km²) and contained 47% (range 29-61%) of calving locations.

There was no concentrated calving area in 2001 when the spring was very late and the extent of calving was almost completely snow covered. Density of parturient females in the concentrated calving area ranged approximately 13-106/km² over the years and averaged 7 times (range 3.7-10.8) higher than outside the concentrated calving area each year (Table 3.1). None of these estimates differed between the increase and decrease phases of the herd (P > 0.05). Since 1972, there have been only 2 years (2000, 2001) when all calving occurred in Canada and 1 additional year (1982) when all concentrated calving occurred in Canada.

Neither the areas of annual calving grounds nor areas of concentrated calving areas were correlated (P > 0.05) with the number of calving sites, with the estimated number of parturient females in the herd, with the percent of the extent of calving that was snow free, or with any greenness (NDVI) estimate in either the extent of calving or the annual calving grounds. Thus, neither herd size nor habitat characteristics were clearly related to calving ground size. Factors affecting calving ground size remain unclear.

Distribution of calving sites differed (MRPP, P < 0.05) among all successive years, 1983-2001, except 1983-1984 when the number of calving sites obtained from radiocollared females was lowest and 2000-2001 when late springs restricted calving to Canada (Table 3.1). There was no uni-directional trend to shifts in location of annual calving grounds or concentrated calving areas (Rayleigh's Test, P = 0.870 and 0.740, respectively). During 1983-1994, parturient females displayed no among-year fidelity to the concentrated calving area (P = 0.951) nor any habitat attribute for calving (P > 0.135), but females that calved in the 1002 Area returned there for calving in the following year more often than expected (P = 0.024).

The percent of females calving in the 1002 Area in the years 1983-2001 was quite variable, averaging 43% (range 0-92%) but not differing (P = 0.128) between the decrease (50%, SE = 32%) and the increase phase (30%, SE = 23%) of the herd (Fig. 3.14). The proportion of the concentrated calving area that was in the 1002 Area followed a similar trend. As the relative amount of green biomass at calving within the extent of calving (NDVI_calving) increased because of earlier springs, the percent of females calving in the 1002 Area increased ($r^2 = 0.68$, P < 0.001) (Fig. 3.15). Thus, the average proportion of Porcupine caribou herd females that calve in the 1002 Area may increase if the climate continues to warm.

The general location of calving in the years 1983-2001 was related to the winter Arctic Oscillation (January, February, March) during previous calendar year, approximately 15 months before calving. In years when



Figure 3.12. Minimum median daily movement rate of parturient satellite-collared females of the Porcupine caribou herd, 1985-1995. Values calculated from no more than one location per day. An average of 10 animals (range 4-17) were collared each year yielding 14,447 observations; 87% of these observations were obtained 1985-1990. Not included are the data for 3 females that each spent one winter with the adjacent Central Arctic herd.

the Arctic Oscillation was positive, more than half of the concentrated calving area was likely to be located on the Alaska portion of the coastal plain (83.3% of the years, Fisher's Exact Test, P = 0.045). Similarly, there was a tendency (66.7% of years, Fisher's Exact Test, P = 0.057) for more than half the females to calve in the 1002 Area when the Arctic Oscillation in the previous calendar winter was positive.

The time delay in correlation between the Arctic Oscillation and calving location and between the Arctic Oscillation and NDVI_calving (Fig. 3.6) may have been related to a 1-year delay between tiller formation and flower production for *Eriophorum vaginatum* (cottongrass) (Billings and Mooney 1968, Bliss 1971). Immature cottongrass flowers have been a dominant food item for Porcupine caribou herd when they have calved on the Arctic Refuge coastal plain. Cottongrass tiller formation is probably related to the availability of resources (moisture and soil nutrients).

Positive phases of the Arctic Oscillation may have enhanced resource availability, increased tiller production in the previous year, and resulted in increased flower production during the current spring. We would expect that the increased greenness at calving (NDVI_calving) might reflect leaf area of cottongrass tillers, rather than the pale green immature flowers.

During post-calving (>3 weeks after calf birth), Porcupine herd caribou (regardless of calving location) tended to move westward (Fig. 3.11). Even in exceptional years when calving occurred far to the east in Canada (e.g., 2000, 2001) (Fig. 3.13) caribou reached the Arctic Refuge coastal plain and portions of the 1002 Area by late-June or July (S. A. Arthur, Alaska Department of Fish



Figure 3.13. Calving distributions of the Porcupine caribou herd, 1983-2001, as estimated from fixed kernel analyses of the sites where radiocollared females were first observed with calves during repeated aerial surveys in May and June. There are 3 zones: 1) concentrated calving area (shown in dark gray), the contour enclosing calving sites with greater than average fixed kernel density, 2) annual calving ground (medium gray), the 99% fixed kernel utilization distribution for a year, and 3) aggregate extent of calving (light gray), the outer perimeter of all annual calving grounds. No concentrated calving was detected in 2001.

Table 3.1. Number of calving sites, number of calving sites in the concentrated calving area (CCA), area (km ²) of CCA, area (km ²) of annual
calving ground (ACG), ratio of sizes of CCA to ACG, population size of the Porcupine caribou herd, percent of radio-collared female caribou that
calved in the CCA, percent of radio-collared female caribou that calved in the 1002 Area, percent of the CCA within the 1002 Area, and percent of
the ACG within the 1002 Area, 1983-2001, Alaska, USA, and Yukon Territory, Canada.

Year	Calving Sites	Sites in CCA	CCA Area	ACG Area	Ratio CCA/ACG	Population Size (K)	%females In CCA	%females In 1002	%CCA In 1002	%ACG In 1002
1983	18	11	2,584	10,064	0.25	135	55.6	61.1	62.4	42.8
1984	18	11	839	6,599	0.13		61.1	33.3	19.8	39.2
1985	34	16	1,585	10,784	0.15		47.1	55.9	69.2	36.8
1986	20	8	419	5,432	0.08		40.0	10.0	28.8	8.4
1987	36	15	479	6,048	0.08	165	44.4	13.9	14.2	15.7
1988	61	24	267	3,823	0.07		39.3	1.6	0.0	5.9
1989	51	15	255	3,672	0.07	178	29.4	33.3	59.3	30.1
1990	53	22	1,167	8,379	0.14		39.6	69.8	100.0	47.2
1991	43	21	731	5,767	0.13		48.8	88.4	92.5	68.6
1992	43	18	2,174	16,667	0.13	157	41.9	41.9	79.1	22.5
1993	35	18	1,401	9,098	0.15		51.4	57.1	70.2	40.3
1994	79	33	814	6,602	0.12	152	41.8	64.6	77.3	54.8
1995	60	31	827	5,141	0.16		51.7	91.7	100.0	71.2
1996	65	30	1,354	9,453	0.14		46.2	53.8	90.6	33.9
1997	29	15	530	5,661	0.09		51.7	31.0	33.7	31.8
1998	39	20	789	6,316	0.12	128	51.3	84.6	93.4	73.1
1999	20	9	601	7,820	0.08		45.0	20.0	9.3	30.4
2000	22	13	791	6,541	0.12		59.1	0.0	0.0	0.0
2001	41	а		10,602		123		0.0		0.0
average	40	18	976	7,604	0.12	148	47.0	42.7	55.5	34.3
minimum	18	8	255	3,672	0.07	123	29.4	0.0	0.0	0.0
maximum	79	33	2,548	16,667	0.25	178	61.1	91.7	100.0	73.1
SE	18	7	630	3,060	0.04	20	7.8	30.1	35.9	22.5

a No concentrated calving was detected in 2001



Figure 3.14. Percent of radio-collared Porcupine caribou herd females that calved in the 1002 Area of the Arctic National Wildlife Refuge, Alaska, 1983-2001.



Figure 3.15. Percent of radio-collared Porcupine caribou herd females that calved within the 1002 Area of the Arctic National Wildlife Refuge, Alaska, in relation to the median Normalized Difference Vegetation Index at calving (NDVI_calving) within the aggregate extent of calving, 1985-2001. Point legends indicate the year of the estimates.

and Game, personal communication). As a result of these westward movements, essentially the entire 1002 Area was eventually used by late June or early July. Most of the use of the westernmost portion of the 1002 Area by satellite-collared females of the Porcupine caribou herd occurred during 24 June-14 August (Fig. 3.11).

Foraging on the Calving Ground

The calving season diet of Porcupine herd caribou during 1993-1994, when concentrated calving was primarily in the 1002 Area (Fig. 3.13), was dominated (76-82%) by immature flowers of cottongrass from the time the caribou arrived on the calving ground until about 16-18 June (Figs. 3.16a, 3.17a). Similar diets were observed in 1973 (Thompson and McCourt 1981), but the location of concentrated calving in that year was not documented (Clough et al. 1987).

Diet was relatively consistent between years, but somewhat more variable in 1994, and not related to average daily weight-gain of calves in 1993 and 1994. Both cottongrass flowers and young willow (*Salix* spp.) leaves are easily digestible and are common forage of upland calving caribou when they are available (e.g.,



Figure 3.16. Porcupine caribou herd *a*) diet composition and *b*) median phenology of major forage items, 1993. Diet composition estimated from microhistological analysis of fecal pellets, corrected for digestibility. Phenology scores for cottongrass: 1 = leaves only, 2 = flowers in boot, 3 = early flower, 4 = full flower; and for willow: 1 = dormant, 2 = bud swelling, 3 = leaf unfolding, 4 = full leaf.



Figure 3.17. Porcupine caribou herd *a*) diet composition and *b*) median phenology of major forage items, 1994. Diet composition estimated from microhistological analysis of fecal pellets, corrected for digestibility. Phenology scores for cottongrass: 1 = leaves only, 2 = flowers in boot, 3 = early flower, 4 = full flower; and, for willow: 1 = dormant, 2 = bud swelling, 3 = leaf unfolding, 4 = full leaf.

Thompson and McCourt 1981, Kuropat 1984, Russell et al.1993). Cottongrass flowers were most common in the vegetation type herbaceous tussock tundra, and willow was most common in shrub tussock tundra and riparian shrub vegetation types (Jorgensen et al. 1994). Herbaceous plants were ubiquitous.

Dietary shifts within the 1993 and 1994 calving seasons apparently allowed caribou to increase nutrient concentration in their diet as the season progressed. By mid-June, 1993-1994, as cottongrass flowers matured, the leaves of willows unfolded (Figs. 3.16*b*, 3.17*b*). Then, within about 4 days (Figs. 3.16*a*, 3.17*a*), caribou diet shifted to an approximate 50:50 mix of willow and herbaceous plants.

The diet shift resulted in an increase of dietary nitrogen concentration (from 3% to 4%) and a decrease in Neutral Detergent Fiber (NDF) concentration (from 57% to 27%) based on nutritional analyses of cottongrass and willow of appropriate phenological stages from the calving ground. Available biomass of willow likely exceeded the biomass of cottongrass flowers during the diet shift and thereafter. Caribou maintained the willow and herbaceous diet until they departed the calving ground near the end of June. Because climate warming and earlier greening may increase the carbon:nitrogen ratios of individual forage species and reduce their quality on fixed dates (Walsh et al. 1997), rapid shifting among forage species may allow caribou to accommodate time-specific reduction in nutritional quality of individual plant species that accompanies climate warming.

Diet of Porcupine herd caribou was substantially different when they used the Canadian portion of the extent of calving than when they used the Arctic Refuge coastal plain and the 1002 Area. Regardless of timing of snowmelt in Canada, calving diet there was dominated by mosses and evergreen shrubs (58.4-73.5%, Russell et al. 1993). These forage groups were much less digestible than the immature cottongrass flowers and willows (Russell et al. 1993) that dominated the calving diet of the Porcupine caribou herd in 1993 and 1994. This implied that diet quality during calving was reduced when the Porcupine caribou herd used the Canadian portion of the extent of calving rather than the Arctic Refuge coastal plain and the 1002 Area.

Habitat Selection

Habitat selection may be assessed at several orders (Johnson 1980); selection at each order implies disproportionate use of some component(s) of the habitats that are available. For migratory barren-ground caribou, selection orders might be defined as follows from highest to lowest order:

First Order – the species distribution on earth.

Second Order – area use by herds within the species range.

Third Order - annual range use within herd ranges.

Fourth Order – seasonal range use within annual ranges of herds.

Fifth Order – annual use within the aggregate extent of a seasonal range.

Sixth Order – annual concentrated use within an annual seasonal range.

Seventh Order – patch use within a concentrated use area. Eighth Order – plant species use within habitat patches. Ninth Order – plant part use within plant species.

Higher order selection may constrain the choices at lower orders (Johnson 1980). The basis of selection may or may not be consistent among orders and, when the basis of selection changes among orders, habitat selection is considered to be scale-dependent (O'Neil and King 1998). In this work, we assessed habitat selection at fifth and sixth orders as defined above. Much discussion has focused on fourth order selection (cf. Bergerud and Page 1987; Fryxell 1991, 1995), but analysis of selection at the fourth order for the Porcupine caribou herd was beyond the scope of this report.

For the purposes of the material that follows, we define *fifth order selection* as the comparison of use within the annual calving grounds (ACG) to availability in the extent of calving (EC), written as ACG/EC (hereafter called *calving ground selection*). We define *sixth order selection* as the comparison of use within annual concentrated calving areas (CCA) to habitat availability within the annual calving grounds (CCA/ACG, hereafter called *concentrated calving selection*).

Because there was spatial dependency among habitats (vegetation, NDVI estimates, snowcover; all inventoried from the same 1-km² pixels) we present the results for each habitat attribute separately. Selection was assessed by comparing mean use/availability ratios among years with the null use/availability ratio of 1.0.

Habitat conditions within the extent of calving have been variable during 1985-2001. There was substantial snowcover throughout the extent of calving in 1986, 2000, and 2001, but greening was early in 1990, 1994, 1995, and 1998 (Fig. 3.18).

There was scale dependency in habitat selection by the Porcupine caribou herd during calving. Parturient females selected annual calving grounds with proportionately greater area of high (>median) rate of greening (NDVI_rate, 1.33x, P = 0.005) (Fig. 3.19*a*) and proportionately less area with high forage biomass both at calving (NDVI_calving, 0.60x, P < 0.001) (Fig. 3.19*b*) and during peak lactation (NDVI_621, 0.70x, P = 0.002) (Fig. 3.19*c*) than available in the extent of calving.

Parturient females also selected annual calving grounds with proportionately more area in the 26-50% (1.76x, P = 0.001) and 51-75% (1.71x, P = 0.008) snowcover classes and proportionately less area in the 0-25% (0.84x, P = 0.008) snowcover class than available in the extent of calving (Fig. 3.20).

Analysis of vegetation types in annual calving grounds showed that parturient females selected wet sedge (1.42x, P = 0.004), herbaceous tussock tundra (1.42x, P < 0.001), and riparian (1.37x, P < 0.001) vegetation types, avoided the alpine vegetation type (0.60x, P < 0.001), and did not respond (P > 0.05) to the shrub tussock tundra or moist sedge vegetation types (Fig. 3.21).

In contrast, at the next lower selection order (sixth), parturient females of the Porcupine caribou herd selected concentrated calving areas with proportionately greater area of high forage biomass both at calving (NDVI_calving, 2.35x, P < 0.001) (Fig. 3.19b) and during peak lactation demand (NDVI_621, 2.59x, P < 0.001) (Fig 3.19c) than available in the annual calving grounds. The females were non-selective (P > 0.05) for rate of greening (NDVI_rate) (Fig. 3.19a) and all snowcover classes (Fig. 3.20), selected herbaceous tussock tundra



Figure 3.18. Annual conditions of snowcover and vegetation phenology derived from Advanced Very High Resolution Radiometer (AHVRR) satellite imagery during the calving period (30 May - 5 June), 1985-2001, for the Porcupine caribou herd. No concentrated calving was detected in 2001.



Figure 3.19. Average percent of area in low (\leq median) or high (> median) classes of *a*) daily rate of increase in the Normalized Difference Vegetation Index (NDVI_rate) *b*) NDVI at calving (NDVI_calving), and *c*) NDVI on 21 June (NDVI_621) for the aggregate extent of calving, annual calving grounds, and concentrated calving areas of the Porcupine caribou herd, Alaska, 1985-2001. Statistically significant selection or avoidance (P < 0.05, overall experiment) in comparison with the category to the left is indicated by "+" or "-" above the bars. For example, female caribou on the annual calving ground avoided low NDVI_rate and selected high NDVI_rate in comparison with availability in the aggregate extent of calving. No significant selection of NDVI_rate for the concentrated calving area when compared with the annual calving ground was detected.



Figure 3.20. Average percent of area in 4 exclusive snowcover classes for the aggregate extent of calving, annual calving grounds, and concentrated calving areas of the Porcupine caribou herd, 1985-2001. Statistically significant selection or avoidance (P < 0.05, overall experiment) in comparison with the category to the left is indicated by "+" or "-" above the bars. For example, female caribou on the annual calving ground avoided areas of 0-25% snowcover and selected areas of 26-50% and 51-75% snowcover when compared with availability in the aggregate extent of calving. No significant selection of any snowcover class was detected for the concentrated calving area when compared with availability in the annual calving ground.

(1.68x, P = 0.001), avoided alpine vegetation (0.34x, P < 0.001), and were non-responsive (P > 0.18) to the remaining vegetation types (Fig. 3.21).

Although selection of vegetation types was scaleindependent, there was scale dependency in the selection of forage quantity (NDVI_calving, NDVI_621) and quality (NDVI_rate). Parturient Porcupine caribou herd females selected annual calving grounds with a high proportion of easily digestible forage (NDVI_rate), then selected concentrated calving areas with relatively high plant biomass at calving (NDVI_calving) and on 21 June (NDVI_621).

The basis of habitat selection shifted from forage quality to forage quantity between the fifth (ACG/EC) and sixth (CCA/ACG) orders. The work of White et al. (1975) and White and Trudell (1980b) at the levels of microhabitats (~seventh order, selection for biomass) and plant species within microhabitats (~eighth order, selection for digestibility) suggests that the basis of selection continues to be dynamic across successively smaller scales.

Forage quality appears to be the basis of selection at both relatively large (fifth order) and relatively small (eighth order) scales. Forage quantity appears to be the basis of selection at intermediate scales of analysis within this range. Specification of the scale of analysis is critical to developing an understanding of the basis of forage selection by ungulates, and Porcupine herd caribou demonstrated a variable functional response to forage (NDVI estimates) within the extent of calving.



Figure 3.21. Average percent of area in 6 vetetation types for the aggregate extent of calving, annual calving grounds, and concentrated calving areas of the Porcupine caribou herd, 1985-2001. Vegetation types: Wsedge = wet sedge; Msedge = moist sedge; HerbTT = herbaceous tussock tundra; ShrubTT = shrub tussock tundra, Alpine, and Riparian. Statistically significant selection or avoidance (P < 0.05, overall experiment) in comparison with the category to the left is indicated by "+" or "-" above the bars. For example, the female caribou on the annual calving ground avoided the Alpine vegetation type and selected the HerbTT vegetation type when compared with availability in the aggregate extent of calving, and on the concentrated calving area the caribou showed similar selection when compared with availability in the annual calving ground.

There were no clear differences in patterns of selection of any types of habitats between the increase and decrease phases of the herd. This observation is tempered by the fact that habitat selection was assessed for only the last 5 years (1985-1989) of the increase phase, but has been assessed for all 12 years of the current decline (1990-2001).

The shifting location of annual calving grounds within the extent of calving was apparently a functional response to annually variable landscape patterns in the quantity of easily digestible forage (NDVI_rate). The location of concentrated calving areas within annual calving grounds was an apparent functional response to forage biomass (NDVI calving, NDVI 621).

This functional response to habitats allowed Porcupine caribou herd females to attain substantial intakes of nitrogen (Fig. 3.22) based on estimated diet composition (Figs. 3.16*a*, 3.17*a*), estimated nitrogen content of consumed forages, and consumption rates presented by White et al (1975), White and Trudell (1980*a*,*b*), and Trudell and White (1981). Thus, the Porcupine caribou herd calving ground was clearly important to the annual nitrogen budget of lactating females and was likely important to the annual energy budget.

The adjacent Central Arctic herd obtained only about one-quarter as much dietary nitrogen from its calving



Figure 3.22. Estimated total intake of dietary nitrogen (g) from the calving ground (25 May - 14 June) for 4 North American caribou herds. Forage composition of diet and nutritional composition of forages were estimated from locally collected samples. Intake rates were estimated from White et al. (1975).

ground as did the Porcupine caribou herd (Fig. 3.22). It is likely that the proportion of the annual nitrogen budget obtained from a calving ground is positively correlated with the relative value of the calving ground to the nutrition of a herd within its annual range.

Effects of Insect Harassment on Habitat Use

Mosquitoes (*Cuculidae*) and flies of the family *Oestridae* are known to harass caribou, although harassment by Oestrid flies may occur primarily after Porcupine herd caribou leave the calving ground. Lactating females that are disturbed by insects may experience a negative energy balance due to increased movement rates when trying to escape harassment by insects (White et al. 1975, Russell et al. 1993). When harassment causes lactating females to substantially reduce foraging time, calf growth may be reduced (Helle and Tarvainen 1984, Fancy and White 1987, Russell et al. 1993).

During warm and calm days (mean temperature >13°C and mean wind speed <6m/sec) when conditions were such that caribou were likely harassed by insects (Nixon 1990), Porcupine herd caribou preferred dry prostrate shrub vegetation types on ridge tops in the foothills and mountains of the Brooks Range, elevated sites on the coastal plain, and areas adjacent to the Beaufort Sea coast, apparently to gain relief from mosquitoes (Walsh et al. 1992).

Porcupine herd caribou did not display as strong a tendency to move to the coastline during potential insect harassment as has been seen for the adjacent Central Arctic herd. Observations of movements of unmarked animals during survey flights, however, indicate that
segments of the herd often follow the coastline while moving along the coastal plain of the Arctic Refuge in July (F. J. Mauer, U.S. Fish and Wildlife Service, personal communication).

Individual radio-collared caribou showed at least partial fidelity (i.e., caribou repeatedly returned to specific areas) to either the coastal plain, foothills, or mountain zones during the insect harassment season in different years (Walsh et al. 1992). The negative energetic consequences of insect harassment (Helle and Tarvainen 1984) suggest that free access to insect relief habitat is important to caribou (Walsh et al. 1992), but in some herds the energetic cost of insect harassment may be low (Toupin et al. 1996).

Calf Performance in Relation to Habitat Use

Mean calf weights within 1-2 days of birth were remarkably similar among years. On average, female calves caught during 1992-94 when the herd was declining weighed 6.2 kg, slightly less (P = 0.003) than \leq 2-day-old female calves caught during 1983-85 (6.7 kg, Whitten et al. 1992) when the herd was increasing.

The increase/decrease classification, however, explained only about 9% of the variance in calf weights. The difference in female calf weights between the increase and decrease phases of the herd was due solely to a cohort of heavy calves in 1985 (7.2 kg). Female calves caught in 1983-84 weighed an average of 6.3 kg (Whitten et al. 1992).

There was a significant interaction among years and between periods (0-3 weeks and 4-5 weeks after birth) (P < 0.001) in daily weight-gain of female calves, 1992-94 (Fig. 3.23). Daily gain was particularly low during the fourth and fifth weeks of life for calves born in 1993 (Fig. 3.23).

Daily weight-gain of calves did not differ between calves born in the concentrated calving areas and in the peripheral calving areas (P = 0.214). Much higher relative densities of caribou (7x on average) in the concentrated calving areas compared to peripheral calving areas may have reduced forage available to individual lactating females.

Even though concentrated calving areas had a greater proportion of area with high plant biomass (both NDVI_calving and NDVI_621) than did the annual calving grounds, the differential in forage abundance was evidently not sufficient to overcome the higher densities of caribou in the concentrated calving areas and to enhance the weight-gain of calves born there.

Patterns of habitat use by calves varied significantly (P < 0.01) between periods and among years, 1992-1994 (Fig. 3.24a-c), but were generally similar to use of sites for calving (Fig. 3.21). Weight-gain of calves during calving ground use was not associated with the percent of



Figure 3.23. Daily gain (kg) of caribou calves of the Porcupine herd, 1992-1994, during 2 periods (0-3 weeks post-birth and 4-5 weeks post-birth). Gain was estimated from sequential weights of recaptured radio-collared animals. Means are listed above the appropriate bars.

time that calves spent in any particular vegetation type or in any class of forage at calving (NDVI_calving), rate of increase in forage during lactation (NDVI_rate), forage available at the peak of lactation (NDVI_621), or snowcover (P > 0.05).

Although individual calf weight-gain was not explained by within-annual-calving-ground habitat use, several characteristics of parturient females and calves were related to habitat conditions in the annual calving grounds, 1992-1994. The rank orders of 1) NDVI_621 in the annual calving ground, 2) average parturient female weights (Fig. 3.25), 3) parturient female body condition score, and 4) average calf weights, all at 3-weeks postcalving, were all the same (1993 > 1994 > 1992).

Lack of correlation between individual calf weightgain and use of annual calving ground habitat suggests that the location of annual calving grounds may have maximized calf weight-gain, given the conditions of the annual habitat available within the extent of calving. Once the annual calving ground was located in an area that provided a high proportion of easily digestible forage (high NDVI_rate), then variation in caribou density and forage biomass (NDVI_calving, NDVI_621) may have interacted to reduce variation in performance among the individual study animals.

Factors Associated with Calf Survival on the Calving Ground

During 1983-1985, average mortality of calves during June was 29% (Whitten et al. 1992), slightly higher than the 1983-2001 average of 25%. In those early years, about 61% of mortality on the calving ground was due to predation and the remainder (39%) was due to nutritional or physical characteristics of calves (Whitten et al. 1992, Roffe 1993). The interaction between nutritional status of the calves and predation mortality was not known.



Figure 3.24. Availability of 6 vegetation types in the aggregate extent of calving for the Porcupine caribou herd and use by radio-collared calves during 2 periods (0-3 weeks post-birth and 4-5 weeks post-birth) for *a*) 1992, *b*) 1993, and *c*) 1994. Vegetation types: Wsedge = wet sedge; Msedge = moist sedge; HerbTT = herbaceous tussock tundra; ShrubTT = shrub tussock tundra, Alpine, and Riparian.

Predation occurred further south and at higher elevations near the foothills during 1983-1985 (Whitten et al. 1992).

During 1983-1985, golden eagles caused most predation mortality of calves on the annual calving grounds (~60%), grizzly bears ranked second (~24%), and wolves ranked third (~16%) (Whitten et al. 1992). Young and McCabe (1997) estimated that bears killed about 2% of calves during 1994, a year with relatively high overall calf survival (Fig. 3.10*b*).

Immature golden eagles ranged throughout the coastal plain and foothills (Clough et al. 1987), while golden eagle nests and wolf dens were primarily restricted to the foothills (*see Fig. 6.1*). Grizzly bear densities were moderate and their distributions were concentrated in the foothills (Young and McCabe 1997). In late summer through winter, the source and distribution of predation mortality of calves were unknown, but wolves were probably the dominant predator.

We used multiple scales to analyze factors associated with calf survival during June: 1) fate of individual calves within the population of calves; and 2) the proportion of the annual population of calves that survived until the end of June in relation to a) habitat characteristics within the extent of calving and b) habitat characteristics within each annual calving ground. These latter 2 classifications are conceptually equivalent to the fifth and sixth order habitat selection analyses.

Several factors were associated with enhanced survival of individual calves, 1983-1994 (n = 345 calves). Survival was greater (10.8%, P = 0.004) if the calf was born in a high density concentrated calving area rather than in the low density peripheral portion of the calving ground; greater (11.0%, P = 0.008) if born near the median calving date rather than being born early or late in the calving season; greater (11.2%, P = 0.006) if born on



Figure 3.25. Median Normalized Difference Vegetation Index on 21 June (NDVI_621) within the annual calving grounds of the Porcupine caribou herd and weights of parturient female caribou when captured within the annual calving ground on 21 June, 1992-1994.

the coastal plain with lower suspected density of wolves, eagles and bears; and greater (8.3%, P = 0.026) if born in the 1002 Area.

The survival advantage of high density calving to individual calves tended to be greater when calves were born in the foothills and mountains than when they were born on the coastal plain (14.3% advantage vs. 7.9% advantage, respectively).

Individual calf survival was not related (P = 0.160) to the frequency of use of its birth site as a portion of the concentrated calving area, 1983-1994, but calf survival was lower (9.9%, P = 0.026) if the birth site was in an area never used as a concentrated calving area. In a stepwise logistic regression analysis that simultaneously considered calving density, time of birth, zone of birth (coastal plain or foothills), and in or out of the 1002 Area, only calving density (P = 0.004), time period of birth (early, middle, late; P = 0.012), and zone (P = 0.008) entered the model that predicted individual calf survival, 1983-1994.

The survival advantage of both high calving density and being born near the middle of the calving period may have been due to predator swamping where high spatial and temporal densities of calves may make it difficult for predators to capture individual calves (Hamilton 1971). Bears tended to be less successful at capturing calves in the concentrated calving areas of the Porcupine caribou herd (Young and McCabe 1997).

When assessing the proportion of the annual population of calves that survived during June, the timing of birth in relation to other calves was not applicable, but median calving date, 1983-1996, was available. In addition, we could consider the relative amount of food (NDVI_calving, NDVI_rate, and NDVI_621), winter range conditions prior to calf birth (snow properties), and the proportion of calves born in coastal plain or foothill zones.

Analyses of the proportion of calves surviving in relation to these independent variables were conducted separately at 2 scales: a) the extent of calving and b) the annual calving grounds.

Within the extent of calving, the relative amount of forage available to females during peak lactation (NDVI_621) provided the best model of calf survival during June ($r^2 = 0.85$, P < 0.001) (Fig. 3.26). No other independent variable that was considered added significant explanatory power.

This model (Fig 3.26) (Percent June Calf Survival = $[0.107 + (2.05 * \text{NDVI}_621 \text{ in the extent of calving})] * 100)$ was the best available estimate of survival of calves during June for the Porcupine caribou herd under undisturbed conditions during the past 2 decades. This model of calf survival was independent of annual calving ground location and, if the 1002 Area is developed, the



Figure 3.26. Calf survival through June for the Porcupine caribou herd, 1985-2001, in relation to median Normalized Difference Vegetation Index on 21 June (NDVI_621) within the aggregate extent of calving (EC). Legends identify the year of the estimate. Calf survival was not estimated in 1986 because inclement weather prevented a complete sample in late June. Calf survival for 1993 was a significant outlier (RStudent = 3.84, see text for biological justification) and was excluded from the estimated regression line ($r^2 = 0.85$, P < 0.0001). Upper and lower dashed lines indicate 95% confidence intervals on the predicted observations.

model can be used to assess whether calf survival during June is affected by development.

Calf survival for 1993 was an outlier (RStudent = 3.84) and excluded from the estimated relationship between NDVI_621 in the extent of calving and calf survival (Fig. 3.26) and from all subsequent models of calf survival. During 1992, atmospheric aerosols from the eruption of Mt. Pinatubo in the Philippines reached the Arctic in the spring (Stone et al. 1993). This resulted in a late spring, cool summer, early and heavy snow deposition in the fall, and near catastrophic conditions for caribou.

We surmise that the consistently bad weather conditions during 1992 and early 1993 resulted in a carryover effect that reduced calf survival in 1993 to levels much lower than would have been expected on the basis of NDVI_621 alone. It was likely that this suspected additional mortality in 1993 affected calves within the first day or two of life; perhaps many calves were of very low birth weight. We draw this conclusion because 0- to 3-week weight-gain of calves that survived to be radiocollared in 1993 was as high as any other year (Fig. 3.23) and the weights of parturient females that were caught with their live calves on ~21 June in 1993 were as high as any weights we observed, 1992-1994 (Fig. 3.25).

At the smaller scale of the annual calving grounds, the proportion of Porcupine caribou herd calves that survived through June was positively related to both NDVI_621 in the annual calving grounds and to the proportion of calves that were born on the coastal plain (assumed lower

predation risk) ($r^2 = 0.70$, P < 0.001). No other variable added significant explanatory power. Median NDVI_621 in the annual calving grounds and the proportion of calves born on the coastal plain were not correlated (P > 0.94). Forage in the annual calving ground accounted for approximately 75% of the total variance explained by this model and assumed predation risk accounted for the remainder (Fig. 3.27).

Thus, in addition to scale dependency in the functional response of caribou to habitats (selection of NDVIs within the extent of calving and within the annual calving grounds), there was scale dependency in the numerical response of calf survival to calving ground location and habitat conditions. Only forage was related to calf survival at the largest spatial scale (extent of calving) that we analyzed.

At the intermediate scale (annual calving ground), forage dominated calf survival, but predation risk added substantial explanatory power. At the smallest scale (individuals within the population of calves), spatial and temporal variance in calf density (indirect predation risk) and direct predation risk most effectively explained calf survival.

This scale dependency in calf survival likely occurred because the annual variance in habitat conditions in both the extent of calving and in the annual calving grounds far exceeded the annual variance in predation risk within the extent of calving and within the annual calving grounds. The scale dependency in calf survival made it impossible to extrapolate across scales. Thus, to develop an understanding of the relative influence of forage and



Figure 3.27. Predicted calf survival for the Porcupine caribou herd, 1985-2001, in relation to median Normalized Difference Vegetation Index on 21 June (NDVI_621) within the annual calving ground and to the proportion of calves born on the Arctic National Wildlife Refuge coastal plain physiographic zone where predator density was lower than in the foothill-mountain physiographic zone ($r^2 = 0.696$, P < 0.001). Calf survival was not estimated in 1986 because inclement weather prevented a complete sample in late June.

predation on calf survival, it is imperative to specify the scale of analysis, and assess multiple scales simultaneously.

The temporal increase in forage during peak lactation (NDVI 621) (Fig. 3.4) was coincident with local climate warming (Fig. 3.3*a*). Forage at calving (NDVI calving) was positively associated with the Arctic Oscillation (Fig. 3.6). There were also positive relationships between climate and NDVI calving, between percent of females calving in the 1002 Area and NDVI calving, and between calf survival and NDVI calving $[r^2 = 0.33, P = 0.011]$ (annual calving ground); $r^2 = 0.60$, P < 0.001 (extent of calving)]. As a result, June calf survival was weakly correlated ($r^2 = 0.22$, P = 0.029) with the proportion of cows that calved in the 1002 Area. Further, because climate affected calving ground location (e.g., Porcupine caribou herd females were more likely to use the western portion of the extent of calving following winters with a positive Arctic Oscillation), both forage availability and predation risk were implicitly related to climate.

In years with substantial snowcover on the coastal plain (Fig. 3.18) and relatively low NDVI_621 in the extent of calving, average calf survival (66%, n = 7, SE = 6%) was 19% less (P = 0.008) than when there was little snowcover at calving and NDVI_621 was high (85%, n = 6, SE = 11%). Thus, climate was an important influence on habitat conditions, on the likely use of the Alaska coastal plain and 1002 Area for calving, and on calf survival during June, 1983-2001, under undisturbed conditions.

Potential Effects of Development on June Calf Survival

In order to assess the potential effects of development of the 1002 Area on the Porcupine caribou herd during calving, we needed a model of caribou behavioral response to oil field infrastructures. The adjacent Central Arctic herd (Fig. 3.2), which calved in the vicinity of Prudhoe Bay - Kuparuk complex of petroleum development areas, provided the only available model of caribou behavioral response to petroleum development during calving.

Parturient female caribou (i.e., those about to give birth or accompanied by very young calves) of the Central Arctic herd repeatedly demostrated their sensitivity to disturbance during the first few weeks of life of their calves (Smith and Cameron 1983, Whitten and Cameron 1983, Dau and Cameron 1986; Cameron et al. 1992; Nellemann and Cameron 1996, 1998).

Parturient females avoided, or were less likely to cross, *infrastructures* (roads and pipelines) during the calving season (Cameron and Whitten 1979, Dau and Cameron 1986, Murphy and Curatolo 1987, Lawhead 1988, Cameron et al. 1992). In addition, densities of caribou during calving (June) were greater than expected beyond 4 km from roads and pipelines (Cameron et al. 1992).

Central Arctic herd caribou may make substantial use of areas in the vicinity of oil field infrastructures during periods of moderate to high insect abundance during postcalving in July (Pollard et al. 1994). That observation is not relevant, however, to the distribution of the Central Arctic herd during calving in June nor to the assessment of Porcupine caribou herd distribution during calving in relation to potential oil development: Caribou of the Porcupine herd generally depart the calving ground during early July.

Historically, 2 zones of concentrated calving of the Central Arctic herd have been recognized (Murphy and Lawhead 2000). The zones were physically divided by the Sagavanirktok River and the trans-Alaska oil pipeline. There was an eastern *reference* zone where development infrastructure was historically absent through 1995, and a western *developed* zone that included the Prudhoe Bay, Milne Point, and Kuparuk petroleum development areas. In 1996, the developed versus reference zone study design was compromised by the completion of pipelines leading to the Badami petroleum development area, east of the trans-Alaska oil pipeline and into the reference zone.

During the late 1980s, concentrated calving in the developed zone shifted from the vicinity of the Kuparuk-Milne Point petroleum development areas to undeveloped areas to the south-southwest of the oil fields (Lawhead et al. 1993, Murphy and Lawhead 2000). Low density calving continued to occur in these petroleum development areas while concentrated calving shifted. That shift was completed by approximately 1987 when the Oliktok Point and Milne Point roads were completed and substantial infrastructure was in place. The unidirectional shift in concentrated calving in the developed zone, 1980-1995, has subsequently been confirmed (P <0.002, Wolfe 2000). During the same years, however, the concentrated calving area in the reference area showed no uni-directional shift (P = 0.14, Wolfe 2000) (see also Fig. 4.7).

Since 1996 the bulk of high density calving in the developed zone has remained south of roads and pipelines although a small zone of high density calving occurred in the Kuparuk-Milne Point area in 1996 (Lawhead and Prichard 2001). The shift in calving distribution in the developed zone occurred even though the Milne Point and Kuparuk petroleum development areas included substantial improvements in field design and layout (e.g., elevated pipes, reduced road density) that should have facilitated caribou passage compared with the design of the older Prudhoe Bay Complex.

No other concentrated calving area of Alaska barrenground herds has demonstrated a statistically significant uni-directional shift during the past 2 decades. Kelleyhouse (2001) showed no uni-directional shift in concentrated calving for the Western Arctic herd, 1987-2000, but was unable to assess shifts in the concentrated calving areas of the Teshekpuk Lake herd due to an inadequate number of years for the test. As noted previously, directional shifts of concentrated calving areas of the Porcupine caribou herd have not differed from randomness, 1983-2001.

Forage during peak lactation (NDVI 621) in the concentrated calving area in the developed zone of the Central Arctic herd declined as the concentrated calving area shifted south-southwest, 1980-1995 (Wolfe 2000). During this shift, forage during peak lactation remained highest in the area used for concentrated calving during 1980-1982 (Wolfe 2000). There was, however, no decline in forage availability on June 21 (NDVI 621) in the concentrated calving areas in the reference zone of the Central Arctic herd during 1980-1995 (Wolfe 2000). No clear biological evidence explained the shift of concentrated calving in the developed zone to an area of reduced forage availability for lactating females. Thus, petroleum development was implicated as a cause of the southerly shift in concentrated calving in the developed zone of the Central Arctic herd, 1980-1995.

Since the first census of the Central Arctic herd in 1978, the herd size has increased from approximately 5,000 to approximately 27,000 animals in 2000 (E. A. Lenart, Alaska Department of Fish and Game, personal communication. *See also Fig 4.2*). There was a sharp decline (from 23,000 to 18,000) in the herd from 1992-1995 and a subsequent recovery. It is unknown whether the Central Arctic herd would have increased at a higher rate than observed had the concentrated calving area in the developed zone not shifted to the south-southwest by 1987.

The observation of either an increase or decrease of any magnitude in the size of the Central Arctic herd or any other herd is not, by itself, sufficient evidence to conclude that there has been an effect of development or lack thereof on herd size. For example, had the 1002 Area been developed in 1989, the subsequent natural decline of the Porcupine caribou herd (Fig. 3.8) would not have constituted evidence of an effect of development.

To assess potential effects of development on the growth curve of the Central Arctic herd, we needed to make comparisons with an ecologically similar herd. The Porcupine caribou herd does not constitute a good ecological comparison and neither does the Western Arctic herd. The Teshekpuk Lake herd (Fig. 3.9) is the most ecologically comparable herd to the Central Arctic herd in Alaska.

The Central Arctic herd and Teshekpuk Lake herd are certainly not identical, however: 1) both herds are relatively small in size and the trajectories of their growth curves suggest exponential growth, 2) both herds have relatively high bull:cow ratios (~80:100), 3) calving ground habitats of both herds showed similar climate trends (Kelleyhouse 2001, Wolfe 2000), 4) both herds exhibited the same dip in herd size during the mid-1990s (Fig. 3.9), 5) neither herd has consistently demonstrated the long distance migrations exhibited by the Western Arctic herd and Porcupine caribou herd, and 6) before 1987, both components of the Central Arctic herd as well as the Teshekpuk Lake herd calved in wet coastal habitats with relatively late snowmelt.

The apparent divergence in the relative sizes of the Central Arctic herd and adjacent Teshekpuk Lake herd after 1987 (Fig. 3.9) suggests that the growth rate of the Central Arctic herd may have slowed after roads and pipelines expanded in the developed zone and the concentrated calving area in the developed zone shifted south-southwest. The relative trajectories of the 2 herds' growth curves were parallel through the mid- to late-1980s when both herds were slightly less than 4 times as large as when first censused. Thereafter, their trajectories diverged slightly. By the late 1990s the Teshekpuk Lake herd was about 7 times larger than when first censused while the Central Arctic herd was only about 5.4 times as large as when first observed. Cronin et al. (1998) noted that exponential growth rate of the Teshekpuk Lake herd was approximately twice as great as the exponential growth rate estimated for the Central Arctic herd (0.152 vs. 0.077, respectively) from the mid-1970s through the mid-1990s.

Several ecological factors may have diluted or obscured any population consequences of avoidance of petroleum development areas by the Central Arctic herd during calving. First, only the half of the herd that used the developed zone was potentially affected. Reduction in available food for lactating females during peak lactation was demonstrated only for the females that used the developed zone concentrated calving area (approximately 25% of all females in the Central Arctic herd; Wolfe 2000).

Second, the Central Arctic herd remained on the coastal plain when it shifted its concentrated calving areas in the developed zone. The parturient females and calves were not displaced to the adjacent foothills where predator densities were assumed to be greatest. Thus, the shift may have incurred little if any additional mortality due to predation.

Third, development of the complex of petroleum development areas from Prudhoe Bay to Kuparuk has occurred during a period of relatively favorable environmental conditions (Maxwell 1996). The resilience of herds to abiotic, biotic, or anthropogenic challenges would be expected to be greatest during favorable environmental conditions. Fourth, because the Central Arctic herd obtained a relatively small proportion of its annual nitrogen budget from its calving ground compared with other herds (Fig. 3.22), the Central Arctic herd calving ground may have had less relative value to herd performance than the calving grounds of other herds.

Fifth, calving ground density of the Central Arctic herd has been, and remains, quite low (approximately one-fifth the effective density of the Porcupine caribou herd; Whitten and Cameron 1985). Thus, even though females of the Central Arctic herd in the developed zone shifted their concentrated calving to an area with reduced total forage, the amount remaining per caribou may have been sufficient to accommodate nutritional requirements.

Because ecological conditions for the Porcupine caribou herd are substantially different than for the Central Arctic herd, it is unlikely that all these ameliorating factors will apply to the response of the Porcupine caribou herd to development within its calving ground. Nevertheless, the avoidance of oil field roads and pipelines by parturient females of the Central Arctic herd during the calving season is transferable to Porcupine caribou herd because sensitivity to disturbance by parturient caribou has been repeatedly noted elsewhere (Wolfe et al. 2000).

To assess the potential effects of petroleum development in the 1002 Area on the Porcupine caribou herd, we assumed that displacement of Porcupine caribou herd's concentrated calving grounds would occur, similar to the shift observed for the concentrated calving area in the developed zone of the Central Arctic herd (Lawhead et al. 1993, Wolfe 2000). We then used empirical habitatdemography relationships developed in the Porcupine caribou herd studies to assess the implications of this hypothetical displacement on calf survival during June for the Porcupine caribou herd.

We based our predictions on an empirical model relating calf survival to forage in the annual calving ground on 21 June and to the proportion of calves born in low predation risk (Fig. 3.27). This empirical model was Percent June Calf Survival = $[-0.0396 + (2.0989 * \text{median NDVI}_621 \text{ in the annual calving ground}) + (0.00283 * proportion of calves born in low predation risk)] * 100, (<math>r^2 = 0.70$; P < 0.001). The spatially explicit nature of this intermediate-scale model subsumed the effects of temporal and spatial caribou density on individual calf survival.

First, we used the empirical model to predict calf survival in each of the 17 observed annual calving grounds of the Porcupine caribou herd, 1985-2001 (Fig. 3.13). Then each concentrated calving area was displaced the minimum distance necessary to provide 4 km clearance from the boundary of each of 4 hypothetical oil development scenarios for the 1002 Area presented in Tussing and Haley (1999; scenarios 2-5) and for the single hypothetical development scenario presented in the 1987 Final Legislative Environmental Impact Statement (Clough et al. 1987). The scenarios in Tussing and Haley (1999) are based on the most recent estimates of the distribution and quantity of oil reserves within the 1002 Area (U.S. Geological Survey 2001).

This protocol assumed oil field design similar to the Kuparuk and Milne Point petroleum development areas within the scenario boundaries. The modeling exercise could be used to assess the potential effects of additional development scenarios that are not presented in Tussing and Haley (1999) or Clough et al. (1987).

Central Arctic herd parturient females actually separated their concentrated calving areas from development infrastructure by about 7-8 km (Wolfe 2000). We used a conservative displacement of 4 km based on observations by Cameron et al. (1992) of increased caribou density from 4 km outward beyond roads and pipelines. Calving sites and the entire annual calving grounds were displaced along with the concentrated calving areas.

Our protocol stated that a concentrated calving area could not be moved onto the Beaufort Sea. We made no changes in shape of the concentrated calving areas or annual calving grounds. As a result of these shifts, relatively small portions of the peripheral, low-density calving areas were occasionally moved onto the Beaufort Sea along with some associated calving sites. We treated these ocean sites as missing data when assessing the potential effects of displacement on calf survival.

Modeled displacement for the Porcupine caribou herd was to the east and south, parallel to the Beaufort Sea coastline, because that is the direction of the herd's migratory approach to the annual calving grounds in spring. Displacement of the developed-zone concentrated calving areas of the Central Arctic herd has been primarily to the south, the direction of approach to that calving ground from winter range.

Our protocol minimized displacement of the Porcupine caribou herd calving grounds into the foothills and mountain zone. This tended to keep the annual calving grounds on the coastal plain in the best remaining foraging habitats. In some cases, observed concentrated calving areas (e.g., in 1988, 2000, and 2001) did not overlap the boundaries of any of the hypothetical development scenarios, and in those cases the annual calving ground was not displaced.

Once the concentrated calving areas and associated annual calving grounds and calving sites were displaced, the forage during peak lactation (NDVI_621) within the displaced annual calving ground was re-inventoried, the median was recalculated, and the proportion of calves born in the low predation risk zone (coastal plain) was recalculated.



Figure 3.28. Estimated change in calf survival during June for the Porcupine caribou herd, 1985-2001, as a function of the distance of displacement of the annual calving ground and associated concentrated calving area and calving sites. Upper and lower dashed lines indicate 95% confidence intervals on the mean effect.

Then the empirical model was again used to predict calf survival for the displaced calving ground. The difference between the calf survival estimate for the displaced and observed calving ground was calculated and a dataset of 46 displacement distances and associated changes in calf survival was generated for analysis.

The model showed a significant ($r^2 = 0.47$, P < 0.001) inverse relationship between displacement distance and predicted change in calf survival (Fig. 3.28).

The simulations indicated that a substantial reduction in calf survival during June would be expected under full development of the 1002 Area. Eighty-two percent of observed calving distributions would have been displaced and the average distance of these displacements would have been 63 km (range 16-99 km). This would have yielded a net average effective displacement of 52 km and an expected mean reduction in calf survival of 8.2% (SE = 0.7%).

It is remotely conceivable that calving caribou of the Porcupine caribou herd could select habitats that yielded equivalent forage and predation risk after displacement. Forage for lactating females of the Central Arctic herd, however, declined as the concentrated calving area in the developed zone shifted to the south-southwest (Wolfe 2000). This suggests that such compensatory habitat use by the Porcupine caribou herd would be unlikely if their calving grounds were displaced by oil development.

Because there was no empirical basis for changing the shape of the observed calving distributions, it was impossible to estimate the magnitude of the effect of considering the peripheral calving areas and calving sites as missing data when they were displaced onto the ocean. The effect was expected to be small. Arbitrarily assigning calving sites that were displaced onto the ocean back onto the coastal plain and making no other adjustments would have increased displaced calf survival by only about 0.6% on average. This probably constituted the maximum possible effect of treating areas and calving sites that were displaced to the Beaufort Sea as missing data.

Stochastic simulation modeling (Walsh et al. 1995) indicated that a 4.6% reduction in Porcupine caribou herd calf survival during June, all else held equal, would have been sufficient to halt growth of the Porcupine caribou herd during the best conditions observed to date. A 10-km average displacement in our simulations would have been sufficient to bring the upper confidence interval on the mean effect below a 0% predicted change in calf survival (Fig. 3.28). A mean displacement of 27 km in our modeled predictions would have been sufficient to reach the threshold of 4.6% mean reduction in calf survival sufficient to halt growth of the Porcupine caribou herd under best observed growth conditions to date. This latter level of displacement could occur well before full development of the 1002 Area.

The estimated effect of displacement of the Porcupine caribou herd on calf survival during June was conservative for several reasons. First, we used the conservative estimate of a 4 km displacement of concentrated calving areas from infrastructure (Cameron et al. 1992) versus 7-8 km (Wolfe 2000). Second, we displaced the concentrated calving areas parallel to the Beaufort Sea coastline thus maintaining calving distributions on the best remaining coastal plain habitat and minimizing displacement into the foothills where predation would be expected to increase calf mortality. Finally, relatively low density calving was allowed to overlap developed areas, as has been observed for the adjacent Central Arctic herd (Wolfe 2000, Lawhead and Prichard 2001).

Because the assumptions were conservative, the results were conservative. Substantial (10 to 27 km) displacement of concentrated calving areas and associated annual calving grounds and calving sites of the Porcupine caribou herd is likely to negatively affect calf survival during June. At the upper end of this range of displacement (27 km), recovery of the herd from the current decline (Fig. 3.8) would be unlikely. These conclusions are consistent with those found in the 1987 Final Legislative Environmental Impact Statement (Clough et al. 1987).

The Porcupine caribou herd has demonstrated substantial natural variability in size and demography (Figs. 3.5, 3.8, 3.10*a-c*). Because development of the 1002 Area would take time, any effects on the herd's performance may take decades to detect. Reduced calf survival may slow the rate of increase during positive phases of the growth curve of the herd and increase the rate of decline during the negative phases of the herd's growth curve. The period of natural cycles in herd size may increase and the amplitude of herd size may be affected.

The best empirical tool available for detecting potential effects of development is the modeled relationship between calf survival and forage for females during peak lactation demand (NDVI_621) within the extent of calving (Fig. 3.26). This model is independent of actual annual calving ground location and encompasses a near full cycle of herd size as well as substantial variation in hemispheric weather patterns (Fig. 3.5) and variation in calving ground location (Fig. 3.13).

With industrial development, if observed calf survival falls below the lower 95% confidence limit on the predicted observations from this model (Fig. 3.26), or if a parallel pattern of calf survival yields a significantly lower intercept term, then an effect of development on calf survival would be indicated.

Individual observations that fall below the lower confidence limit and which can be satisfactorily explained by exceptional environmental characteristics (e.g., carryover effects of near-catastrophic conditions in 1992 to 1993 after eruption of Mount Pinatubo) (Fig. 3.26) need not be considered evidence for effects of development on calf survival. A pattern of observed calf survival below the lower confidence limit would be cause for concern.

Statistical methods for making these types of decisions are currently in development (Rexstad and Debevec 2001). This assessment will require continued intensive calving ground surveys and calf survival estimates.

Conclusions

Our research has shown that the Porcupine caribou herd has significant annual variance in calving ground location (Fig. 3.13), faces annual variance in habitat conditions, selects areas with abundant high quality forage for calving, has increased survival of calves born in the concentrated calving areas, and shows a correlation between calf survival and both forage for females during peak lactation and predation risk in the annual calving grounds. All this implies that unrestricted access to annual calving grounds and concentrated calving areas maximized performance of lactating Porcupine caribou herd females and their calves. Because the Porcupine caribou herd has shown limited capacity for growth, free access to calving ground habitats may have compensated for less than optimal wintering habitats.

Location of the concentrated calving areas during the past 19 years (1983-2001) is the best estimate of the area that has provided the highest quality calving habitat for females and their calves. Calf survival within the aggregate extent of concentrated calving areas has been higher than for calves born in areas never used as a concentrated calving area (83.8% vs.73.9%, respectively,



Figure 3.29. Aggregate extent of annual calving (light green shading) and aggregate extent of concentrated calving (dark green shading) for the Porcupine caribou herd, 1983-2001. The deformed/undeformed geological boundary is discussed in USGS Fact Sheet FS-028-01 (U.S. Geological Survey 2001).

1983-1994, P = 0.026). Thus, the aggregate extent of all observed concentrated calving areas (Fig. 3.29) identifies the most valuable portion of the extent of calving in terms of calf survival during June.

Our model prediction of a reduction in calf survival when calving grounds were displaced supports the concept that caribou made a critical "decision" in locating their annual calving grounds within the extent of calving, 1983-2001. It appears that actual calving ground location maximized June calf survival given the habitat conditions within the extent of calving for a given year.

Weight-gain of calves provided further evidence for the importance of unrestricted location of annual calving grounds. The lack of a relationship between calf weightgain and habitat use within annual calving grounds suggests that weight-gain was optimized by selection of the annual calving grounds, particularly during the first 3 weeks of life.

Comparative growth of captive and wild Porcupine caribou herd calves (Parker et al. 1990) has shown that wild Porcupine caribou herd calves attain their maximum genetic potential for daily weight-gain during early- to mid-lactation (Gerhart et al. 1996). Therefore unrestricted selection of the annual calving ground may optimize weight-gain of calves for a year. The matching rank orders of NDVI_621 in the annual calving grounds and calf weights at 3 weeks of age, 1992-1994, support this concept.

Unrestricted selection of annual calving grounds likely had significant implications for the parturient females as well as for their calves. The matching rank orders of 1) NDVI_621 within annual calving grounds, 2) parturient female weights, and 3) parturient female body condition scores during peak lactation, 1992-1994, suggest substantial contribution of the calving ground to parturient females' nutritional status. Because fall weights of parturient females influence their probability of conception (Cameron et al. 1993, Cameron and ver Hoef 1994, Russell et al. 1998), calving ground habitats may contribute to parturition rates in the following year.

Petroleum development will most likely result in restricting the location of concentrated calving areas, calving sites, and annual calving grounds. Expected effects that could be observed include reduced survival of calves during June, reduced weight and condition of parturient females and reduced weight of calves in late June, and, potentially, reduced weight and reduced probability of conception for parturient females in the fall.

Whether these factors are additive to annual performance or are compensated on winter range will determine the net value of the annual calving grounds to herd performance. Determining the additive/ compensatory nature of annual calving ground value, through field and simulation studies, should be the first research priority in future work

Still unclear is the cause of the decline of the Porcupine caribou herd (Fig. 3.8) during a period when calving ground habitat conditions were favorable as a result of summer warming. Increased winter mortality was implicated by the herd decline because sub-adult and adult mortality on the calving ground has been inconsequential (Fancy et al. 1994, Walsh et al. 1995), and parturition rate and calf survival during June has remained high during the decline.

Possible mechanisms for this suspected increase in off-calving-ground mortality include: 1) reduced longevity of adult females as a result of the cumulative energetic costs of persistent high parturition and calf survival during climate warming, 2) increased energetic costs of insect harassment as the climate has warmed, 3) reduced availability of winter forage or other adverse effects associated with increasing frequency of freezethaw events, 4) the herd exceeded forage carrying capacity of winter range, or 5) an increase in some form of predation (human or natural) on the winter range.

Increased frequency of spring and fall icing events on non-calving habitats of the Porcupine caribou herd (Figs. 3.7a,b) supports the third hypothesis and may be implicated in the fifth hypothesis (increased predation mortality). Increased frequency of icing was not evident on the non-calving ranges of other Alaska barren-ground caribou herds that have not declined significantly during the 1990s (Central Arctic herd, Teshekpuk Lake herd, Western Arctic herd). Testing the remaining hypotheses will require substantial additional fieldwork. In summary, 4 research-based ecological arguments indicate that the Porcupine caribou herd may be particularly sensitive to development within the 1002 portion of the calving ground:

Low productivity of the Porcupine caribou herd - The Porcupine caribou herd has had the lowest capacity for growth among Alaska barren-ground herds (Porcupine caribou herd = 4.9%, Central Arctic herd = 10.8%, Teshekpuk Lake herd = 13%, Western Arctic herd = 9.5%) and is the only barren-ground herd in Alaska known to be in decline throughout the 1990s. This low growth rate (Fig. 3.9) indicates that the Porcupine caribou herd has less capacity to accommodate anthropogenic, biological, and abiotic stresses than other Alaska barren-ground herds. Any absolute effect of development would be expected to have a larger relative effect on the Porcupine caribou herd than on the other herds. For example, an approximate 4.6% reduction in calf survival, all else held equal, would be enough to prevent Porcupine caribou herd growth under the best conditions observed to date (Walsh et al. 1995) or prevent recovery from the current decline. A similar reduction in calf survival, all else held equal, for other Alaska barren-ground herds, however, would not be sufficient to arrest their growth.

Demonstrated shift of concentrated calving areas of the Central Arctic caribou herd away from petroluem development infrastructures - It is assumed that the Porcupine caribou herd caribou will avoid roads and pipelines during calving in a manner similar to the Central Arctic herd if development of the 1002 Area occurs. Avoidance of petroleum development infrastructure by parturient caribou during the first few weeks of the lives of calves is the most consistently observed behavioral response of caribou to development.

Lack of high-quality alternate calving habitat -Calving areas in Canada and away from the Alaska coastal plain were used only when the Arctic Refuge coastal plain, including the 1002 Area, were unavailable due to late snowmelt. Diet quality on the Canadian portions of the calving ground was substantially lower than on the Arctic Refuge coastal plain and 1002 portions of the calving ground. When snow cover reduced access by females to the Arctic Refuge coastal plain and 1002 Area for calving, calf survival during June was 19% lower than when they could calve on the Arctic Refuge coastal plain and 1002 Area.

Strong link between calf survival and free movement

of females - The location of the annual calving grounds and concentrated calving areas was variable among years in response to variable habitat conditions and was often coincident with the 1002 Area. Empirical relationships between calf survival, forage available to females in the annual calving grounds, and predation risk derived from 17 years of ecological data predict that June calf survival for the Porcupine caribou herd will decline if the calving grounds are displaced, and that the effect will increase with displacement distance. This prediction (Fig. 3.28) is a function of displacement: 1) reducing access to the highest quality habitats for foraging and 2) increasing exposure to risk of mortality from predation during calving (first 3 weeks of June).

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Section 4: The Central Arctic Caribou Herd

Raymond D. Cameron, Walter T. Smith, Robert G. White, and Brad Griffith

From the mid-1970s through the mid-1980s, use of calving and summer habitats by Central Arctic herd caribou (*Rangifer tarandus granti*) declined near petroleum development infrastructure on Alaska's arctic coastal plain (Cameron et al. 1979; Cameron and Whitten 1980; Smith and Cameron 1983; Whitten and Cameron 1983*a*, 1985; Dau and Cameron 1986).

With surface development continuing to expand westward from the Prudhoe Bay petroleum development area (Fig. 4.1), concerns arose that the resultant cumulative losses of habitat would eventually reduce productivity of the caribou herd. Specifically, reduced access of adult females to preferred foraging areas might adversely affect growth and fattening (Elison et al.1986; Clough et al. 1987), in turn depressing calf production (Dauphiné 1976, Thomas 1982, Reimers 1983, White 1983, Eloranta and Nieminen 1986, Lenvik et al. 1988, Thomas and Kiliaan 1991) and survival (Haukioja and Salovaara 1978, Rognmo et al. 1983, Skogland 1984, Eloranta and Nieminen 1986, Adamczewski et al. 1987).

Those concerns, though justified in theory, lacked empirical support. With industrial development in arctic Alaska virtually unprecedented, there was little basis for predicting the extent and duration of habitat loss, much less the secondary short- and long-term effects on the well-being of a particular caribou herd.

Furthermore, despite a general acceptance that body condition and fecundity of the females are functionally related for reindeer and caribou, it seemed unlikely that any single model would apply to all subspecies of *Rangifer*, and perhaps not even within a subspecies in different geographic regions. We therefore lacked a complete understanding of the behavioral responses of arctic caribou to industrial development, the manner in which access to habitats might be affected, and how changes in habitat use might translate into measurable effects on fecundity and herd growth rate.



Figure 4.1. Petroleum development infrastructure in the Prudhoe Bay and Kuparuk petroleum development areas, Alaska, showing primary and secondary roads, pipelines, and gravel pads, 1994.

Our study addressed the following objectives: 1) estimate variation in the size and productivity of the Central Arctic herd; 2) estimate changes in the distribution and movements of Central Arctic herd caribou in relation to the oil field development; 3) estimate the relationships between body condition and reproductive performance of female Central Arctic herd caribou; and 4) compare the body condition, reproductive success, and offspring survival of females under disturbance-free conditions (i.e., east of the Sagavanirktok River) with the status of those exposed to petroleum-related development (i.e., west of the Sagavanirktok River).

Status of the Central Arctic Herd

Photocensus results indicate net growth of the Central Arctic herd from 1978 through 2000 (Fig. 4.2). Within



Figure 4.2. Photocensus estimates of the Central Arctic caribou herd, 1978-2000 [Whitten and Cameron 1983b; Alaska Department of Fish and Game (ADF&G) files] and net calf production based on observations of radio-collared adult (i.e., sexually-mature) females from 10 June through 15 August (ADF&G files). Note: Productivity data not adjusted for differences in sample sizes east and west of the Sagavanirktok River, Alaska.

that long-term trend, however, there was an abrupt decrease from 1992 to 1995. This decrease coincided with calf production estimates at or below approximately 70%. Steady growth thereafter was associated with productivity estimates consistently exceeding 70%.

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Development-related Changes in Distribution

Since 1978, changes in the distribution of calving caribou associated with the Kuparuk petroleum development area, west of Prudhoe Bay (Fig. 4.1), have been quantified using strip-transect surveys flown by helicopter.

After construction of a road system near Milne Point, mean caribou abundance declined by more than twothirds within 2 km from a road and was less than expected, overall, within 4 km; but nearly doubled 4-6 km from roads (Fig. 4.3) (Cameron et al. 1992b). Prior to road placement, caribou were found in a single, more-orless continuous concentration roughly centered where the Milne Point Road was subsequently built. After construction of the road, a bimodal distribution with separate concentrations east and west of the road was clearly apparent (Fig. 4.4) (Smith and Cameron 1992), indicating avoidance of infrastructure by calving caribou.

These results suggest that roads spaced too closely will depress calving activity within the entire oil field complex. In fact, relative occurrence of caribou in the heavily-developed western portion of the Kuparuk petroleum development area declined significantly from 1979 through 1987, independent of total abundance (Fig. 4.5) (Cameron et al. 1992*b*).



Figure 4.3. Fractional changes in mean density of caribou from the Central Arctic herd between pre-construction (1978-81) and post-construction (1982-87) periods for 1-km-distance intervals from the Milne Point road system in the Kuparuk petroleum development area, Alaska. (*from* Cameron et al. 1992b)



Figure 4.4. Changes in mean relative distribution of caribou from the Central Arctic herd in the Kuparuk petroleum development area, Alaska, during calving: 1979-1981, 1982-1986, and 1987-1990. Shown only are those 10.4-km²-transect segments in which the occurrence of caribou exceeded the area contribution to total coverage (0.9%). Gradations in line spacing depict multiples of observed use relative to availability: wide = <3X; narrow = >3X-5X; solid = >5X. (*from* Smith and Cameron 1992)

An exponential decline in the occurrence of caribou as density of roads increased (Fig. 4.6) (Nellemann and Cameron 1998) underscores the sensitivity of the females during the calving period. The probable consequence is reduced access to preferred habitats (Bishop and Cameron 1990, Nellemann and Cameron 1996, 1998).

Incremental redistribution and local habitat loss within the Kuparuk petroleum development area may have triggered changes on a regional scale. Wolfe (2000) reported an inland shift in concentrated calving activity



Figure 4.5. Decline in percentage abundance of caribou from the Central Arctic herd west of the Milne Point Road, Kuparuk petroleum development area, Alaska (Spearman's Rank, P < 0.02), and changes in total numbers of caribou observed north of the Spine Road (*see Fig. 4.3*), 1979-1987. (*from* Cameron et al. 1992b)

away from the Milne Point petroleum production unit (Fig. 4.7), apparently in response to the increasing density of infrastructure.

Ground observations within the Kuparuk petroleum development area in 1978-1990 provided additional insights on changing distribution and movements. Caribou increasingly avoided zones of intensive activity, especially during the calving period (Smith et al. 1994), corroborating data from strip-transect surveys. Lower success in crossing road/pipeline corridors by large insect-harassed groups (Smith and Cameron 1985, Curatolo and Murphy 1986, Murphy and Curatolo 1987, Murphy 1988) may have contributed to a general shift from the central Kuparuk petroleum development area to peripheral areas with less surface development and human activity. Routes of summer movement are now primarily south of Oliktok Point and along the Kuparuk River floodplain (Smith et al. 1994).



Figure 4.6. Relationship between mean (SE) density of caribou from the Central Arctic herd and road density within preferred rugged terrain, Kuparuk petroleum development area, Alaska, 1987-1992. Different letters indicate a significant difference (P < 0.05). (from Nellemann and Cameron 1998)

An analysis of the summer distribution of radiocollared females in 1980-1993 (Cameron et al. 1995) suggests that caribou use of the oil field region at Prudhoe Bay has declined considerably from that noted during the 1970s by Child (1973), White et al. (1975), and Gavin (1978). Caribou abundance within the main industrial complex as well as east-west movements through that area were significantly lower than for other areas occupied by caribou along the arctic coast (P = 0.001 and P < 0.001, respectively). Conservative calculations yielded an estimated 78% decrease in use by caribou and a 90% decrease in their lateral movements (Cameron et al. 1995), all changes apparently in response to intensive development of the Prudhoe Bay to Kuparuk oil field region over the past 3 decades. Occurrence of caribou that use the complex, however, is reportedly unrelated to distance from infrastructure (Cronin et al. 1998).

Body Condition and Reproductive Performance

Reproductive success of caribou is highly correlated with nutritional status. The probability of producing a calf varies directly with body weight and/or fat content of sexually-mature females during the previous autumn (Cameron et al. 1993, 2000; Cameron and Ver Hoef 1994; Gerhart et al. 1997). In contrast, calving date and perinatal survival are more closely related to maternal weight shortly after parturition (Cameron et al. 1993) (Fig. 4.8). The likelihood of conceiving is probably determined by body condition at breeding, whereas parturition date and calf survival reflect maternal condition during late gestation.



Figure 4.7. Shifts in concentrated calving areas, Central Arctic caribou herd, Alaska, 1980-1995. (adapted from Wolfe 2000)

These relationships link the nutritional consequences of changes in distribution to the reproductive success of caribou of the Central Arctic herd. West of the



Figure 4.8. Logistic regressions (solid lines are significant at P < 0.05) of parturition rate, incidence of early calving (i.e., on or before 7 June), and perinatal (>2 days post partum) calf survival on autumn and summer body weights of female caribou, Central Arctic caribou herd, Alaska, 1987-1991. The empirical percentages are shown at arbitrary 10-kg intervals of body weight. Numbers in parentheses are sample sizes. The asterisk indicates inclusion of one female weighing 57 kg. (*from* Cameron et al. 1993)

Sagavanirktok River, in the petroleum development zone, caribou had reduced access to preferred foraging habitats near roads (Nellemann and Cameron 1996) and shifted their concentrated calving area into habitats with lower plant biomass (P < 0.001) (Wolfe 2000). In contrast, forage biomass remained constant (P = 0.23) within concentrated calving areas east of the Sagavanirktok River where no development was present (Wolfe 2000) (Fig. 4.9).

Repeated use of lower-quality calving habitats may reduce forage intake by females calving west of the Sagavanirktok River. Likewise, impaired summer movements between insect relief habitat and inland feeding areas could depress energy balance (Smith 1996) and, hence, rates of weight-gain.

Indeed, several data sets suggest reduced nutritional status and fecundity of radio-collared females exposed to oil development west of the Sagavanirktok River. Estimates of July and October body weights, oversummer weight-gain, the incidence of 2 successive-year pregnancies, and perinatal calf survival all tended to be



Figure 4.9. Changes in median Normalized Difference Vegetation Index (NDVI) on 21 June for concentrated calving areas of the Central Arctic caribou herd in the study *reference zone* (relatively undeveloped) and *treatment zone* (developed) east and west of the Sagavanirktok River, Alaska, respectively, 1985-1995. (*from* Wolfe 2000)

lower for females to the west than for those under disturbance-free conditions to the east, although individual differences were not significant at the 95% confidence level (Cameron et al. 1992*a*).

In a more recent analysis of data for 1988-1994, however, mean parturition rate of females calving west of the Sagavanirktok River was less than that of females calving east of the Sagavanirktok River, 64% vs. 83%, respectively (P = 0.003, Table 4.1) (Cameron 1995). Corresponding frequencies of reproductive pauses (Cameron 1994, Cameron and Ver Hoef 1994) were significantly higher (P < 0.02, *t*-test, ratio method) in the west (36%, 26 of 73 observations) compared with the east (19%, 12 of 64 observations), or approximately one pause every 3 and 5 years, respectively (Cameron 1995).

The key constraint on reproduction is lactation, which exacts a substantial cost on summer weight-gain, in turn influencing the probability of conceiving that autumn. During 1988-1991, weights of all lactating Central Arctic herd females sampled averaged 9 kg less than

Table 4.1. Parturition status of 43 radio-collared female caribou^a, Central Arctic herd, west and east of the Sagavanirktok River^b, Alaska, 1988–1994. West includes the Prudhoe Bay and Kuparuk oil fields; east was generally free of disturbance during that time. (data *from* Cameron 1995)

· · · · ·	% Parturient (<i>n</i>)				
Year	West	East			
1988	72.7 (11)	100.0 (8)			
1989	53.8 (13)	77.8 (9)			
1990	83.3 (12)	100.0 (7)			
1991	45.5 (11)	75.0 (12)			
1992	72.7 (11)	75.0 (12)			
1993	55.6 (9)	62.5 (8)			
1994	66.7 (6)	87.5 (8)			
Mean parturition rate%	64.3 ^{**} ± 5.0	82.5 ^{**} ± 5.3			

^a All sexually mature.

^b Individual locations consistently west or east for 2-7 years during the calving period.

** t-test, paired comparisons, P=0.003.

nonlactating females (Fig. 4.10). This resulted in a projected 28% lower parturition rate for the lactating females (Fig. 4.11) (Cameron and White 1992).

Lower parturition rates of females west of the Sagavanirktok River during 1988-94 (Table 4.1) may reflect a failure to compensate for the metabolic burden of milk production (i.e., through increased forage intake or reduced energy expenditure). Hence, those females of the Central Arctic herd that used the development zone were in consistently poorer condition in autumn, experienced more frequent reproductive pauses, and produced fewer calves (Fig. 4.2).

Yet the degree to which lactation constrains weightgain does vary. An increase in net calf production during



Figure 4.10. Mean (SE) body weights of lactating and nonlactating female caribou from the Central Arctic herd, Alaska, in summer (July) and autumn (October). (*from* Cameron and White 1992) *Significant at P < 0.001.



Figure 4.11. Distributions of observed autumn (October) body weights for lactating and nonlactating female caribou from the Central Arctic herd. The associated parturition rates are integrated estimates derived from the logistic model (Fig. 4.8). (*from* Cameron and White 1992)

1996-2000 (Fig. 4.2) suggests the prevalence of forage and insect conditions that enhanced growth and fattening despite the demands of milk production and presence of industrial activity. With the opening of the Badami petroleum development area east of the Sagananirktok River in 1996, however, the undisturbed status of that area was compromised, rendering further comparisons questionable.

Overview

Clearly, anthropogenic impacts on caribou must be identified and assessed within the framework of a variable natural environment. Favorable foraging and insect conditions would attenuate the consequences of disturbance-induced changes in quality of occupied habitats. Conversely, adverse conditions would exacerbate those same types of consequences. Unless analyses are based on multi-year observations of marked individuals and incorporate comparative data on an undisturbed control or reference group, conclusions will be equivocal at best. For example, absent a valid baseline, net growth of the Central Arctic herd (Fig. 4.2) is no better evidence of compatibility with development than a net decline would be evidence of a conflict.

The crucial consideration for the future of the Central Arctic herd and other arctic caribou herds is whether changes in distribution associated with surface development, by depressing reproduction or survival, will either retard an increase in herd size or accelerate a decrease.

Our data, in fact, indicate that productivity can and will decline if the cumulative loss of preferred habitat, when superimposed on natural forces, is sufficient to compromise nutrition.

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Section 5: Forage Quantity and Quality

Janet C. Jorgenson, Mark S. Udevitz, and Nancy A. Felix

The Porcupine caribou herd has traditionally used the coastal plain of the Arctic National Wildlife Refuge, Alaska, for calving. Availability of nutritious forage has been hypothesized as one of the reasons the Porcupine caribou herd migrates hundreds of kilometers to reach the coastal plain for calving (Kuropat and Bryant 1980, Russell et al. 1993).

Forage quantity and quality and the chronology of snowmelt (which determines availability and phenological stages of forage) have been suggested as important habitat attributes that lead calving caribou to select one area over another (Lent 1980, White and Trudell 1980, Eastland et al. 1989). A major question when considering the impact of petroleum development is whether potential displacement of the caribou from the 1002 Area to alternate calving habitat will limit access to high quantity and quality forage.

Our study had the following objectives: 1) quantify snowmelt patterns by area; 2) quantify relationships among phenology, biomass, and nutrient content of principal forage species by vegetation type; and 3) determine if traditional concentrated calving areas differ from adjacent areas with lower calving densities in terms of vegetation characteristics.

We investigated caribou forage in 2 areas: an historically traditional calving area entirely within the 1002 Area and an adjacent displacement area entirely outside of the 1002 Area (Fig. 5.1).

The traditional calving area was defined during the 1002 Area baseline biological studies as the area of intensive calving use during 10 of the 14 years studied from 1972 to 1985. Importance of this area was upheld by data on calving locations from later years.

Availability of potential displacement areas is limited here because the coastal plain narrows as the rugged



Figure 5.1. Map of caribou forage study area, Porcupine caribou herd, on the coastal plain of the Arctic National Wildlife Refuge, Alaska.

Brooks Range mountains approach the Beaufort Sea. The displacement area chosen for comparison was located to the south and east of the 1002 Area in the only part of Alaska's North Slope that is a designated Wilderness Area.

The displacement area had topography similar to the traditional area: a mix of rolling foothills and coastal plains. It lay along the spring migration route typically traversed by the Porcupine caribou herd. Female caribou have calved in this area, especially during years when snow melted late (Fig. 3.18).

We gathered data at both study areas during the caribou calving period in early June of 1990 and 1991. Fifty-five 30m x 30m study sites in 1990, and 45 in 1991, were located at the intersections of grids positioned randomly over the entire study area. We sampled during 3 periods in 1990 (31 May-3 June, 8-12 June, and 19-22 June), and 2 periods in 1991 (4-6 June and 9-13 June).

Data were collected on 4 prevalent plant species identified in the literature as important forage for caribou on Alaska's North Slope: *Eriophorum vaginatum* (tussock cottongrass), *E. angustifolium* (tall cottongrass), *Carex aquatilis* (aquatic sedge), and *Salix planifolia* ssp. *pulchra* (diamond-leaf willow) (Thompson and McCourt 1981, Russell et al. 1993).

At each study site, forage quantity data were collected in 14 1-m² quadrats along 2 randomly-located transects. Phenology data were collected at the same 14 quadrats, plus 20 3-m² quadrats located on 2 additional random transects. Tussock cottongrass inflorescences and diamond-leaf willow leaves were collected on transects for analyses of nutrient and fiber content at a random subsample of sites during 1990 only.

We compared the traditional and displacement calving areas by measuring the following characteristics: distributions of vegetation types, snowcover, plant biomass, nutrient and fiber content, and phenology.

Non-parametric analysis of variance using a repeated measures design was used to test for differences between the calving areas and between sampling periods (time). Analyses were conducted individually for each parameter in each year.

Interactions between area and time were tested with Mann-Whitney tests (Conover 1980) of area differences for each time contrast in a full orthogonal set. If interactions were insignificant (P > 0.05), area differences were tested with Mann-Whitney tests based on the mean value for all sampling periods. The differences between the first and last sampling periods were tested with the sign test using data from both areas. If any interactions were conducted separately for each sampling period, and sign tests were conducted separately for each area.

Forage Comparisons Within and Outside the 1002 Area

Spring snowmelt was very early in 1990 and was nearly complete before the calving period. Snowmelt in 1991 was slightly earlier than normal. In 1991, we found the traditional calving area had more area with partial snowcover remaining during the calving period than the displacement area (40% vs. 33%, P = 0.02). Some plants were in earlier phenological stages in the traditional area (Table 5.1).

The quantity of new green forage was low throughout both study areas during the calving period in both years even though snow melted earlier than normal (Table 5.2). Only tussock cottongrass flowers appeared to be readily available for forage during the peak of calving. The 2 other sedges had very little new growth. The willow, which is the major forage species later in the summer, leafed out only at the end of the calving period. The tundra appeared brown and no other plant species were producing abundant new growth during the calving period.

Four forage species were quantified (Table 5.3). Tussock cottongrass flowers had much higher biomass in the traditional calving area than in the displacement area in both years, although the difference was statistically significant only in 1991. Tussock cottongrass was uncommon at the displacement area sites. The 2 other sedges had very low cover and no significant differences. Diamond-leaf willow did not leaf out during the study period in 1991, but in 1990 willow leaves had greater biomass in the traditional calving area when they leafed out.

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Tussock cottongrass flowers and diamond-leaf willow leaves were tested for forage quality throughout the study period in 1990 (Table 5.4). Higher nutrient concentrations increase forage quality, while higher fiber and lignin concentrations decrease digestibility. Both plant species tended to have greater forage quality in earlier phenological stages than in later stages. Tussock cottongrass flowers had greater forage quality in the traditional calving area than in the displacement area.

Distributions of vegetation types were distinctly different between the 2 areas (Table 5.5). The traditional calving area had greater cover of 2 vegetation types important for caribou forage: tussock tundra and moist sedge-willow tundra. The displacement area had greater cover of early succession vegetation types such as Dryas river terraces and barren or partially vegetated ground due to the greater extent of floodplains in that area. Tussock tundra is a late-succession vegetation type and is nearly absent from floodplain terrain (Jorgenson et al. 1994).

The displacement area also included the highest elevation foothills where development of tussocks is

1990	31 May	- 03 June	08 – 12	June	19 – 22	June		
	С	D	С	D	С	D	Area ^b	Time ^C
Tussock cottongrass	3	3 ^{**d}	3	3 ^{**d}	3	4**	<i>P</i> < 0.01	*
Tall cottongrass	1	1	2	2	2	2	<i>P</i> = 0.60	ns
Aquatic sedge	1	1	2	1	2	2	<i>P</i> = 0.44	*
Diamond-leaf willow	1	2	1	2**	2	3**	<i>P</i> = 0.01	*
1991	04 — 06	June	09 – 13	June	(no san	npling)		
	С	D	С	D			Area ^b	Time ^C
Tussock cottongrass	2	2	3	3			<i>P</i> = 0.85	*
Tall cottongrass	1	2*	1	2*			<i>P</i> = 0.04	ns
Aquatic sedge	1	2	2	1			P = 0.83	ns
Diamond-leaf willow	0	0 ^{**d}	0	1**			<i>P</i> < 0.01	*

Table 5.1. Median phenological stages^a of major forage species in the Porcupine caribou herd's traditional caribou calving area (C) and potential displacement area (D) on the coastal plain of the Arctic National Wildlife Refuge, Alaska.

* P < 0.05, ** P < 0.01, ns = no significant difference.

a Phenological stages: Tussock cottongrass, 1 = boot stage, 2 = early flower, 3 = full flower, 4 = seed; Tall cottongrass and Aquatic sedge, 1 = vegetative < 5cm, 2 = vegetative > 5cm, 3 = early flower, 4 = full flower; Diamond-leaf willow, 0 = no new growth, 1 = bud swollen, 2 = leaf unfolding, 3 = full leaf.

b Significance level for difference between areas averaged over all periods.

c Significance level for change between first and last sampling period.

d Phenological stage significantly advanced, although median values were the same.

Table 5.2. Median^a biomass (g/m²) and percent cover of 4 major caribou forage species in the 5 most common vegetation types on the coastal plain of the Arctic National Wildlife Refuge, Alaska, during the Porcupine caribou herd's calving period, June 1990.

•		• ·	-								
		Vegetation Types ^b									
Species	WG	MS	MSD	Π	ST						
Tussock cottongrass											
g/m²	0.00 ^A	< 0.01 ^{AB}	< 0.01 ^{AB}	0.04 ^C	0.03 ^{BC}						
Tall cottong	rass										
% cover	1.2 ^{AB}	1.4 ^A	0.5 ^C	0.4 ^c	0.5 ^{BC}						
Aquatic sec	dge										
% cover	0.9 ^A	0.7 ^A	0.0 ^B	0.0 ^B	0.0 ^B						
Diamond-leaf willow											
g/m²	0.00 ^A	0.88 ^{BC}	0.00 ^{AB}	0.83 ^C	3.25 ^c						

 Values are medians for all sites, with site values obtained as means for 3 times. Medians with the same superscript were not significantly different (*P* < 0.05).

b Vegetation types: WG = wet graminoid tundra, MS = moist sedge-willow tundra, MSD = moist sedge-Dryas tundra, TT = tussock tundra, ST = low shrub tundra. poorer than in the lower foothills of the traditional calving area. Glacial lobes covered about one-fifth of the foothills in the displacement area during the most recent glaciation that ended $\sim 10,000$ years ago. These recently deglaciated areas have very little tussock tundra (Jorgenson 1984).

Different distributions of vegetation types may explain most of the differences found in forage quantity and quality between the traditional and displacement areas. Tussock cottongrass flowers had greater biomass and forage quality in the tussock tundra type compared with other vegetation types (Tables 5.2 and 5.6). The greater biomass of flowers in the traditional area mainly resulted from the greater extent of tussock tundra. No consistent differences in flower quantity or quality between tussock tundra in the traditional calving area and tussock tundra in the displacement area were observed.

The location of the Porcupine caribou herd traditional calving area is greatly influenced by vegetation type distributions and snowmelt patterns across the Arctic Refuge coastal plain. These factors appear to determine the quantity and quality of forage available to the caribou during calving.

Because of the low amount of forage available during the calving period, the differences in vegetation

Table 5.3. Median density (no/m²), biomass (g/m²), and percent cover of major forage species in the Porcupine caribou herd's traditional caribou calving area (C) and potential displacement area (D) on the coastal plain of the Arctic National Wildlife Refuge, Alaska.

1990	31 May–	03 June	08 – 12	June	19 — 2	2 June		
	С	D	С	D	С	D	Area ^a	Time ^b
Tussock cottongrass flowers	· ·	·				•		
no/m2	0.6	0	0.5	0.2	0.2	0	P = 0.87	ns
g/m2	0.02	0	0.01	< 0.01	0.01	0	<i>P</i> = 1.00	ns
Tall cottongrass								
% cover	0.4	0.4	0.6	0.3	0.6	0.2	P = 0.93	ns
Aquatic sedge								
% cover	0	0	0	0	0	0	<i>P</i> = 0.72	*C
Diamond-leaf willow leaves								
g/m2	0	0	0	0	2.0	0.3	<i>P</i> = 0.10	*
1991	04 – 06 、	June	09 – 13	June	(no sa	mpling)		
	С	D	С	D	С	D	Area ^a	Time ^b
Tussock cottongrass flowers								
no/m2	2.7	0.0**	3.5	0.0**			<i>P</i> < 0.01	ns
g/m2	0.09	0.00**	0.11	0.00**			<i>P</i> < 0.01	ns
Tall cottongrass								
% cover	0.2	0.3	0.3	0			P = 0.68	ns
Aquatic sedge								
% cover	0	0	0	0			P = 0.08	*C

* *P* < 0.05, ** *P* < 0.01, ns = no significant difference.

a Significance level for difference between areas averaged over all periods.

b Significance level for change between first and last time periods. If the significance levels differed between areas, both are shown (C/D).

c Last sampling period with significantly higher cover, although median values were the same.

Table 5.4. Median nutrient and fiber concentrations (percent of dry weight) of 2 major forage species in different phenological stages in the Porcupine caribou herd's traditional caribou calving area (C) and potential displacement area (D) on the coastal plain of the Arctic National Wildlife Refuge, Alaska.

	Early Flo	ower	Full Flo	wer	See	<u>ل</u>		
Tussock cottongrass	С	D	С	D	С	D	Area ^a	Time ^b
Nitrogen	2.8	2.6	2.5	2.2**	2.4	2.2**	<i>P</i> = 0.01	ns
Phosphorus	0.49	0.45	0.46	0.38 [*]	0.38	0.36 [*]	<i>P</i> = 0.03	*/ns
Calcium	0.18	0.16	0.13	0.12	0.14	0.11	P = 0.25	ns
Neutral detergent fiber	55.8	58.0	58.2	62.7	66.8	65.9	P = 0.07	*
Acid detergent fiber	16.5	18.4	19.0	20.4**	22.8	23.2**	<i>P</i> = 0.01	*
Lignin	2.3	2.6	2.5	2.3	1.9	1.9	P = 0.43	ns
n (# of sites)	6	7	8	15	8	14		
	Leaf Un	folding	Full Lea	Full Leaf				
Diamond-leaf willow	С	D	С	D				
Nitrogen	3.7	3.4	2.2	2.2			P = 0.27	*
Phosphorus	0.50	0.47	0.18	0.17			P = 0.79	*
Calcium	0.51	0.49	0.62	0.59			P = 0.34	*
Neutral detergent fiber	22.2	22.4	25.0	25.6			<i>P</i> = 0.71	*
Acid detergent fiber	16.3	15.6	17.0	17.7			<i>P</i> = 0.71	*
Lignin	10.3	9.4	8.8	9.4			P = 0.43	*
n (# of sites)	8	8	8	8				

* *P* < 0.05, ** *P* < 0.01, ns = no significant difference. a Significance level for difference between areas averaged over all periods.

Significance level for change between first and last time periods. If the significance levels differed between areas, both are b shown (C/D). All tests for tussock cottongrass inflorescences were of full flower and seed stages only.

Table 5.5. Distribution of vegetation types (percent of area) in the caribou habitat study area (Fig. 5.1) based on an independent sample of 756
systematically-located vegetation plots on the coastal plain of the Arctic National Wildlife Refuge, Alaska.

Vegetation Type	Entire Coastal Plain	Calving Habitat Study Area	Traditional Calving Area	Displacement Calving Area
Tussock Tundra	22	30	39	21
Moist Sedge-Willow Tundra	30	25	31	19
Low Shrub Tundra	7	11	8	13
Moist Sedge-Dryas Tundra	12	9	7	12
Wet Graminoid Tundra	13	8	8	7
Dryas River Terrace	3	7	1	13
Riparian Shrublands	2	3	3	3
Barren	2	3	3	4
Partially Vegetated	2	2	<1	5
Water	<1	2	<1	4

	Full Flower		See		
	Πª	Other	Π	Other	Stage
Nitrogen	2.4	2.0**	2.4	2.1**	<i>P</i> < 0.01
Phosphorus	0.43	0.34**	0.39	0.35**	<i>P</i> < 0.01
Neutral detergent fiber	60.0	63.6	66.2	66.7	<i>P</i> = 0.25
Acid detergent fiber	19.7	21.8*	22.8	23.6*	<i>P</i> = 0.04
Lignin	2.6	1.1**	1.9	1.9	<i>P</i> = 0.03
n (# of sites)	17	6	16	6	

Table 5.6. Median nutrient and fiber concentrations (percent of dry weight) of tussock cottongrass inflorescences in different phenological stages compared between tussock tundra and other vegetation types on the coastal plain of the Arctic National Wildlife Refuge, Alaska.

* P < 0.05, ** P < 0.01

a TT = tussock tundra; Other = all other vegetation types that had tussock cottongrass inflorescences including moist sedge-willow tundra, moist sedge-Dryas tundra, and shrub-dominated tundra.

characteristics found between the 2 areas studied are probably biologically important and could affect calving success of the herd if petroleum development causes the displacement of calving caribou out of the 1002 Area into adjacent areas with lower forage value.

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Section 6: Predators

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Calving caribou (*Rangifer tarandus*) of the Central Arctic herd, Alaska, have avoided the infrastructure associated with the complex of petroleum development areas from Prudhoe Bay to Kuparuk (Cameron et al. 1992, Nellemann and Cameron 1998, and Section 4 of this document). Calving females of the Porcupine caribou herd may similarly avoid any oil field roads and pipelines developed in areas traditionally used during the calving and post-calving periods. This may displace the caribou females and calves to areas east and south of the 1002 Area of the Arctic National Wildlife Refuge.

Increased calf mortality could occur if calving caribou are displaced into areas that have a higher density of predators, higher rates of predation, or where a higher proportion of the predators regularly use caribou as a food source (Whitten et al. 1992).

Our study assessed predation risks to caribou calving in the 1002 Area versus calving in potential displacement areas. Due to funding constraints, our research focused on grizzly bears (*Ursus arctos*), with wolves (*Canus lupus*) and golden eagles (*Aquila chrysaetos*) receiving only cursory attention. Our research objectives were 1) to compare relative abundance of predators within the 1002 Area with that in adjacent peripheral areas, 2) to determine factors affecting predator abundance on the calving grounds, and 3) to quantify the use of caribou as a food source for predator populations using the coastal plain of the Arctic National Wildlife Refuge.

To accurately describe the activities of predators relative to calving caribou, we divided the study area into 3 naturally occurring physiographic zones: coastal plain, which included virtually all of the 1002 Area (< 300 m elevation); foothills (301-900 m elevation); and mountains (> 900 m elevation).

Landscape use distributions were estimated with fixedkernel analyses using Least Squares Cross Validation (Silverman 1986, Seaman et al. 1996, 1998, 1999). *Concentrated use areas* were defined as the utilization contour that included sites with greater than average density (Seaman et al. 1998). In all cases, sampling was limited to the north slope of the Brooks Range.

Eagle distribution estimates were based on aerial survey locations of 202 nest structures that were no closer than 1 km from adjacent structures. Wolf distribution estimates were based on aerial survey locations of 22 dens in the Arctic Refuge and northwestern Yukon Territory, Canada. Additional wolf dens in the foothills and mountains to the east of the estimated wolf concentrated use area probably existed, but were not documented in the analyzed data set.

Grizzly bear distributions were estimated annually, based on 23-60 annual locations of radio-collared bears during the first week of June, 1983-1994. No grizzly bears were radio-collared in Canada. Grizzly bear habitat use was investigated using Chi-square tests (Neu et al.1974). Distance-based tests of independence (Diggle and Cox 1983) as well as analysis of variance procedures were used to compare grizzly bear and calving caribou distributions.

Predator Distributions

Predators (grizzly bears, wolves, and nesting golden eagles) in general were more abundant in the foothills and mountains than on the coastal plain (Fig. 6.1). The distribution of grizzly bear radio-locations relative to the coastal plain, foothill, and mountain zones was non-random (P < 0.0001, Chi-square).

In all years, the foothills received greater use by bears than expected, whereas the coastal plain received less use than expected (P < 0.05), except in 1990 when the coastal plain was used in proportion to its availability. We hypothesize that bears were more abundant in the foothills because the rolling hills provided greater diversity in topography, vegetation, and phenology than the flatter coastal plain. Other studies have reported lower grizzly bear densities on the arctic coastal plain than in the foothills of the Brooks Range (Miller et al. 1997, Reynolds 1979).

Radio-collared wolves were more likely to be found in the foothills (55%) and mountains (36%) than on the coastal plain (9%). All active wolf dens (n = 11) were located in the mountains, with the exception of one den located in the foothills. Since 1982, there have been no reported cases of wolf dens on the coastal plain of the Arctic Refuge.

All 170 golden eagle nest structures, including 22 active nest sites, that were located within 30 km of the 1002 Area were found in the foothills and mountains (Young et al. 1995). Subadult golden eagles, however, were abundant on the Arctic Refuge coastal plain and foothills where their distributions coincided with those of calving caribou.

Factors Associated with Predator Distributions

Grizzly bear distributions during the caribou calving period in early June appeared to be influenced by a combination of factors including seasonal habitat selection patterns, annual variations in snowmelt, and annual distribution patterns of calving caribou.

Within-year (1983-1993) spatial distribution patterns of radio-collared grizzly bears did not differ among time



Figure 6.1. Distribution of *a*) golden eagle (*Aquila chrysaetos*) nest structures, *b*) wolf (*Canis lupus*) dens, and *c*) grizzly bears (*Ursus arctos*) near the calving grounds of the Porcupine caribou herd. Solid yellow lines enclose *concentrated use areas* (CUA, sites with greater than average observation density), solid white lines delineate 99% *use distributions* (UD), and the dashed red line delineates the approximate 300-m-elevation boundary between the coastal plain and foothill/mountain physiographic zones. The outer perimeters of all annual grizzly bear fixed kernel estimates of CUA and 99% UD are depicted.

periods, whereas concurrent distributions of calving caribou did differ. This suggests that annual grizzly bear distributions were influenced less by the distribution of calving caribou than by other factors (e.g., annual snowmelt patterns). Among-year differences (P < 0.05) in grizzly bear spatial distribution patterns suggest that annual variations in snowmelt contribute to annual bear distribution patterns.

Radio-collared grizzly bears were relocated more frequently on the coastal plain in years when snowmelt occurred early (38.9%) or normally (23.8%), as in 1990 and 1989, respectively, than in years when snowmelt occurred late (12.7%), as in 1988. Distributions of radiocollared bears and caribou cows with calves tended to be positively associated in 1988 and 1989 (i.e., years of late and normal snowmelt, respectively, when calving occurred primarily in the foothills), and negatively associated in 1990 (i.e., a year of early snowmelt when calving occurred primarily on the coastal plain) (Young et al. 1994).

Analyses of concurrent grizzly bear and calving caribou distributions in 1983-1993 indicated that bears

selected high or medium caribou density zones in 5 of 9 (56%) years, but avoided the highest density of caribou in 2 (22%) years. Two years were not comparable.

During the caribou calving period, radio-collared wolves were located primarily in the mountains and foothills where their activity was associated with den sites. All known wolf den sites on the North Slope of the Arctic Refuge have been located in the mountains and foothills. Thus, the availability of suitable den sites appears to be the primary factor influencing wolf distributions during the calving period.

Factors affecting the distribution of nesting golden eagles differed from those of subadult birds. Nesting or adult birds sought suitable nesting habitat on cliffs found primarily in the foothills and mountains in proximity to colonies of Arctic ground squirrels (*Spermophilus parryi*), their primary prey (Young et al. 1995). Subadult birds appeared to be associated primarily with distributions of calving caribou.

Rates of predation

Use of caribou as a food source varied among and within predator species. Of 26 grizzly bear observation surveys that were successfully completed (>1 hr), 8 (31%) included a kill of a caribou calf (Young and McCabe 1997). Kill rates of caribou calves ranged from 1.0 to 6.3 kills/bear unit/day; a *bear unit* being a solitary individual, a family group, or a male with 1 or more consorts.

Trends in the data suggested that bears were more likely to encounter and kill caribou calves as calving density decreased. This suggests that predator swamping may be an effective anti-predator strategy by calving females of the Porcupine caribou herd with respect to predation by grizzly bears.

Radio-collared wolves were relocated in the vicinity of caribou 34% of the time and on caribou carcasses 9% of the time. Productivity was similar (P > 0.05) between 3 wolf packs with access (4.3 pups/litter) and 1 pack without access (4.2 pups/litter) to the traditional caribou calving grounds. Because there are few wolves (20-40) and their distributions are usually separated from those of calving caribou, wolves kill relatively few caribou during the calving period.

Based on prey remains collected at nest sites, 1988-1990, we observed little evidence of use of caribou by nesting golden eagles. Ground squirrels were their predominant prey (Young et al. 1995). Subadult birds, however, are important predators of calving caribou (Whitten et al. 1992; *see also section 3 of this report*).

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Section 7: Muskoxen

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Dynamics and Range Expansion of a Reestablished Muskox Population

Muskoxen (Ovibos moschatus) disappeared from Alaska in the late 1800s, but returned to the Arctic National Wildlife Refuge when animals were reestablished into areas of former range in 1969-1970 (Klein 1988). Released at Barter Island (Kaktovik) and the Kavik River, muskoxen initially moved into regions that encompassed the 1002 Area on the coastal plain of the Arctic Refuge. From 1974 to 1986 the muskox population grew rapidly. By 1987, however, numbers declined in the regions that they had first occupied (Reynolds 1998*a*).

Petroleum exploration and development could occur in muskox habitat in the 1002 Area of the Arctic Refuge. Status of the muskox population and factors related to trends in local abundance need to be determined if changes resulting from natural processes are to be separated from those that might result if industrial development is permitted in the Arctic Refuge.

We developed a study with the following objectives to understand the dynamics of the muskox population in and near the 1002 Area of the Arctic Refuge: 1) determine abundance and rates of population increase, production, and survival; 2) document changes in population distribution over time; and 3) evaluate factors associated with changes in the number of muskoxen.

Numbers of muskoxen seen during annual censuses in 1982-2001, combined with data from earlier studies, were used to estimate animal abundance and population trends of muskoxen in the 1002 Area (regions first occupied) and adjacent areas to the east and west (regions occupied later) (Reynolds 1998*a*). *Rates of successful calf production* (defined as calves:100 females >2 years old present in late June), survival of calves and yearlings, and long term reproduction patterns by marked female muskoxen were determined from annual sex and age composition counts made from the ground in 1983-2001.

Radio-collared adult muskoxen were relocated 6 times/year from 1982 to 1994 to determine seasonal and annual variability in population distribution and to document adult mortalities. Locations were determined from the air with a global positioning system (GPS) or were plotted on 1:63,360-scale maps. The adaptive-kernel technique within the computer program CALHOME (Kie et al.1996) was used to delineate the size and locations of regions used by mixed-sex groups of muskoxen in 1969-1981, 1982-1985, 1986-1989, and 1990-1993. Core areas of use (70% adaptive-kernel contour) and total range (95% contour) were used to document changes in distribution and range expansion over time.

Locations of muskoxen seen during seasonal muskox surveys in the Arctic Refuge, as well as locations of mixed-sex groups seen during other studies, were used to document the continued expansion of the population distribution from 1994-2001. Reconstructed models of the population estimating maximum and predicted population growth were used to evaluate how changes in calf production, survival, and emigration affected local abundance of muskoxen.

The Arctic Refuge's reestablished population of muskoxen grew slowly for a few years and then increased rapidly for more than a decade (Reynolds 1998*a*). Between 1977 and 1981, the population grew at r = 0.24, a rate approaching maximum growth. In 1986, 368 muskoxen were counted in the 1002 Area, but after 1986, numbers of muskoxen declined (Fig.7.1). The rate of increase slowed to 0.14 in 1982-1986 and to <0.00 in 1987-1995.

The rate of population growth (r = 0.14) in 1972-1996 (Reynolds 1998*a*) was similar to rates recorded for other expanding populations of muskoxen in Alaska and Canada (Spencer and Lensink 1970, Gunn et al. 1991). An introduced population of muskoxen in Greenland was still irrupting 25 years after release, but those animals were in an area of abundant high-quality forage with no predation and low snowfall (Olesen 1993).

In 1996-2001, numbers of muskoxen counted in the 1002 Area ranged from 168 to 212 (P. E. Reynolds, U.S. Fish and Wildlife Service, unpublished data) and indicate that muskox abundance is still declining slowly (Fig. 7.1).

Factors affecting changes in the number of muskoxen in the 1002 Area of the Arctic Refuge included changes in rates of successful reproduction and survival as well as changes in animal distribution.

Calf production was the only source of increase in this reestablished population; a lack of adjacent populations



Figure 7.1. Number of muskoxen observed in the regions first occupied after reintroduction — the 1002 Area, Arctic National Wildlife Refuge, Alaska, USA, during spring censuses, 1982-2001

of muskoxen precluded immigration. Growth of the population during its most rapid increase was due to high rates of reproduction and survival of muskoxen in newly occupied habitats. In the 1002 Area, indices of successful calf production reached a maximum between 1977 and 1980 (87 calves:100 females >2 years old) during years when successful reproduction by some 2-year-old females and 100% reproduction among females >2 years old occurred in some groups (Jingfors and Klein 1982).

Calf production declined between 1983 and 2001 (Fig. 7.2). In 1983-1986, as the rate of population increase began to slow, calf production in the 1002 Area averaged 61 calves:100 females >2 years old compared with 49 in 1987-1990, 41 in 1991-1994, and 28 in 1995-1999 (Reynolds 1999). In June 2000 and 2001, very few calves (<5 calves per 100 females >2 years old) were seen. Because calves were counted several weeks after birth, we could not determine if changes in the production of muskox calves were due to lower fecundity or increased neonatal mortalities.

Reproductive patterns of radio-collared females in the 1002 Area showed similar trends. Mean reproductive intervals (number of years between successful reproductive events in a 3-year period) increased significantly ($r^2 = 0.95$, n = 6, P = 0.0009) between 1982 and 1999. By 1991-1993, most marked females successfully reproduced at intervals of 2 to 3 years, rather than every year (Reynolds 2001). Percentages of marked females without calves for 3 or more consecutive years were 0% in 1982-1987, 15% in 1988-1990, and 25% in 1994-1996 (Reynolds 2001). In summer, body weights of 8 lactating muskoxen (mean = 223 kg, range = 188-254 kg) were not different (t = 2.2, df = 10, P = 0.167) from 8 non-lactating females (mean = 196 kg, range = 136-254 kg) and were similar to weights of female muskoxen in other wild and captive populations (Reynolds and Reynolds 1999).



Figure 7.2. Changes in rates of successful production of muskox calves in the regions first occupied after reintroduction – the 1002 Area, Arctic National Wildlife Refuge, Alaska, 1983-2001. Successful calf production was measured by counting the number of calves per 100 females >2 years of age in late June.

Unlike calf production, which declined in 1983-1995 $(r^2=0.75, P < 0.001)$, calf and yearling survival did not decline over time (calf survival: $r^2 = 0.01, P = 0.71$; yearling survival: $r^2 = 0.01, P = 0.82$). Annual variability in young animal survival followed the same annual trends as calf production and was related to snow depth and the length of the snow season (Reynolds 1998*a*).

Between 1983 and 1999 the percentages of radiocollared muskoxen dying each year were variable but showed an increased trend (Reynolds 1999). Sources of mortality included kills by predators, including humans.

Legal hunting of muskoxen in the Arctic Refuge began in 1982. Over time, the number of permits issued each year increased from 5 males only to 12 males and 3 females. The season was expanded from 2 to 8.5 months. An average of 7 muskoxen was killed in 1985-1989 compared with an average of 10 in 1995-1999. About 3% of the muskox population in the Arctic Refuge was harvested annually from 1990-1999 (P. E. Reynolds, U.S. Fish and Wildlife Service, unpublished data).

Kills or scavenging of muskoxen by grizzly bears (Ursus arctos) in and near the Arctic Refuge increased significantly between 1986 and 2001 ($\beta = 0.504$, df = 18, P < 0.001) (Fig. 7. 3). Known kills of muskoxen by grizzly bears ranged from 0-2 deaths per year before 1993, 1-4 deaths per year in 1993-1996, and 5-10 deaths per year in 1997-2001 (Reynolds et al. 2002).

Forty-seven deaths of adult or sub-adult muskoxen from known grizzly bear predation occurred between 1982-2001. Of these, 28 muskoxen died during 10 incidents of multiple kills in which bears killed more than one muskox from a group. Most of these kills (79%) took place between May 1998 and June 2001 (Reynolds et al. 2002).

Grizzly bears likely also killed muskox calves and caused other mortalities of young calves that were



Figure 7.3. Number of muskoxen killed or scavenged by grizzly bears from April 1982 through June 2001 in northeastern Alaska, USA. (*from* Reynolds et al. 2002)

deserted during predation events. Multiple kills of calves were observed in Canada (Clarkson and Liepins 1993). The increase in kills by grizzly bears suggests that predation may have been one factor that resulted in very low numbers of calves in late June of 2000 and 2001. Deep snow and a prolonged winter season in 2000 and 2001 also likely contributed to the low numbers of calves seen in those years and may have exacerbated the number of predation events (Reynolds et al. 2002).

Shifts in distribution and emigration also affected numbers of muskoxen in the 1002 Area of the Arctic Refuge. Following their release in 1969 and 1970, most muskoxen became associated with 1 of 3 mixed-sex groups in 3 regions of the Arctic Refuge. The regions first occupied were located between the Canning and Aichilik Rivers within the boundaries of the 1002 Area (Fig. 7.4*a*) (Reynolds 1998*a*). After 1986, muskoxen in mixed-sex groups colonized new regions east and west of the 1002 Area (Fig. 7.4*c*,*d*) (Reynolds 1998*a*).

In 1995, about 800 muskoxen were counted in the entire range of the population (Table 7.1), which had expanded westward to the Itkillik River, Alaska, and eastward to the Babbage River in northern Yukon Territory, Canada (Reynolds 1998a). In 1998-2001, mixed-sex groups of muskoxen continued to expand their range west to the Colville River, southwest along the Sagavanirktok River, and south and east of the Babbage River in northwestern Canada. During these years, <700 muskoxen were counted throughout the total range of the population (Table 7.1) (P. E. Reynolds, U.S. Fish and Wildlife Service, unpublished data, E. A. Lenart, Alaska Department of Fish and Game, unpublished data, and D. A. Cooley, Yukon Renewable Resources, unpublished data).

Differences between the observed and predicted abundance in the 1002 Area, based on reconstructed population projections, suggest that changes in muskox calf production and animal survival caused most of the decline in the rate of population growth (Reynolds 1999). Density dependent factors as well as annual variability in snowfall and increasing rates of predation all likely influenced observed changes in calf production and animal survival.

Emigration of mixed-sex groups of muskoxen also reduced the number of muskoxen in the 1002 Area (Reynolds 1998*a*, 1999). In 2000 and 2001, the additional emigration of mixed-sex groups containing marked animals and the low rates of successful calf production (<5 calves per 100 females > 2 years old) contributed to the declining trend in numbers of muskoxen in the 1002 Area (P. E. Reynolds, U.S. Fish and Wildlife Service, unpublished data).

Although muskoxen are continuing to expand into their former range in northern Alaska and northwestern Canada, numbers of muskoxen in the 1002 Area are not likely to increase from their present level of <250 animals in the near future.

If exploration and extraction of petroleum resources are permitted in the Arctic Refuge coastal plain, associated industrial activities could further reduce the number of muskoxen in the 1002 Area either through induced dispersal or decreased productivity and survival. Muskoxen are year-round residents of the 1002 area, which heightens their vulnerability. In addition, their small numbers make it less likely that the muskoxen can recover from perturbations.

Status and distribution of muskoxen in and near the 1002 Area should continue to be monitored to document future trends.

Seasonal Strategies of Muskoxen: Distribution, Habitats, and Activity Patterns

Seasonal shifts in distribution, habitat use, and activity are means by which animals maximize energy intake and avoid conditions that risk their survival. The muskox is an energetically conservative species (Klein 1992) and its seasonal habitat use and energy budgets influence its reproduction and survival (White et al. 1989). Limited forage availability and energy constraints in winter as well as potential cumulative effects of disturbance contribute to its susceptibility.

As year-round residents of the coastal plain of the Arctic Refuge, muskoxen are vulnerable to human activities in both winter and summer. Information is needed about their seasonal patterns of distribution and activity to evaluate and minimize potential effects associated with oil and gas exploration and development proposed for the Arctic Refuge's 1002 Area.

Our study to determine seasonal patterns of muskoxen on the coastal plain of the Arctic Refuge had the following objectives: 1) compare distribution and habitat use of muskoxen in different seasons, and 2) determine seasonal movements and activity patterns of muskoxen.

In the Arctic Refuge, snow is present from 8-9 months each year (September - May). Five seasons were defined for muskoxen based on ecological and biological conditions: *calving* (late March to mid-June), *summer* (late June to mid-September), *early winter* (late September to mid-November), *mid-winter* (late November to mid-January), and *late winter* (late January to mid-March).

To identify population distribution in different seasons, 19-25 radio-collared muskoxen were monitored and 4 to 6 radio-relocation surveys were flown each year from 1982 to 1995. Locations of groups of muskoxen, both marked and unmarked, were determined using a global positioning system or were plotted on 1:63,360 scale maps.



Figure 7.4. Range expansion of muskoxen in mixed-sex groups in and near the Arctic National Wildlife Refuge, Alaska, 1969-1993. *Total ranges* were defined by 95% adaptive kernel contours. *Core areas* were defined by 70% adaptive kernel contours. (*from* Reynolds 1998a)

Table 7.1. Number of muskoxen seen in different regions in northeastern Alaska, USA, and northwestern Canada in 1982-2000 during precalving surveys. *GMU 26B* and 26C are State of Alaska game management units. The muskox population originated from animals released adjacent to the Arctic National Wildlife Refuge, Alaska, in 1969 and 1970. The muskoxen began to disperse into new regions east and west of the Arctic Refuge by 1986 (Reynolds 1998a).

Year	West of the Arctic Refuge: Itkillik River to Canning River (GMU 26B) ^a	1002 Area in the Arctic Refuge: Canning River to Aichilik River ^b	All Arctic Refuge: Canning River to Canada (GMU 26C)	East of the Arctic Refuge in northern Yukon Territory, Canada ^C	Arctic Refuge + west + east
1982		219	219		219
1986	9	386	399	23	431
1990	122	273	332	41	495
1995	330	228	321	146	797
1998	207	213	331	136	674
2000	277	189	246	146	669

a data source: E. A. Lenart, Alaska Department of Fish and Game, Fairbanks, Alaska, USA

b regions first occupied; numbers included in Arctic Refuge numbers

c data source: D. A. Cooley, Department of Renewable Resources, Yukon Territories, Canada

Seasonal distribution and movement rates were determined from 15 female muskoxen fitted with *satellite collars* (ultra-high frequency platform transmitter terminals that were relocated by satellite) (Reynolds 1989). Three to 5 animals carrying satellite collars were monitored yearly from October 1986 through March 1992. These collars transmitted information about animal location and activity every second or third day for 6 hr/ day (Reynolds 1998*b*).

Seasonal distribution of the population and seasonal home ranges of satellite-collared muskoxen were delineated with an adaptive-kernel technique and the program CALHOME (Kie et al. 1996). Seasonal differences in population distribution were compared as the overlap of *core areas* (70% contour), distances between core-area centers, and core-area sizes.

Mean movement rates (km/day) for each season and each month were calculated from distances moved by satellite-collared muskoxen. Distances were calculated between consecutive locations at 40-55 hr intervals. Mean activity indices for each season and each month were derived. Activity counts from 5 satellite-collared muskoxen with >10 days of activity counts per month were used to estimate mean activity (Reynolds 1998b).

Land-cover and terrain types, extracted from a landcover map derived from Landsat-Thematic Mapper data (Jorgenson et al. 1994), were used to determine seasonal differences in habitat use at a landscape scale. Selection ratios of 6 land-cover classes and 5 terrain types were based on proportions present in core areas (habitats used) divided by proportions in the entire study area (habitats available) (Reynolds 1998b).

The average size of core areas used by muskoxen carrying satellite collars was significantly larger (P < 0.05) in summer (223 km²) than in calving season or the 3 winter seasons (27-70 km²) (Reynolds 1998b). The size of

core areas was highly variable in summer, but means differed by almost an order of magnitude between summer and other seasons. The minimum size of core areas used in summer was >4 times larger than minimum core areas occupied in winter or calving.

Muskoxen were conservative in their daily movements throughout the year. Most (95%, n = 2314) movements made by satellite-collared muskoxen were <5 km/day (Reynolds 1998b). Of these, 46% were <1 km/day. Moderate movements of 5-10 km/day took place primarily between June and September (77 of 108). Only 1 (<1%) moderate movement of 5-10 km/day was recorded between January and April. Movement rates >10 km/day, resulting in relatively long moves, were rare (18 of 2314); 16 (89%) movements >10 km/day occurred in July.

Mean daily movements in summer (2.6 km/day) were greater (P < 0.05) than in other seasons (1.1–1.4 km/day) (Reynolds 1998b). Mean rates of movement were significantly higher (P < 0.05) in July than in other months (Fig. 7.5). Activity counts/minute from satellite-



Figure 7.5. Seasonal changes in rates of movement and activity counts of satellite-collared female muskoxen in and near the Arctic National Wildlife Refuge, Alaska, 1986-1992. (*from* Reynolds 1998b)

collared muskoxen were also greater in summer (P < 0.001) than in other seasons. Activity counts differed among months (P = 0.001) and were highest in July and lowest in April during the onset of the calving season.

Seasonal home ranges occupied by females with satellite-collars overlapped less (P = 0.01) between calving and summer than between early winter and mid-winter and between mid-winter and late winter (Reynolds 1998b). This reflected the sedentary nature and small home range size of the muskoxen in winter. Distances between seasonal home ranges were also small. The distribution of the population of muskoxen occupying the coastal plain of the Arctic Refuge showed little change between seasons.

At a landscape scale, muskoxen used riparian cover along river corridors, floodplains, and foothills in all seasons. Moist sedge was selected in late winter and calving; tussock tundra was avoided in late winter. Wet sedge was used in proportion to availability in summer and early winter but avoided in other seasons. Upland shrub was selected only during the calving season and avoided in other seasons. Bare cover (including bare ground, water, and ice) was selected in all seasons except spring. Mountain terrain was avoided in all seasons (Reynolds 1998b).

Ground-based studies (Wilson 1992) provided more information at regional and local scales (*see next subsection on winter habitat use*). Locations of mixed-sex groups of muskoxen during summer and winter surveys demonstrated the importance of river corridors and adjacent uplands to this population (Fig. 7.6).

The small seasonal shifts in distribution and low movement rates observed in this study confirmed that muskoxen are energetically conservative throughout the year (Jingfors 1980, Thing et al. 1987) and that they have a high fidelity to geographic regions. Seasonal changes in movements, activity, and habitat use were related to



Figure 7.6. Locations of mixed-sex groups of muskoxen seen during winter and summer surveys in the Arctic National Wildlife Refuge, Alaska, USA, 1982-1999.

availability of forage and the energy budgets of muskoxen.

In winter, snow limits forage availability and habitat selection (Jingfors 1980). In late winter, muskoxen selected feeding sites with soft shallow snow (Biddlecomb 1992, Wilson 1992). These sites were frequently narrow windblown bluffs adjacent to rivers where snow accumulation was low (Nellemann and Reynolds 1997). By mid- to late winter, riparian willows and wet-sedge communities may be unavailable to muskoxen as snow depths increase (Wilson 1992, Evans et al. 1989).

Winter forage of muskoxen is of low quality (Staaland and Olesen 1992). Graminoids were a dominant component of the late winter diet of muskoxen in northeastern Alaska (O'Brien 1988, Biddlecomb 1992, Wilson 1992). Muskoxen, however, can digest low quality graminoids efficiently and may have a fasting metabolic rate lower than other ruminants (Adamczewski et al. 1994, Lawler 2001). In winter, muskoxen conserve energy by reducing movements and activity, decreasing the size of use areas, and concentrating in a few habitats where forage is not covered with deep snow.

Unlike caribou that calve in early June when nutritious vegetation is emerging, most muskoxen give birth several weeks before high quality green forage is available. In Alaska, Dall's sheep (*Ovis dalli*) (Rachlow and Bowyer 1994) and moose (*Alces alces*) (Bowyer et al. 1998) have similar calving strategies to muskoxen. To reproduce successfully, female muskoxen must be in good body condition at calving time to fuel the high cost of lactation. Their energy-conserving strategy of restricting movements and activity and selecting habitats with low snowcover allows female muskoxen to maintain body condition throughout the winter and spring (Thing et al. 1987).

Most muskoxen in the Arctic Refuge give birth in April and May and lactate under conditions of poor quality forage and harsh weather. Their increased use of foothill terrain and upland shrub during the calving season reflected shifts into areas where snowcover was shallow or blown free and their energetic costs of foraging were lower. Muskoxen with young calves also may avoid flooded riparian areas during calving and postcalving periods. Movement rates of muskoxen carrying satellite collars reached a yearly low in April at the onset of the calving season.

During the snow-free summer when food quality and quantity are high, muskoxen increase their movement and activity, occupy larger areas, and use diverse habitats as they forage on a variety of high-quality vegetation (Robus 1981, O'Brien 1988). They track the changing plant phenology in local areas to obtain high quality forage and rapidly regain body weight lost during winter, pregnancy, and early lactation. Muskoxen that fail to regain body weight are less likely to breed or successfully reproduce (White et al. 1997) and are less likely to survive a severe winter.

In our study we found that movement rates and activity increased in June as plants began to leaf out and were highest in July as live plant biomass peaked (Chapin 1983). Movement rates and activity of muskoxen carrying satellite-collars began to decline in August as plant senescence and rut occurred (Reynolds 1998b).

Seasonal strategies that emphasize energy intake in summer and energy conservation in winter, combined with physical adaptations for cold weather and the ability to process low quality forage, permit muskoxen to survive year-round in locations seasonally avoided by most other animals. Muskoxen are present during all seasons in the potential oil exploration and development area of the Arctic Refuge.

This study did not quantify the effects of petroleum development on muskoxen. But human activities that increase energetic costs to muskoxen in winter or decrease foraging opportunities in summer have the greatest probability to affect the muskox population. Riparian habitats frequently used by muskoxen are also likely to be used as sites for gravel and water extraction and winter road construction if exploration and development of petroleum resources occur on the coastal plain of the Arctic Refuge.

Exploratory and construction activities in northern Alaska often take place in winter. Muskoxen are particularly vulnerable to disturbance in winter because of limited habitat, the length of the arctic winter, and their need to conserve energy throughout the winter including the calving season. The average size of muskox groups is larger in winter than in mid-summer (Reynolds 1993). Large groups of animals often are more easily disturbed than small groups because large groups contain more individuals responsive to perturbations.

Effects of human activities on muskoxen are likely related to the scale of the activity and the availability of alternate habitats that can be used if animals are displaced. Muskoxen that expanded westward from the Arctic Refuge use the wide Sagavanirktok River valley in summer despite the presence of the Dalton Highway and the trans-Alaska oil pipeline. Habitats available to muskoxen in the Arctic Refuge, however, are geographically constricted: The coastal plain is narrower because the mountains of the Brooks Range are closer to the Beaufort Sea (Fig. 1.1).

If undisturbed, muskoxen generally stay in relatively small areas throughout the winter. Avoidance by industry of these areas used by muskoxen could reduce the probability of disturbance and displacement of muskoxen. Minimizing human activities in areas occupied by muskoxen from mid-winter through the calving season could reduce the likelihood of disturbance during the
period when energy conservation is critical to survival. Locating permanent facilities away from river corridors, flood plains, and adjacent uplands could also help to reduce potential effects of industrial development on muskoxen.

Winter Habitat Use by Muskoxen: Spatial Scales of Resource Selection

During the snow season, which lasts up to 9 months in the Arctic Refuge, muskoxen remain in small areas, restricted by the availability of forage and by strategies needed to conserve energy (Reynolds 1998b). Human disturbance or destruction of their habitat could displace muskoxen from these limited wintering areas.

To determine what kinds of sites are used by muskoxen in late-winter and why these sites are selected, we set the following research objectives: 1) determine selection of vegetation types based on use and availability, and 2) compare snow depth and hardness, vegetation biomass, and environmental variables at feeding and non-feeding sites. Our study sites were located in the eastern half of the Arctic Refuge coastal plain and 1002 Area, between the Jago River and the Kongakut River.

Fieldwork was conducted in March, April, and July 1989-1990 at 44 late-winter foraging sites used by muskoxen. These sites included *feeding zones* (with feeding microsites or craters), *non-used adjacent zones* (contiguous to the feeding zone), and *non-used nonadjacent zones* (100 m beyond the adjacent zone). At each foraging site, a randomly-oriented transect was laid across the site, passing through the center of the feeding zone and defining unused zones.

Foraging sites were located from observations and tracks of muskox groups in March and April. Fecal pellets were collected for diet selection analysis. Winter foraging sites were relocated the following July when vegetation and environmental characteristics along transects were measured (Wilson 1992). Snow conditions, environmental characteristics, forage cover, and non-vegetated cover were included in an analysis of variables related to habitat selection.

In late winter, muskoxen fed most commonly in moist sedge tundra (37%) and tussock sedge tundra (37%) and used these types in proportion to availability. Dryas terrace (9%), riparian grass forb gravel bars (7%), wet sedge (5%), partially vegetated tundra (2%), and shrub tundra (2%) were selected less frequently than their availability. Muskoxen were not observed feeding in riparian shrub, Dryas ridge, barren ground, or water (Wilson 1992).

Total vegetation cover was greater in feeding zones than in unused adjacent and non-adjacent zones. Cover of evergreen shrubs, sedges, and dead vegetation was greater in feeding zones. Non-vegetative cover was greater in adjacent and nonadjacent zones (Wilson 1992).

Diet selection based on fecal analysis of winter pellets (corrected for digestibility) indicated a high use of sedges (39.1%) and mosses (24.6%) (Wilson 1992). Sedges and grasses were *selected* (use > availability); and horsetails, lichens, willows, and other shrubs were *avoided* (use < availability). Although selection for grasses was high, grasses did not make up a large proportion of the diet or the available habitat.

Analysis of rumen samples indicated that sedges (31%), grasses (19%), mosses (15%), and forbs (13%) comprised most of the diet. The proportion of willows was 8% in rumen samples. In other studies, riparian willows were used by muskoxen in late winter (O'Brien 1998, Robus 1991). During our study, however, snow limited the use of most riparian shrub communities. Willows were browsed in areas where they protruded through the snow (Wilson 1992).

Snow depth was shallower and softer in feeding zones than in nonadjacent zones, and shallower in feeding zones than in adjacent zones (Fig. 7.7). Snow depth and



Figure 7.7. Snow depth (cm) in muskox feeding zones (areas containing feeding sites), *adjacent zones* (unused areas adjacent to and surrounding feeding zones) and *nonadjacent zones* (unused areas 100 meters beyond adjacent zones) in late winter 1989 (n = 20) and 1990 (n = 24) on the coastal plain of the Arctic National Wildlife Refuge, Alaska, USA. (from Wilson 1992)

hardness were less in microsites than in unused portions of feeding sites. Snow depth was the single variable most influential in discriminating between used and non-used areas. Muskoxen also appeared to avoid walking through areas of soft deep snow. Most feeding zones were near some type of topographic relief that had been subjected to wind scarring. Snow depth was shallower in feeding zones of tussock sedge tundra and moist sedge tundra, suggesting that within vegetation types, muskoxen chose feeding zones based on snow depth alone. No differences were detected between feeding zones and adjacent and nonadjacent zones in wetness, slope, micro-relief, or aspect (Wilson 1992).

Snow depth in feeding zones was deeper in 1989 than in 1990 (34.5 cm versus 23.0 cm, respectively), and total vegetation cover was greater in 1990 than in 1989 (Wilson 1992). In 1990, forb cover was greater in feeding zones compared with a greater cover of sedges and nonvegetative material in 1989 feeding zones. Muskoxen did not select for areas of high total vegetative cover in 1989, indicating that detection of vegetation characteristics may require shallow snow cover. In 1989, mean crater depths (29.7 cm) and mean feeding zone depths (34.5 cm) approached or exceeded the maximum snow depths in feeding areas (>30 cm) observed in other muskox studies (Rapota 1984, Smith 1984).

Partially vegetated tundra and Dryas terraces had the shallowest snow; the deepest snow occurred in shrub tundra and moist sedge tundra. Gravel bars with riparian forbs and grass had the greatest total cover of vegetation; moist sedge tundra had the least. Muskoxen selected feeding zones with shallower snow and greater vegetation cover compared with what was available (Wilson 1992).

Winter habitat for muskoxen is limited in quantity because animals must select foraging areas with shallow soft snow and a high cover of vegetation. Areas with little vegetation or deep hard-packed snow were not used. In this study, feeding zones were primarily along narrow bands of windblown vegetated bluffs adjacent to creeks, rivers, and the coastline, reflecting the importance of terrain features to habitat selection (Nellemann and Reynolds 1997).

Snow depth was one of the most important variables distinguishing used and unused area in this study of muskox habitat (Wilson 1992). Snow depth influences the availability of forage and can limit accessibility to some forage types (Evans et al. 1989). Snow depth affects energy budgets. Digging through snow to find forage is energetically costly for ungulates (Fancy 1986). The time lost while digging craters also reduces the daily rate of forage intake (Fleischman 1988).

In high snow years, when some habitats are not available and muskoxen spend more energy moving and foraging, muskoxen may be energetically constrained, resulting in lower survival and less successful reproduction. As winter progresses and snow accumulates, or if deep snow falls early in the winter, muskoxen may be forced to select foraging areas with deep snow or low plant biomass.

If muskoxen are limited in their accumulation of body reserves during summer, effects of a severe winter or overuse of winter range will have greater impacts on reproductive success and survival. If, in addition, animals are disturbed by human activities and cannot optimally use available habitats, the effects of a severe winter likely will be magnified.

Activities associated with the extraction of petroleum resources on the coastal plain of the Arctic Refuge have the potential to displace muskoxen into areas of deeper snow where forage availability is low and energetic costs to procure food are high. Displacement from, or permanent loss of, limited winter habitat could affect reproductive success and survival of muskoxen on the coastal plain of the Arctic Refuge.

To minimize potential effects of petroleum exploration and development on muskoxen in the Arctic Refuge, areas occupied by muskoxen in winter should be avoided; and areas of potential winter habitat should not be selected as sites for permanent facilities.

Summary

Muskoxen are year-round residents of the 1002 Area on the coastal plain of Arctic National Wildlife Refuge. Numbers of muskoxen in the Refuge have declined over time with <300 currently living on the coastal plain including <250 in the 1002 Area. Calf production has also declined over time.

Severe winters (deep snow and prolong snow seasons) and increasing rates of predation are important factors in the dynamics of this population. Muskoxen have expanded their range east and west of the Arctic Refuge coastal plain and emigration has contributed to declining numbers.

Most calves are born in April and May, several weeks before green forage is available. To survive the long months of winter and to maintain body reserves needed for successful reproduction, muskoxen conserve energy in winter by reducing activity and movements. In winter, muskoxen feed on dried sedges and other low quality forage in areas of low snow. Windblown ridges adjacent to rivers are frequently used in winter. During the short weeks of summer, when green forage is available, muskoxen increase their movements and activity and feed on a variety of high quality forage to regain body weight before the next winter. River corridors and nearby uplands are often used by muskoxen in summer.

Muskoxen in the Arctic Refuge are vulnerable to disturbance from activities associated with petroleum exploration and extraction because of their year-round residency, their small population numbers and their need to conserve energy for the 9 months of winter if they are to successfully reproduce.

Disturbances that displace muskoxen from preferred winter habitats into areas of deeper snow or that increase their activity and movements could significantly increase their energetic costs in winter. Female muskoxen that are required to expend greater energy to survive the winter will have fewer reserves for pregnancy and lactation and may not reproduce successfully. Muskoxen frequently use habitats along or adjacent to rivers. These locations may be sites for gravel and water extraction and winter road construction if petroleum development is permitted in the Arctic Refuge.

Avoidance by industry of areas used by muskoxen and the location of permanent facilities away from river corridors, flood plains, and adjacent uplands could reduce the probability of disturbance and displacement of muskoxen. Status and distribution of muskoxen in and near the 1002 Area should be monitored to document future trends.

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Section 8: Polar Bears

Steven C. Amstrup

Movements and Population Dynamics of Polar Bears

Polar bears (*Ursus maritimus*) are hunted throughout most of their range. In addition to hunting, polar bears of the Beaufort Sea region are exposed to mineral and petroleum extraction and related human activities such as shipping, road-building, and seismic testing (Stirling 1990).

Little was known at the start of this project about how polar bears move about in their environment; and although it was understood that many bears travel across political borders, the boundaries of populations had not been delineated (Amstrup 1986, Amstrup et al. 1986, Amstrup and DeMaster 1988, Garner et al. 1994, Amstrup 1995, Amstrup et al. 1995, Amstrup 2000).

As human populations increase and demands for polar bears and other arctic resources escalate, managers must know the sizes and distributions of the polar bear populations. Resource managers also need reliable estimates of breeding rates, reproductive intervals, litter sizes, and survival of young and adults.

Our objectives for this research were 1) to determine the seasonal and annual movements of polar bears in the Beaufort Sea, 2) to define the boundaries of the population(s) using this region, 3) to determine the size and status of the Beaufort Sea polar bear population, and 4) to establish reproduction and survival rates (Amstrup 2000).

One-hundred-fifty-three satellite radio collars (PTTs), fitted to 106 adult female polar bears in the Beaufort Sea, were relocated 37,277 times between 1985 and 1993 (Amstrup 1995, Amstrup 2000, Amstrup et al. 2000). Polar bears were observed to move more than 4 km/hr for extended periods, but mean hourly rates of movement varied from 0.30-0.96 km/hr. Females with cubs had lower hourly rates of movement than females with yearlings and those (single females) without young.

Movement rates varied significantly among months: they generally were lowest in spring and late summer and highest in early winter (Amstrup 1995, Amstrup et al. 2000). Geographic displacements from the beginning to the end of each month were smaller for females with cubs of the year than for single females, and larger in November than in April.

In May, June, July, and August, radio-collared bears shifted locations to the north. Collared bears moved back to the south in October. Mean total distances moved each month ranged from 186-492 km. Total movements in December were larger than those measured in April, May, July, August, and September, and total monthly movements of females with cubs were lower than single females.

Total annual movements ranged from 1,454-6,203 km. Bears that spent part of the year in dens moved less than others, but non-denning classes of bears did not differ in total annual movement (Amstrup 1995, Amstrup et al. 2000).

Females with cubs were generally the most active group, and single females the least active. Highest and lowest levels of activity were recorded in June and September, but there also was a strong activity peak in early winter. Activity levels were lowest in the early morning and higher from mid-day through late evening.

Beaufort Sea polar bears kept their movements within boundaries outside of which they seldom ventured. Annual activity areas ranged from 12,730 km² to 596,800 km². Monthly activity areas ranged from a mean of 344 km² for females with cubs in April to 11,926 km² for females with yearlings in December (Amstrup 1995, Amstrup et al. 2000).

Bears from the Beaufort Sea population occupied an area extending up to 300 km offshore, from Cape Bathurst in Canada to Pt. Hope, Alaska, and enclosing 939,153 km² (Amstrup et al. 1986, Garner et al. 1994, Amstrup 2000).

Animals originally captured along the Beaufort Sea coast spent approximately 25% of their time in the northeastern Chukchi Sea, but animals captured in the Chukchi Sea ventured into the Beaufort Sea only 6% of the time. With few exceptions (Durner and Amstrup 1995) bears captured in the Beaufort Sea were faithful to summer activity areas in the central portion of the Beaufort Sea (Amstrup et al. 1986, Amstrup 1995, Amstrup et al. 1995, Amstrup et al. 2000). Although any bear caught in this region could be relocated anywhere else in the region, individual bears appeared faithful to general geographic regions (Fig. 8.1). Recent analyses of patterns in seasonal fidelity of polar bears (Bethke et al. 1996) suggested that 3 separate populations or stocks could be distinguished.

These 3 relatively discrete stocks overlap to a greater or lesser extent within Alaska waters (S. C. Amstrup, U.S. Geological Survey, unpublished data). Therefore, it is no longer reasonable to refer to only 1 group of polar bears (Amstrup 1995, Amstrup 2000) occupying this region (Amstrup et al. 2001). Although these groups are not distinguishable genetically (Paetkau et al. 1999), they are distinct enough to mandate management recognition.

Two groups, the Chukchi Sea and the Southern Beaufort Sea populations, share the mainland coastal areas of Alaska in the greatest numbers (Amstrup et al. 2001). Recognition of these stocks helps to explain some of the movement patterns previously observed. These 2 groups supply most of the harvest of polar bears that



Figure 8.1. Numbers and relocation positions of satellite radio-collared polar bears (# of individuals) captured in each of 6 longitudinal zones within the Beaufort Sea. Histograms illustrate proportions of those relocations made in each zone. For example, 32% of the 2,226 relocations of bears originally captured in the Lonely zone were recorded in the Barter Island zone, Alaska; 47% of the 1,079 relocations of bears captured in the Wainwright zone, Alaska, were recorded in the Chukchi zone.

occurs in Alaska and much of the harvest along the mainland coast of northwestern Canada.

Data were analyzed for 589 captures of 534 bears between 1967-1974 (a period of hypothesized overharvest) and for 1,087 captures of 789 bears obtained between 1981-1992 (a period when the population should have recovered from over-harvest). Population growth throughout the intervening years was also examined (Amstrup 1995, Amstrup et al. 2001).

Amstrup et al. (2001) and McDonald and Amstrup (2001) suggested that the number of polar bears in the Southern Beaufort Sea population grew at more than 3% per year between 1967 and 1998, reaching an estimated population that could be as high as 2,500 animals.

Although contact with hydrocarbons can have serious ramifications for polar bears (Amstrup et al. 1989), the polar bear's apparent rapid population growth has spanned the entire history of petroleum development in arctic Alaska (Amstrup 2000, Amstrup et al. 2001, McDonald and Amstrup 2001). This suggests that managed resource development can be compatible with healthy polar bear populations. Also encouraging is the new ability to estimate potential impacts that oil spills may have on polar bears. That ability has major ramifications for assessing risks of a variety of potential developments (Durner et al. 2001*b*).

Both long and short-term trends in condition of individual animals were observed during this study. Condition of adult females, as reflected by total mass, showed significant seasonal trends (Durner and Amstrup 1996). Despite seasonal fluctuations, longer-term trends also were suggested. Trends in recruitment and survival rates (in the 1970s compared with those from 1980 through 1992) suggested an inverse compensatory relationship between total population size and recruitment of subadults. Population size alone explained 55% of the variation in proportions of 2- and 3-year-olds in annual samples (Amstrup 1995). Large populations of the latter part of the study appeared to recruit proportionately fewer juveniles, and smaller populations of the early part of the study recruited higher proportions of juveniles.

Condition of single adult females and those with cubs, as reflected in measurements of axial girth, appeared to decline significantly as the population grew. Population size alone explained 75% of the variation in axial girth of reproductive age females.

Although numbers of young produced per female when the population was small (<0.40) and when it was large (<0.38) were similar, litters of more than one yearling were more frequent when the population was small. Sampling inconsistencies during the 2 periods precluded comparison across years for cubs and 2-yearolds but not for yearlings. Observed reproductive intervals of 3.4 and 3.7 years in early and late periods were suggestive of change, but not significantly different (Amstrup 1995). The age structure of the small population was younger than that of the larger population of later years.

Survival of adults, as calculated from life tables, was higher and survival of young lower when the population was large. Survival rates of adult Beaufort Sea polar bears, however, were as high or higher than those measured anywhere else. Annual survival of radiocollared females ranged from 0.946-0.980 (Amstrup and Durner 1995). Survival of cubs ranged between 0.610 and 0.675, while that of yearlings was 0.751-0.903.

In this study hunting explained 85% of the documented deaths of adult female polar bears (Amstrup and Durner 1995). Natural mortalities were not commonly observed among prime age animals (Amstrup and Nielsen 1989), and we still know little about the proximate causes of natural deaths among polar bears.

In the early 1990s, the trends described above suggested a population that could be approaching carrying capacity and was either stable or growing more slowly than in the early 1980s. More recent data suggest an alternate hypothesis: Apparent density dependence was a function of more transitory ecological effects. The apparent continued growth of the population into the late 1990s and the expansion of numbers of maternal dens as well as expanded areas used for denning (*see below*) appear to contradict earlier conclusions regarding carrying capacity and density effects. This suggests that issues related to population status should be revisited (Amstrup et al. 1986, Amstrup 1995, Amstrup et al. 2001, McDonald and Amstrup 2001).

Estimated numbers of bears at the close of the study were relatively large. Effects of the increasing human intrusions into the polar bear environment have not been observed at a population level, suggesting that proactive management can assure coexistence of polar bears and human developments.

Absolute numbers of bears, however, still are small compared to many other species. Early estimates suggested the additional loss of as few as 30 bears each year might push the total take from the population to the maximum sustained yield (Amstrup et al 1986, Amstrup and DeMaster 1988). Excess take did precipitate a decline in the 1960s and 1970s. Hence, although populations may now be near historic highs, managers must be alert to possible changes in human activities, including hunting and habitat alterations that could precipitate future declines.

Reproductive Significance of Maternity Denning on Land

The distribution of polar bears is circumpolar in the Northern Hemisphere, but maternal dens known at the start of this project were concentrated in relatively few, widely scattered locations (Amstrup 1986, Amstrup et al. 1986, Amstrup and DeMaster 1988, Amstrup and Gardner 1994).

Among the best-known denning concentration areas were the Svalbard Archipelago north of Norway; Franz Josef Land, Novaya Zemlya, and Wrangel Island in Russia; and the west coast of Hudson Bay in Canada. Denning was either uncommon or unknown in gaps between known denning concentration areas. The Beaufort Sea region of Alaska and Canada lay in the largest of those gaps, and some had hypothesized that polar bears of this region actually were born in other areas.

Now we realize that the coastal plain area of the Arctic National Wildlife Refuge lies in a region of polar bear denning; and its coastal plain also may contain significant gas and oil resources. Polar bears in dens could be affected in many ways by petroleum development, but neither the distribution of dens nor the sensitivity of bears in dens was known before our research (Amstrup 1986, Amstrup and DeMaster 1988).

To ascertain the number and distribution of denning polar bears that could be impacted by oil development on the Arctic Refuge coastal plain, we established the following research objectives: 1) to determine the distribution of polar bear dens in northern Alaska, 2) to ascertain the time that polar bears enter and emerge from dens, 3) to calculate the relative success rates of dens on land and on sea ice, and 4) to determine whether oil and gas exploration and development of the Arctic Refuge coastal plain would adversely impact polar bears of the Beaufort Sea by disrupting denning activities.

Polar bears were captured and radio-collared between 1981 and 1992. Amstrup and Gardner (1994) determined that denning in the Beaufort Sea region was sufficient to account for the estimated population. They also noted that the proportion of dens on land was higher in the late 1980s and early 1990s than it was earlier in the study (Fig. 8.2). That trend continues, and other distributional changes also may have occurred in the late 1990s and early 2000s. Of a total of 182 dens located by telemetry between spring of 1982 and spring of 2001, 150 were within the study area from 167° to 137° W longitude (Point Hope to Mackenzie River). Polar bear dens in this

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Figure 8.2. Number of polar bear dens located by radio-telemetry in each of 3 substrates, 1981-1990.

region continued to occur on land, pack ice, and land-fast ice.

Seventy-three of the 150 maternal dens discovered by telemetry between 167° W and 137° W were on land or land-fast ice where they were potentially vulnerable to a variety of human disturbances.

The remaining 77 identified maternal dens were on drifting pack ice where they were relatively invulnerable to most human activities. The proportion of pack-ice dens dropped dramatically in the latter half of the study. A decrease in study effort in offshore regions in the late 1990s may explain a portion of the decline in numbers of dens found on pack ice. Bears denning on pack ice drifted as far as 997 km while in dens and were potentially vulnerable to a variety of natural forces that could compromise their security while occupying dens (Amstrup and Garner 1994).

There was no difference in cub production by bears denning on land and pack ice. Mean entry and exit dates were 11 November and 5 April for land dens and 22 November and 26 March for pack-ice dens (Amstrup and Gardner 1994).

Female polar bears captured in the Beaufort Sea appeared to be isolated from those caught east of Cape Bathurst in Canada. Bears followed to >1 den did not reuse sites, and consecutive dens were from 20 km to 1,304 km apart (Fig. 8.3). However, radio-collared bears were usually faithful to substrate (pack ice, land, land-fast ice) and the general geographic area of previous dens (Amstrup and Gardner 1994).

Of the 73 dens found by radio telemetry on the mainland coast of Alaska and Canada (land plus fast-ice dens), 32 (44%) were within the bounds of the Arctic Refuge and 24 (33%) were within the 1002 Area.

The proportion of dens located on the Arctic Refuge dropped from 47% to 41% when the periods before and after 1992 were compared, while the proportion of dens located within the bounds of the 1002 area dropped from 36% to 30%. The decrease in proportion of land dens on the Arctic Refuge was accompanied by an increase in the proportion of dens found on land areas west of the Arctic Refuge. Although this distribution shift is not statistically significant (Chi-square test P = 0.88), it is readily apparent on the map (Fig. 8.4).

The shift may be explained simply by sample size limitations. The continuing growth in polar bear numbers, the continuing trend in proportion of dens on land, and perhaps changing freeze-up conditions in the last decade all may be influencing the distribution of denning efforts. The apparent increase in numbers of bears denning on land and the increased land area used for denning corroborates estimates, reported earlier, that suggested a continued increase in total numbers of polar bears



Figure 8.3. Maternal den locations for 5 polar bears followed to dens for more than one year. All dens were located by radio telemetry. Bears repeatedly denned in the same general geographic area, but not the same place. Likewise, polar bears repeatedly denned in the same substrate. (*from* Amstrup and Gardner 1994)



Figure 8.4. Distribution of maternal dens of radio-collared polar bears along the northern coast of Alaska and Canada, 1981-2001. (updated from Amstrup and Gardner 1994)

throughout the study period. The distribution of maternal denning continues to be a fertile area for future research.

Despite a possible decline in proportional use of the Arctic Refuge for denning, there still appears to be a higher concentration of dens on the Arctic Refuge than on adjacent lands. Development of hydrocarbon resources therefore could increase the potential for disturbance of denning polar bears by human activities.

Because the chronology of denning is now known, however, human activities could be temporally managed to minimize exposure of denning bears (Amstrup 1993, Amstrup and Gardner 1994). Spatial management of industrial activities could further minimize exposure of dens to disturbances because denning occurs in low density (including the Arctic Refuge) within relatively uncommon habitats that can be mapped (Amstrup 1993, Durner et al. 2001*a*).

Available data indicate polar bears are relatively resilient to disturbances coming from outside their dens (Amstrup 1993, Amstrup and Gardner 1994). Data showed that dens exposed to even high levels of activity did not suffer a detectable reduction in productivity (Amstrup 1993). Perturbations resulting from capture, marking, and radio tracking maternal bears did not affect litter sizes or stature of cubs produced; and 10 of 12 denned polar bears exposed to exceptional levels of activity were not measurably affected (Amstrup 1993).

Hence, polar bears in dens may be less vulnerable to human disturbances than previously thought. This finding corroborates the observations of Blix and Lentfer (1992) who reported that polar bears in dens are well insulated from disruptions outside of their dens.

Aggressive and proactive management, therefore, can minimize or eliminate most of the potential adverse effects of human developments on denning polar bears. It will be important to conduct research and monitoring of polar bear denning and ecology concurrent with any approved developments to assure that management efforts do have the desired mitigation effects.

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Section 9: Snow Geese

Jerry W. Hupp, Donna G. Robertson, and Alan W. Brackney

Size and Distribution of Snow Goose Populations

Part of the coastal plain of the Arctic National Wildlife Refuge, Alaska, is used as an autumn staging area by lesser snow geese (*Chen caerulescens caerulescens*) from the Western Canadian Arctic population (hereafter called the Western Arctic population). There were approximately 200,000 breeding adults in the Western Arctic population through the mid-1980s (Johnson and Herter 1989), but the population has recently increased to about 500,000 breeding adults (Kerbes et al. 1999).

Early in their autumn migration, adult and juvenile snow geese from the Western Arctic population feed intensively while staging on the Beaufort Sea coastal plain in Canada and Alaska to build fat reserves needed for migration. Aerial censuses from 1973 to 1985 indicated that up to 600,000 adult and juvenile snow geese used the coastal plain for 2-4 weeks in late August until mid-September (Oates et al. 1987).

We studied annual variation in numbers and spatial distribution of snow geese that staged on the coastal plain of the Arctic Refuge.

Numbers and distribution of snow geese on the Arctic Refuge were assessed from aerial surveys during 9 years from 1982-1993 (Robertson et al. 1997). During surveys biologists estimated the numbers of geese in flocks and marked flock locations on topographic maps. Survey results were digitized on a map of the coastal plain. A grid of 25-km² cells was superimposed over the digitized map. We tallied the numbers of geese observed in a cell during each survey and the number of years each cell was used by geese.

The numbers of snow geese that staged on the Arctic Refuge ranged from 12,800 to 309,200 individuals across years (Fig. 9.1). The numbers were highly variable because in some years most of the population remained in Canada, whereas in other years the majority of the Western Arctic population staged on the Arctic Refuge.

Snow geese occupied approximately 605,000 ha of the Arctic Refuge coastal plain between the Hulahula River and Canadian border. Only 20% of the 25-km² cells were frequently used (i.e., used \geq 5 years) yet 80% of the frequently used cells fell within the boundaries of the 1002 Area (Fig. 9.2). The mid-coastal plain between the Okpilak and Aichilik rivers was used more frequently than areas near the coast or the steep foothills. Areas that were used frequently were also used by larger numbers of geese. Frequently used areas had more of the landscape



Figure 9.1. Numbers of lesser snow geese observed on the coastal plain of the Arctic National Wildlife Refuge, Alaska, USA, during aerial surveys from 1982-1993. Poor weather prevented surveys in 1990 and 1991.

features snow geese selected when feeding (Hupp and Robertson 1998).

Snow Goose Habitat, Food, and Energy Requirements

The staging area on the Beaufort Sea coastal plain provides forage that geese use to build energy reserves prior to continuing their migration south (Patterson 1974). Upon departure from the coastal plain, snow geese make a 2,000-km-nonstop flight to the next stopover area in northern Alberta (Johnson and Herter 1989). Geese that lack sufficient fat reserves may be less likely to survive migration (Owen and Black 1991).

Because snow geese are easily disturbed by human activity (Davis and Wiseley 1974, Wiseley 1974, Bélanger and Bédard 1989), development of the coastal plain could displace geese from feeding habitats. Exclusion from feeding habitats could reduce the likelihood that staging geese would acquire fat reserves needed for migration. To identify snow goose areas that could be impacted by development, we needed data on forage preference as well as the distribution and availability of feeding habitats.

We studied body condition and diet of snow geese in order to understand their energetic and nutritional demands. We also assessed use and availability of feeding habitats and the effects that grazing geese had on vegetation at these sites.

Body condition and diet of 151 snow geese collected during 1984-85 and 1988 were evaluated (Fig. 9.3). Adult snow geese gained an average of 22 g of body fat/day and departed the Arctic Refuge with about 600 g of fat reserves. Juveniles arrived on the Arctic Refuge with smaller fat reserves than adults, acquired lipid reserves at a slower rate (13 g/day), and departed with smaller reserves (375 g). At the end of staging, juveniles had



Figure 9.2. Frequency of use of 25-km² cells by lesser snow goose flocks on the coastal plain of the Arctic National Wildlife Refuge, Alaska, 1982-1993. Use of cells by snow geese was assessed during aerial surveys.

proportionally smaller lipid reserves (15-18% of body mass) than adults (21-24% of body mass) and likely were at greater risk of having inadequate energy reserves for migration.

We examined esophageal contents of snow geese to identify important forage species (Brackney and Hupp 1993). Snow geese primarily consumed 2 food items: the underground stembase of *Eriophorum angustifolium* (tall cottongrass) and the aerial shoots of *Equisetum variegatum* (northern scouring-rush). The birds typically fed on northern scouring-rush during the morning when surface soils and water were frozen, and they consumed underground parts of tall cottongrass during afternoon and evening after soils had thawed.

We examined forage intake and digestibility among captive snow geese to better understand the population's forage requirements (Hupp et al. 1996). Snow geese fed for a high percentage of the day (50-60%) and maintained high rates of forage intake (14 g dry matter/hour). On a daily basis a goose probably consumes the equivalent of about 30% of its body mass in cottongrass stembases. A population of 300,000 snow geese that stages for 3 weeks could consume as much as 4,200,000 kg (wet mass) of cottongrass stembases. Thus the population consumes a very large amount of forage in a short period.

Northern scouring-rush primarily grew on riparian terraces within 400 m of river channels. Riparian terraces adjacent to rivers are important habitat for snow geese as they feed on scouring-rush.

We measured vegetation and soil moisture at sites where snow geese fed on tall cottongrass, and then we developed a statistical model to identify suitable feeding habitat (Hupp and Robertson 1998). The model was tested using captive snow geese. Snow geese typically exploited small, homogeneous patches of cottongrass in flooded areas. They avoided uplands and flooded areas where cottongrass was intermixed with *Carex*, shrubs, or tussocks.

The habitat selection model was used to assess the availability of cottongrass feeding sites along 192 randomly located transects on the 1002 Area east of the Hulahula River. Cottongrass feeding sites occurred in



Figure 9.3. Rates of lipid deposition by lesser snow geese during fall staging on the Arctic National Wildlife Refuge, Alaska. Geese were collected in 1984, 1985, and 1988. Data were pooled across years and size of fat reserves scaled to the date geese were first observed on the Arctic Refuge in each year.

small patches that were highly interspersed with less suitable feeding habitat. They were widely distributed but comprised a small percentage ($\leq 3\%$) of the study area.

Larger-scale micro-relief features were also examined at snow goose feeding areas. Cottongrass feeding sites primarily occurred along narrow (<1 m) edges of flooded thermokarst pits, water tracks, and troughs. When feeding on cottongrass, snow geese selected areas with greater availability of thermokarst pits and avoided uplands, low center polygons, wet meadows, and strangmoor (Hupp and Robertson 1998).

Thermokarst pits and water tracks were widely available in the mid-coastal plain between the Okpilak and the Aichilik rivers. Greater availability of cottongrass feeding habitat in that region likely accounts for its more frequent use by snow geese (Hupp and Robertson 1998).

Snow geese removed the underground portion of cottongrass from which plants regenerate. Four years after an experimental removal, the biomass of stembases in treatment plots was approximately 50% of that in control plots (Hupp et al. 2000). Feeding by snow geese likely

reduces forage availability in subsequent years. Geese may be unable to successfully exploit a site for several years after it has been grazed.

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Snow geese consume large volumes of forage at feeding sites that are small, patchy, and comprise $\leq 3\%$ of the landscape. Feeding on cottongrass at a site reduces forage abundance at that location for at least several years. Snow geese in the Western Arctic population use an extensive staging area because forage availability varies both spatially and temporally. Variation in the numbers of staging geese on the Arctic Refuge is likely due to annual differences in habitat conditions. Poor forage conditions or the presence of snowcover on the Canadian portion of the staging area may contribute to greater number of staging geese on the Arctic Refuge.

Effect and Mitigation of Human Activities on Snow Geese

Staging snow geese are easily disturbed by aircraft activity (Davis and Wiseley 1974, Bélanger and Bédard 1989). Repeated aircraft disturbance can reduce their rate of food intake due to disruption of feeding behavior and displacement from feeding habitats. Reduced fat accumulation and diminished survival during migration could result from repeated aircraft disturbance.

The following objectives were designed to assess snow goose response to experimental aircraft overflights: 1) determine the effect of aircraft on activity patterns and habitat use, 2) calculate the effect of increased stress or displacement caused by aircraft overflights on the energy budgets of the geese, and 3) determine implications of petroleum development to survival of snow geese.

Studies of aircraft disturbance were limited due to low numbers of geese on the Arctic Refuge in most years from 1988-1993, poor weather, and the need to meet other study objectives. Snow geese flushed at a mean distance of 5.2 km (SD = 2.9) from a Bell 206B helicopter during overflights in 1991 (n = 19). Flocks were displaced an average of 1.8 km (SD = 2.0) from their feeding sites.

These results are similar to a 1973 study of aircraft disturbance to the Western Arctic population in Canada in which fixed-wing aircraft and helicopters flushed snow goose flocks within a 6-km radius (Davis and Wiseley 1974). In that study, flocks were displaced an average of 1.9, 1.6, and 5.9 km from feeding sites by helicopters, small, and large fixed-wing aircraft, respectively.

Several studies suggest that human disturbance can displace staging snow geese from feeding habitats and possibly diminish the size of juvenile fat reserves. A study of staging greater snow geese found that >2 disturbances/ hour caused 50% fewer geese to use the disturbed area the following day (Bélanger and Bédard 1989). Energetic reserves of juvenile snow geese staging on the coast of the Beaufort Sea in Canada were projected to diminish approximately 9-20% if aircraft disturbed birds at least once every 2 hours (Davis and Wiseley 1974).

Brackney (1987) estimated that 20-30 aircraft overflights/day would reduce fat reserves of juvenile snow geese on the Arctic Refuge by up to 50%, assuming geese were unable to increase feeding time to compensate for disturbance. Aircraft disturbance would likely have a greater affect on juvenile snow geese because they spend a higher proportion of the day feeding, accumulate fat reserves at a slower rate, and depart with smaller reserves than adults.

Displacement of geese from feeding areas on the Arctic Refuge is of special concern because feeding habitats are limited (Hupp and Robertson 1998) and a large proportion of the frequently used region is within the 1002 Area (Robertson et al. 1997). The Western Arctic population requires access to the entire staging area on the Arctic Refuge to ensure that it can locate adequate feeding habitat in all years. We cannot assume that snow geese would be able to locate adequate feeding habitat in other regions if they were displaced from the Arctic Refuge coastal plain.

Aircraft activity on the Arctic Refuge coastal plain east of the Hulahula River should be closely managed in the event of petroleum development. During autumn staging, aircraft should be restricted within 6 km of frequently used areas between the Okpilak and Aichilik rivers. Aircraft should be restricted across the entire staging area in years when $\geq 100,000$ snow geese are observed on the Arctic Refuge. Surface facilities should not be placed in areas that are frequently used by snow geese.

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