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) radio-collared 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 re-sampled to 1-km^2 pixel size.

NDVI indexes the disproportionate reflectance of near-infrared 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 km^2) 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.

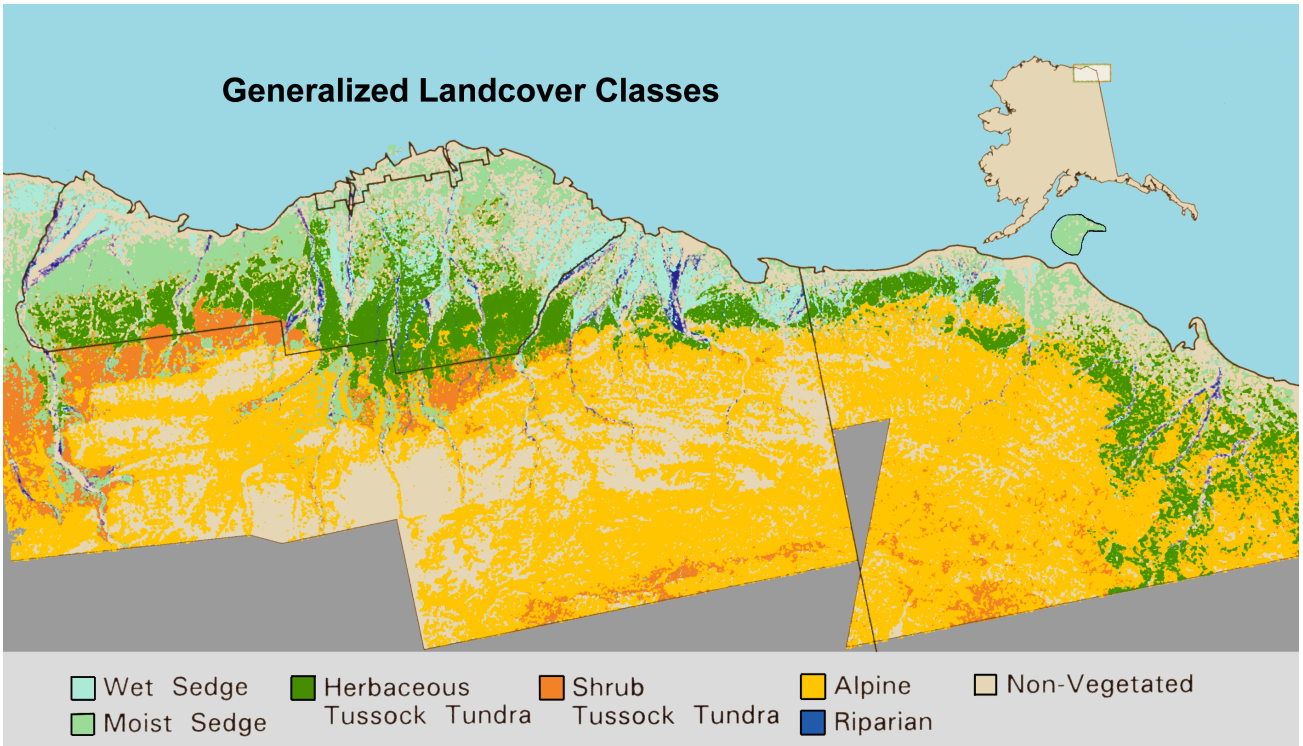

Figure 3.1. Land-cover classes on the coastal plain of the Arctic National Wildlife Refuge, Alaska, and eastward into the Yukon Territory, Canada, as generalized for studies of the Porcupine caribou herd. Classes are based on Jorgensen et al. (1994) as depicted in Fig. 2.1 and are expanded to include 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:

1) 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.

2) 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

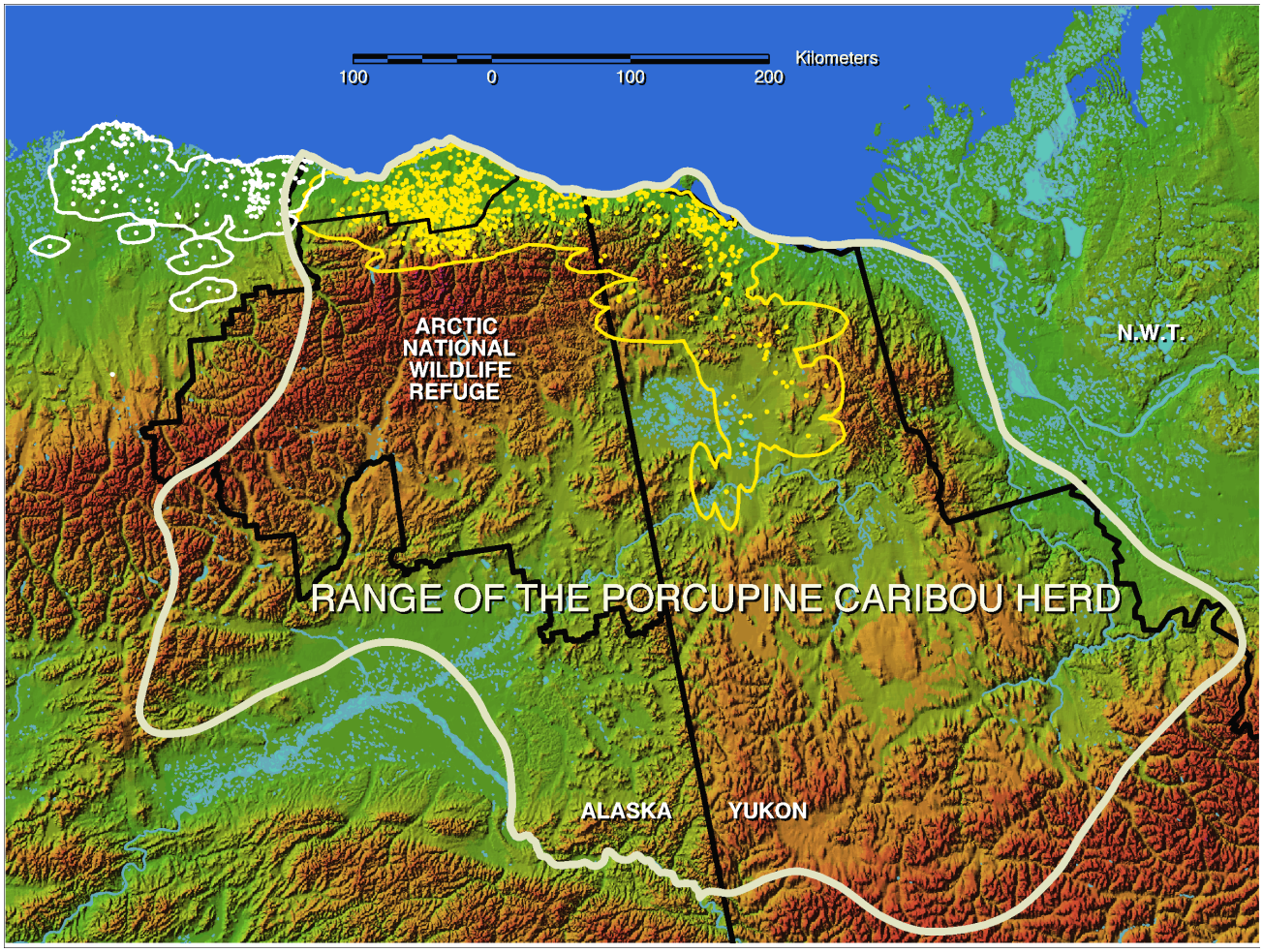

Figure 3.2. For the Porcupine caribou herd: annual range (wide white solid line), calving sites (yellow points), and aggregate extent of calving (thin solid yellow line), 1983-2001. For the Central Arctic caribou herd: aggregate extent of calving (thin solid white line) and calving sites (white points), 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 1980*a,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 1980*b*). 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. 3.3*a*) and winter (Fig. 3.3*b*) 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,

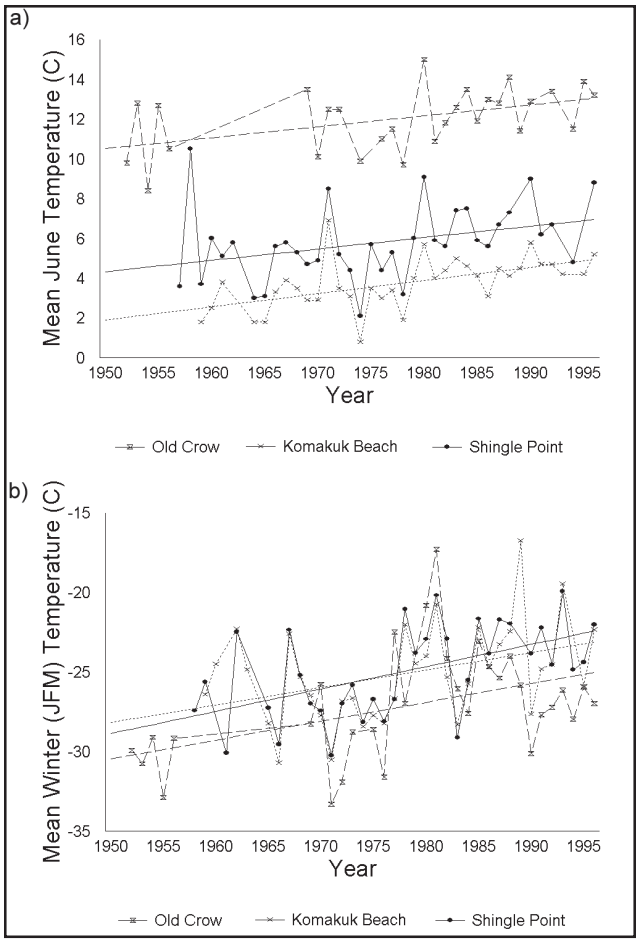

Figure 3.3. Mean temperatures for 2 stations within the Porcupine caribou herd's aggregate extent of calving (Komakuk Beach and Shingle Point, Yukon Territory, Canada) and 1 station within its winter range (Old Crow, Yukon Territory) for *a*) June, and *b*) winter (January, February, March), 1950-1995.

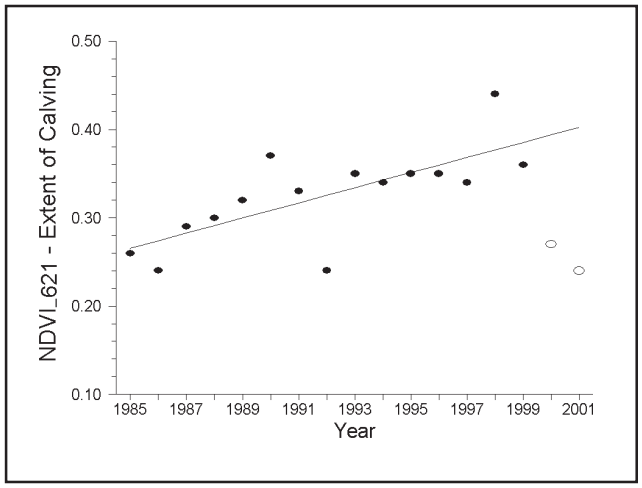

Figure 3.4. Median Normalized Difference Vegetation Index (NDVI) on 21 June within the aggregate extent of calving for the Porcupine caribou herd, 1983-2001. Values for 2000 and 2001 were outliers (RStudent = -2.49, -2.86, respectively) and excluded from the displayed regression line, $r^2 = 0.496$,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

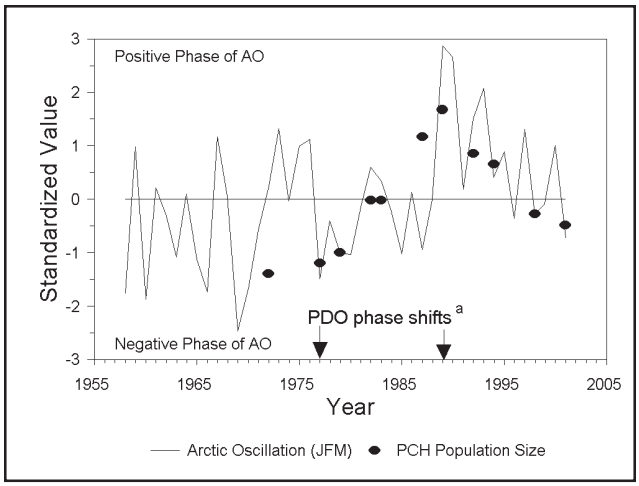

Figure 3.5. Standardized values of the Arctic Oscillation (AO) for winter (January, February, March) and population size of the Porcupine caribou herd, 1958-2001. Mean value indicated by solid horizontal line. [a] PDO is the Pacific Decadal Oscillation (Hare and Matuna, 2000).

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. 3.7*a*) and fall (Fig. 3.7*b*) 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

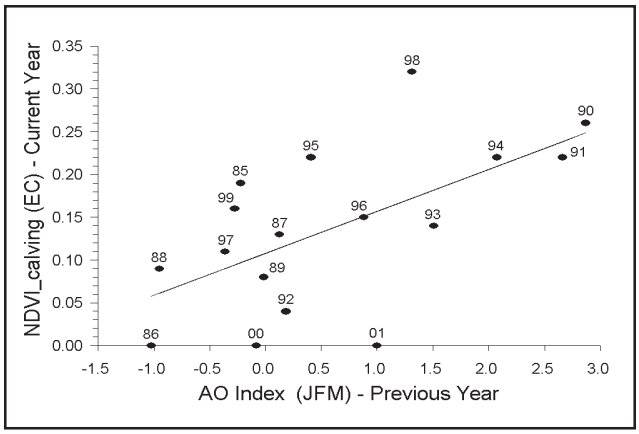

Figure 3.6. Median Normalized Difference Vegetation Index at calving (NDVI_calving) within the aggregate extent of calving (EC) of the Porcupine caribou herd for the current year, and winter Arctic Oscillation index (AO, January, February, March) for the previous calendar year, 1985-2001.

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. 3.7*a*,*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 climate-influenced 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.

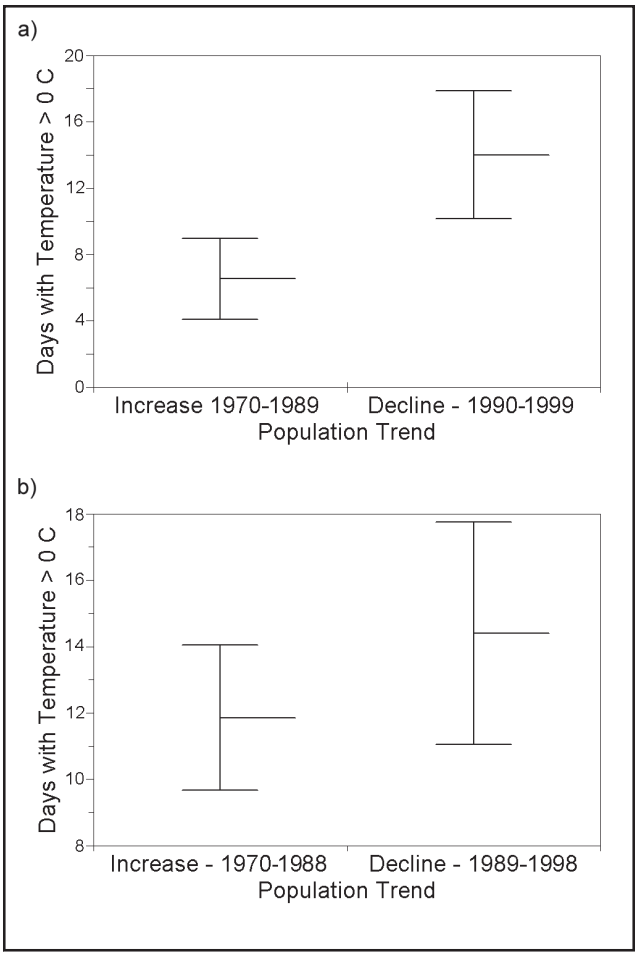

Figure 3.7. Frequency of days with daytime temperatures above freezing in *a*) spring (21 March - 30 April) and *b*) fall (21 September - 20 October) on transitional ranges of the Porcupine caribou herd during the herd increase phase, 1970-1988, and the herd decrease phase, 1989-1998. Brackets indicate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

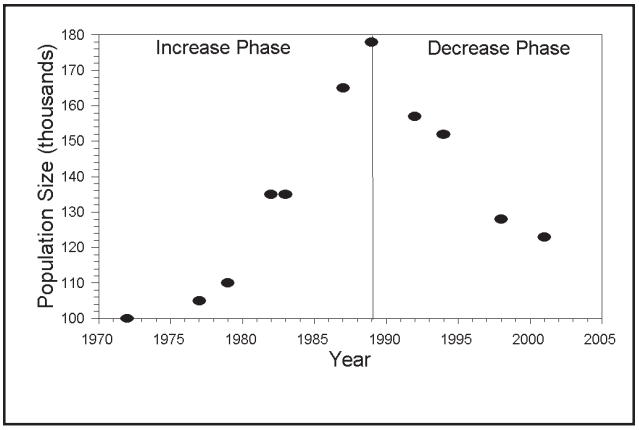

Figure 3.8. Population size of the Porcupine caribou herd, 1972-2001, estimated from aerial photo-censuses by the Alaska Department of Fish and Game.

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).

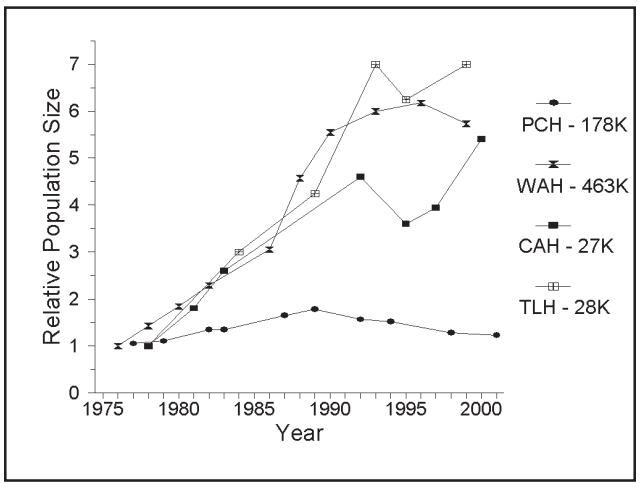

Figure 3.9. Relative post-calving herd sizes (minimum observed = 1.0) of the 4 Alaska barren-ground caribou herds (PCH = Porcupine caribou herd; WAH = Western Arctic herd; CAH = Central Arctic herd; TLH = Teshekpuk Lake herd), 1976-2001. Maximum observed population size for each herd is noted in the 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. 3.10*a-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.

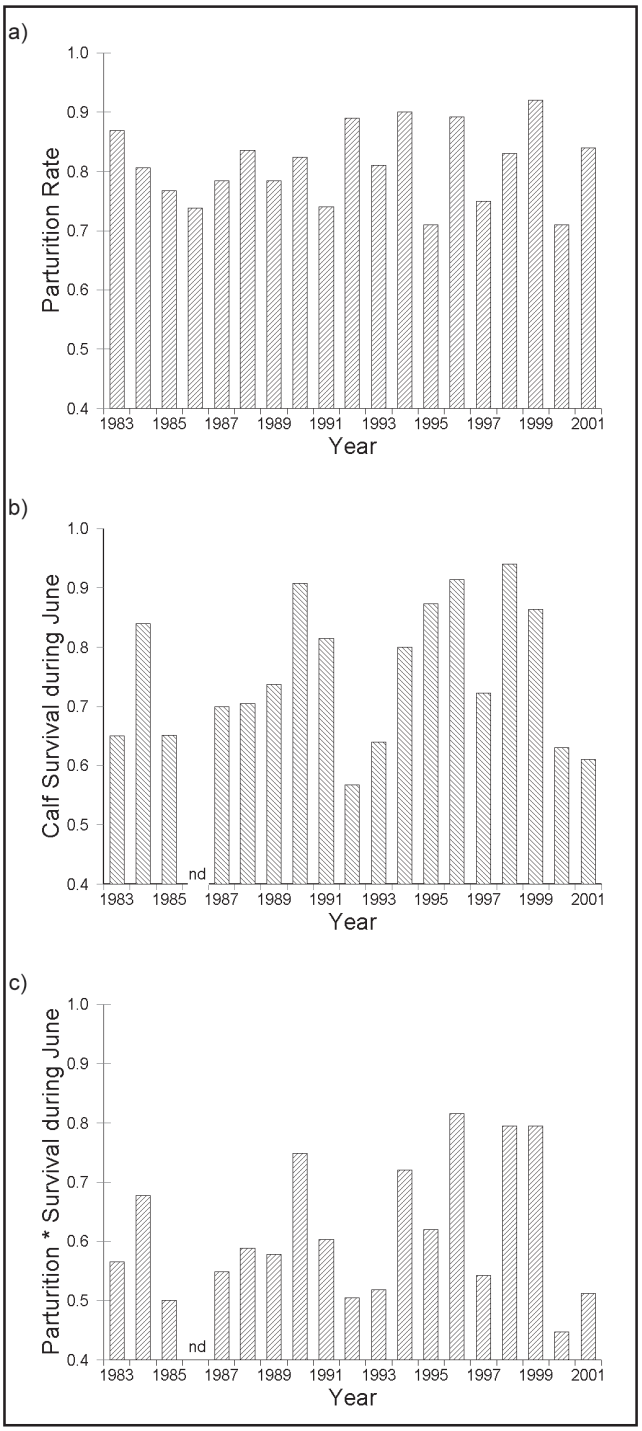

Figure 3.10. Reproductive estimates for the Porcupine caribou herd, 1983-2001: *a*) parturition rate of adult females, *b*) calf survival from birth through the last week of June, and *c*) *net calf production* [the product of parturition rate and calf survival].

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 km^2 (Fig. 3.2). The extent of calving encompassed ~36,000 km^2. 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 km^2 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-

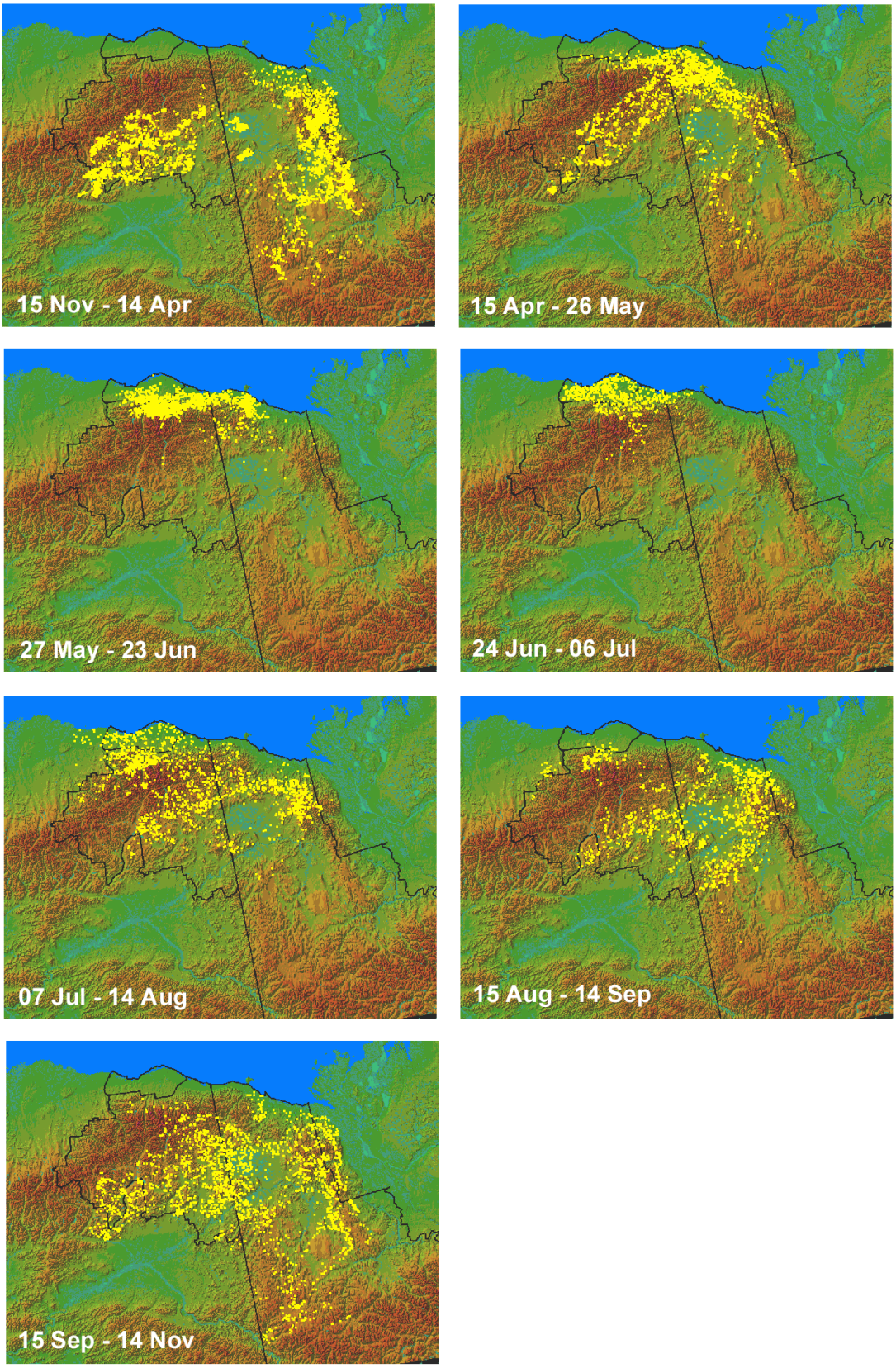

Figure 3.11. Distribution of satellite-collared female caribou of the Porcupine caribou herd during 7 time periods, 1985-1995. An average of 10 animals (range 4-17) were collared each year yielding 14,447 observations; 87% of these observations were obtained 1985-1990. Not included were the locations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

2,548 km^2) 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/km^2 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 radio-collared 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

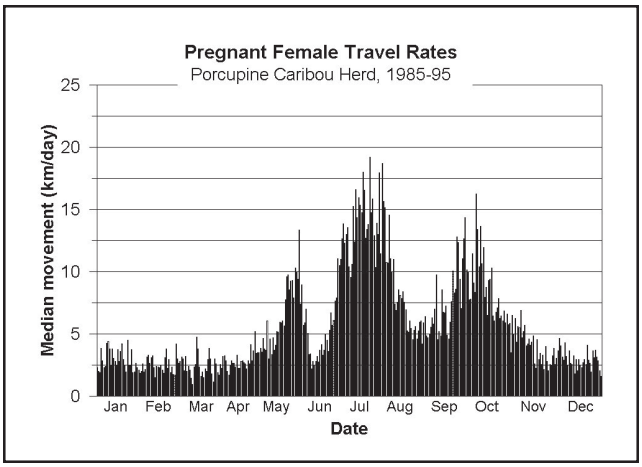

Figure 3.12. Minimum median daily movement rate of parturient satellite-collared females of the Porcupine caribou herd, 1985-1995. Values calculated from no more than one location per day. An average of 10 animals (range 4-17) were collared each year yielding 14,447 observations; 87% of these observations 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

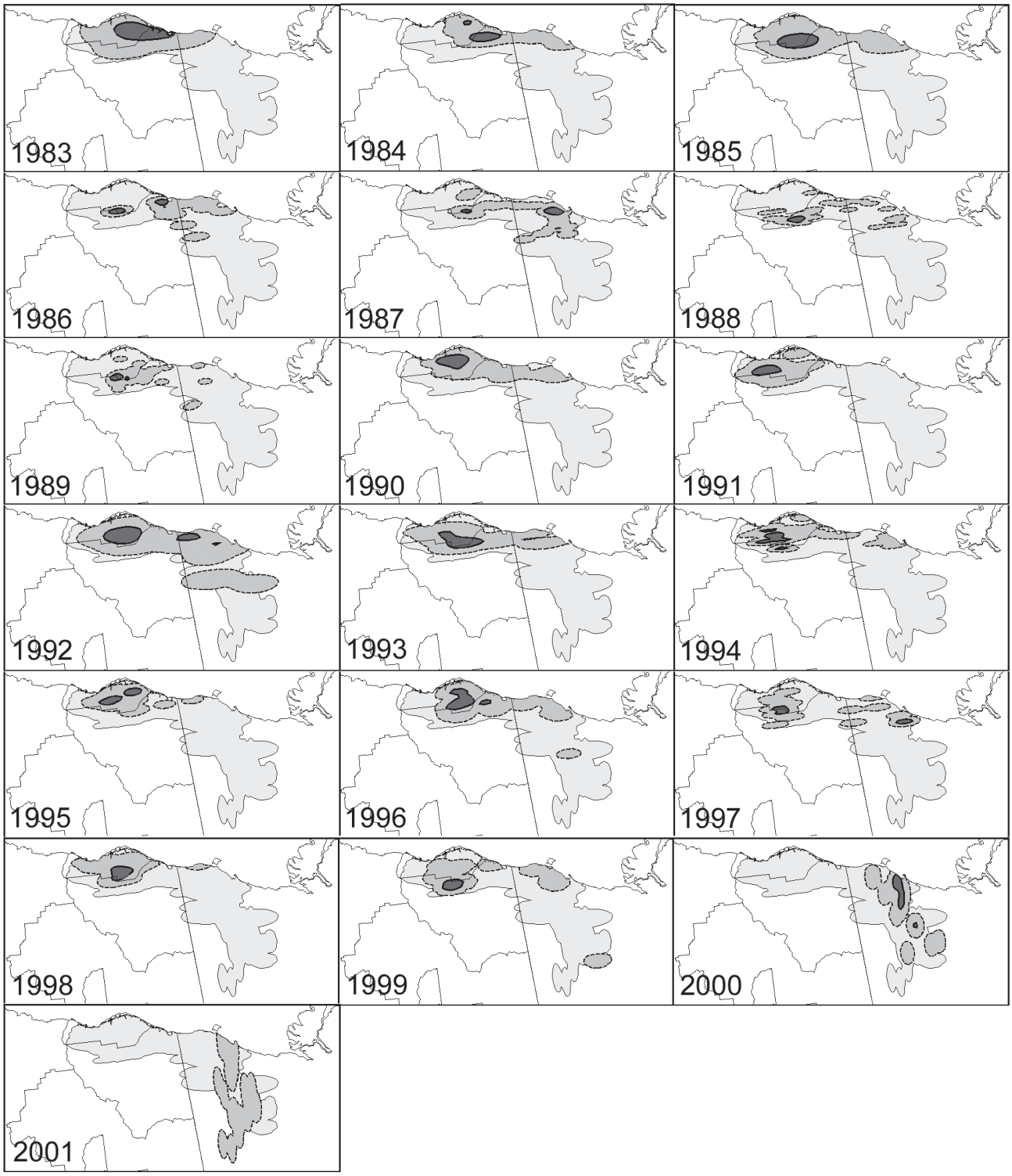

Figure 3.13. Calving distributions of the Porcupine caribou herd, 1983-2001, as estimated from fixed kernel analyses of the sites where radio-collared females were first observed with calves during repeated aerial surveys in May and June. There are 3 zones: 1) *concentrated calving area* (shown in dark 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	a		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

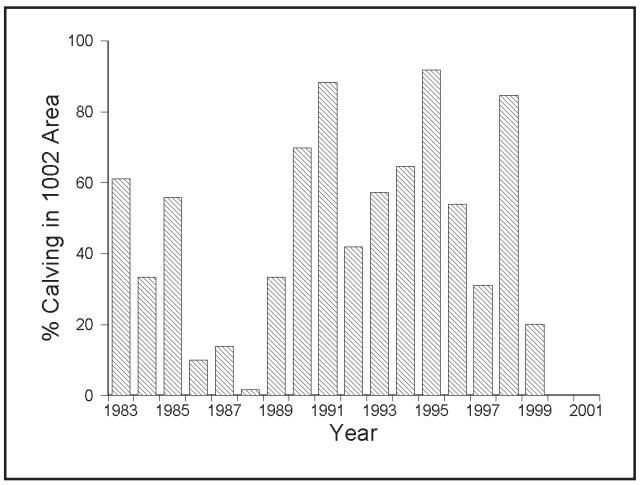

Figure 3.14. Percent of radio-collared Porcupine caribou herd females that calved in the 1002 Area of the Arctic National Wildlife Refuge, Alaska, 1983-2001.

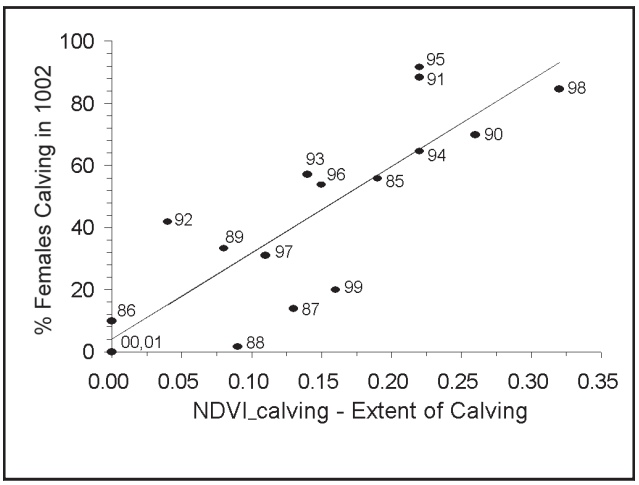

Figure 3.15. Percent of radio-collared Porcupine caribou herd females that calved within the 1002 Area of the Arctic National Wildlife Refuge, Alaska, in relation to the median Normalized Difference Vegetation Index at calving (NDVI_calving) within the aggregate extent of calving, 1985-2001. Point legends 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. 3.16*a*, 3.17*a*). 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., 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.

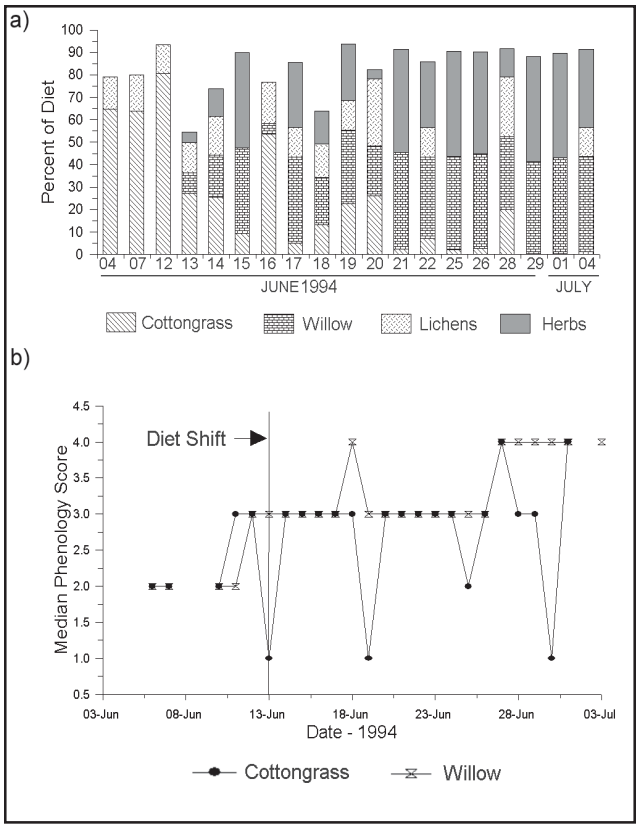

Figure 3.17. Porcupine caribou herd *a*) diet composition and *b*) median phenology of major forage items, 1994. Diet composition estimated from microhistological analysis of fecal pellets, corrected for digestibility. Phenology scores for cottongrass: 1 = leaves only, 2 = flowers in boot, 3 = early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

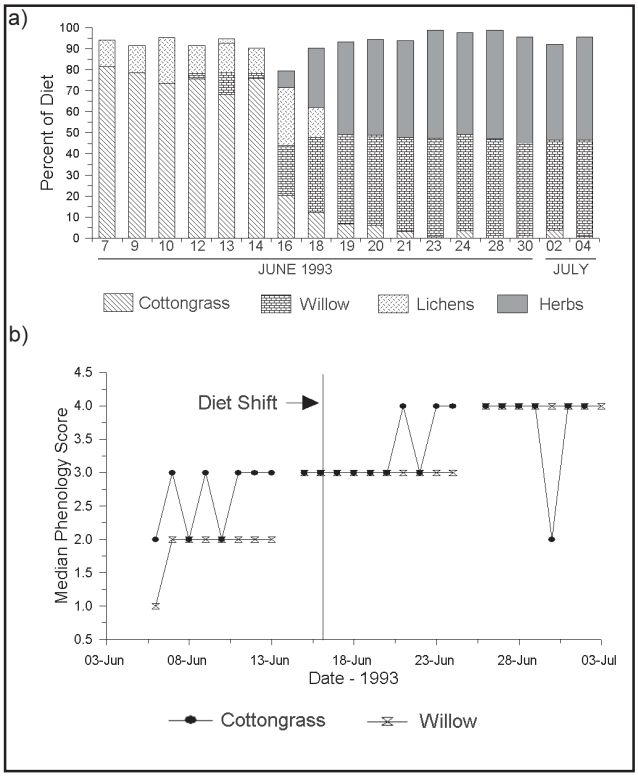

Figure 3.16. Porcupine caribou herd *a*) diet composition and *b*) median phenology of major forage items, 1993. Diet composition estimated from microhistological analysis of fecal pellets, corrected for digestibility. Phenology scores for cottongrass: 1 = leaves only, 2 = flowers in boot, 3 = early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

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-km^2 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. 3.19*b*) and during peak lactation demand (NDVI_621, 2.59x, $P < 0.001$) (Fig 3.19*c*) than available in the annual calving grounds. The females were non-selective ($P > 0.05$) for rate of greening (NDVI_rate) (Fig. 3.19*a*) and all snowcover classes (Fig. 3.20), selected herbaceous tussock tundra

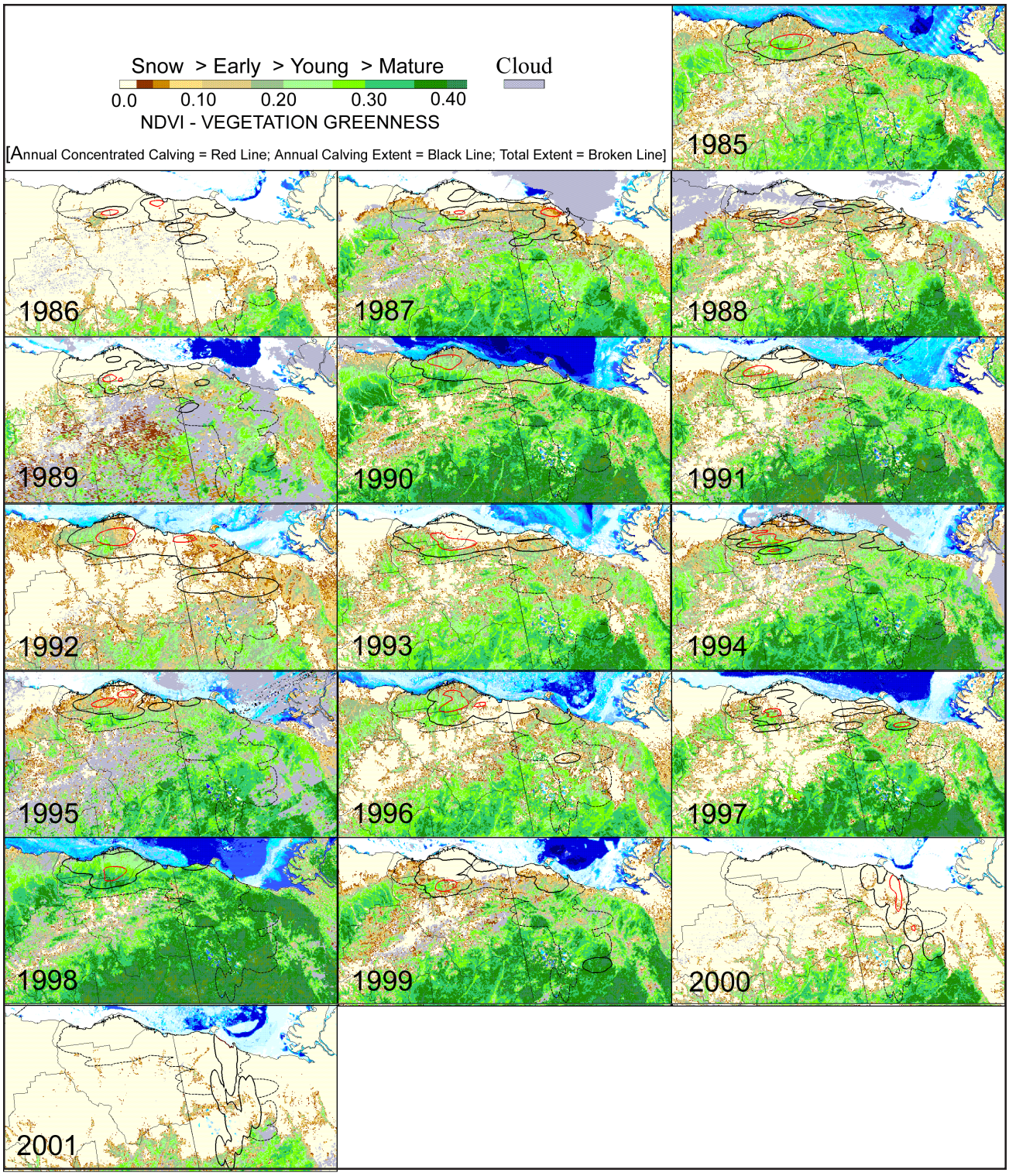

Figure 3.18. Annual conditions of snowcover and vegetation phenology derived from Advanced Very High Resolution Radiometer (AHVRR) satellite imagery during the calving period (30 May - 5 June), 1985-2001, for the Porcupine caribou herd. No concentrated calving was detected in 2001.

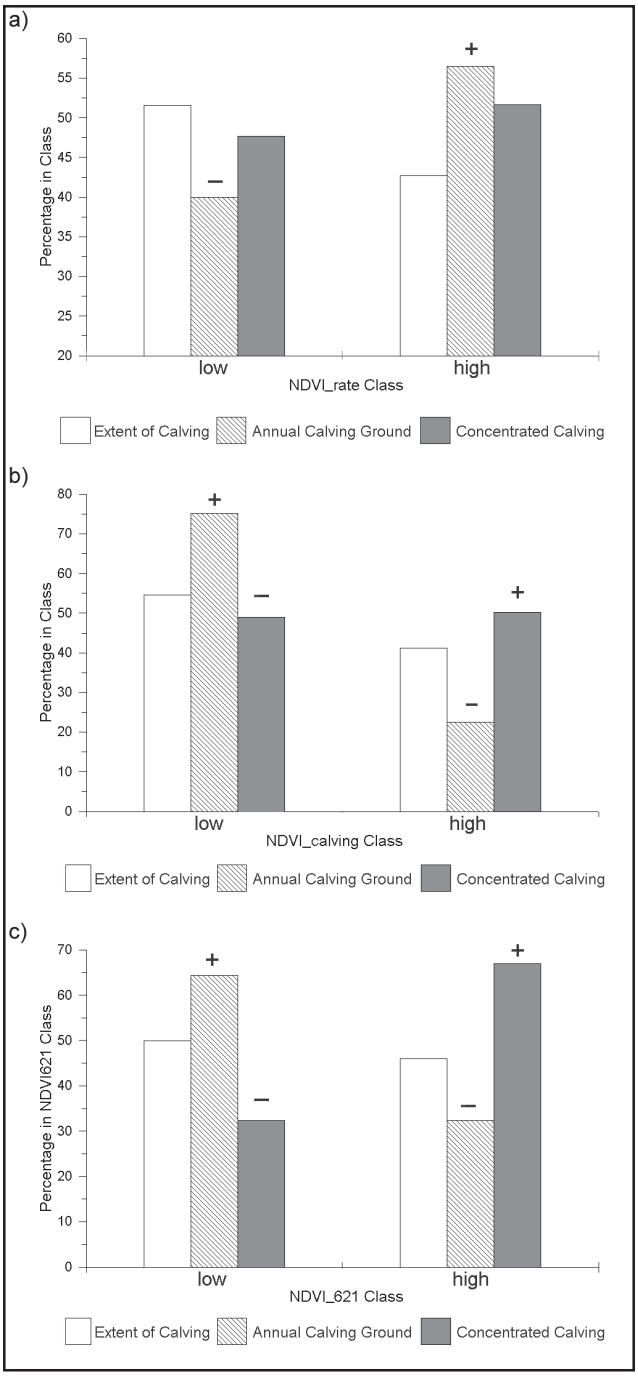

Figure 3.19. Average percent of area in low (≤ median) or high (> median) classes of *a*) daily rate of increase in the Normalized Difference Vegetation Index (NDVI_rate) *b*) NDVI at calving (NDVI_calving), and *c*) NDVI on 21 June (NDVI_621) for the aggregate extent of calving, annual calving grounds, 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.

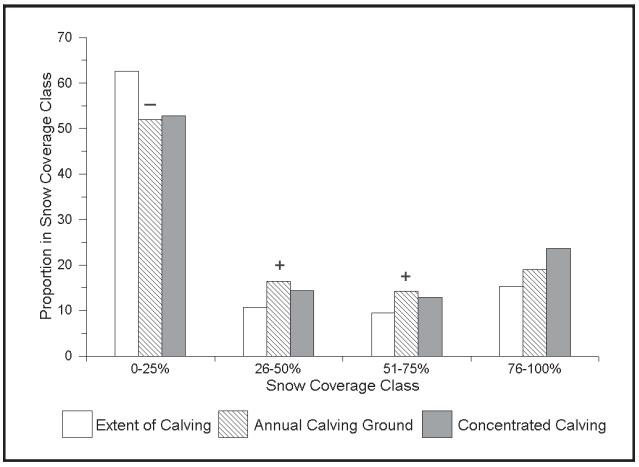

Figure 3.20. Average percent of area in 4 exclusive snowcover classes for the aggregate extent of calving, annual calving grounds, and concentrated calving areas of the Porcupine caribou herd, 1985-2001. Statistically significant selection or avoidance ($P < 0.05$, overall experiment) in comparison with 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 scale-independent, 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 (1980*b*) 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.

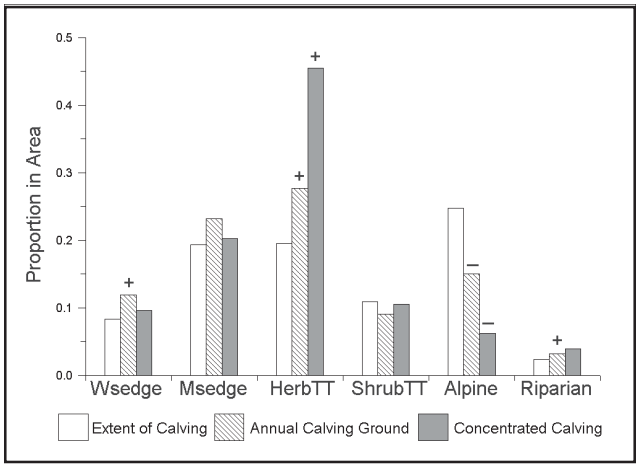

Figure 3.21. Average percent of area in 6 vetetation types for the aggregate extent of calving, annual calving grounds, and concentrated calving areas of the Porcupine caribou herd, 1985-2001. Vegetation types: Wsedge = wet sedge; Msedge = moist sedge; HerbTT = herbaceous tussock tundra; ShrubTT = shrub 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.

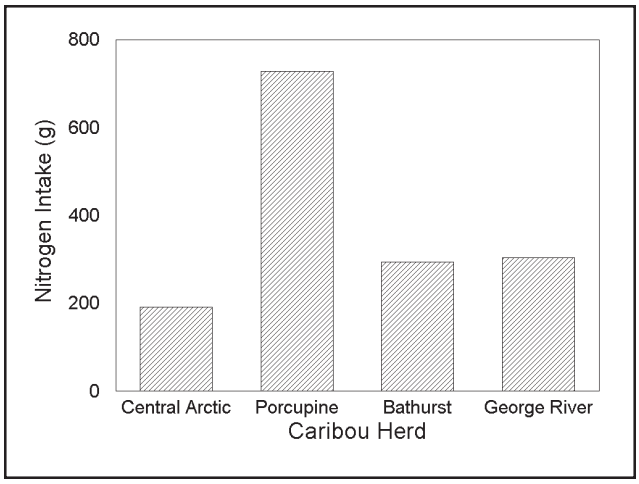

Figure 3.22. Estimated total intake of dietary nitrogen (g) from the calving ground (25 May - 14 June) for 4 North American caribou herds. Forage composition of diet and nutritional composition of forages were estimated from locally collected samples. Intake rates were estimated from White et al. (1975).

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 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 ≤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

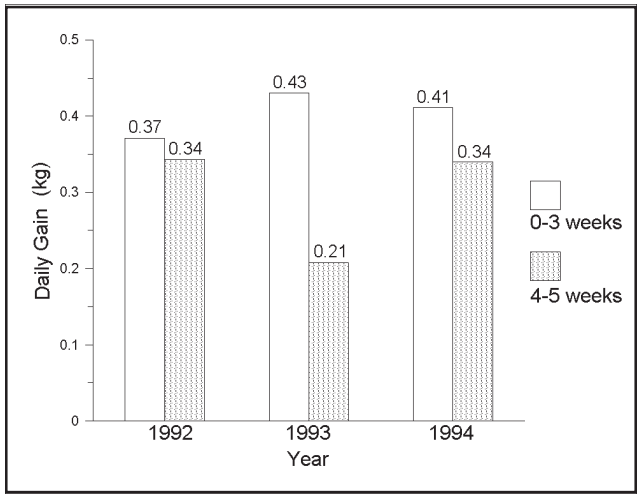

Figure 3.23. Daily gain (kg) of caribou calves of the Porcupine herd, 1992-1994, during 2 periods (0-3 weeks post-birth and 4-5 weeks post-birth). Gain was estimated from sequential weights of recaptured radio-collared animals. Means are listed above the appropriate bars.

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 post-calving, were all the same (1993 > 1994 > 1992).

Lack of correlation between individual calf weight-gain 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.

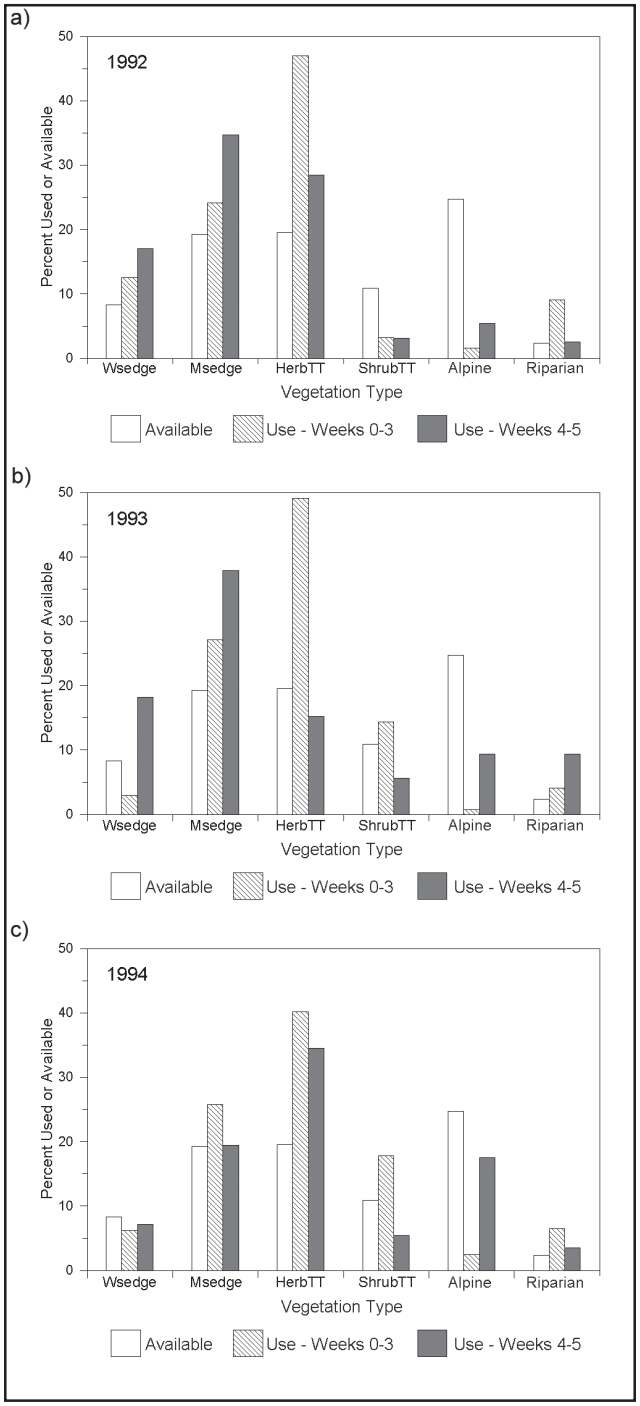

Figure 3.24. Availability of 6 vegetation types in the aggregate extent of calving for the Porcupine caribou herd and use by radio-collared calves during 2 periods (0-3 weeks post-birth and 4-5 weeks post-birth) for *a*) 1992, *b*) 1993, and *c*) 1994. Vegetation types: Wsedge = wet sedge; Msedge = moist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

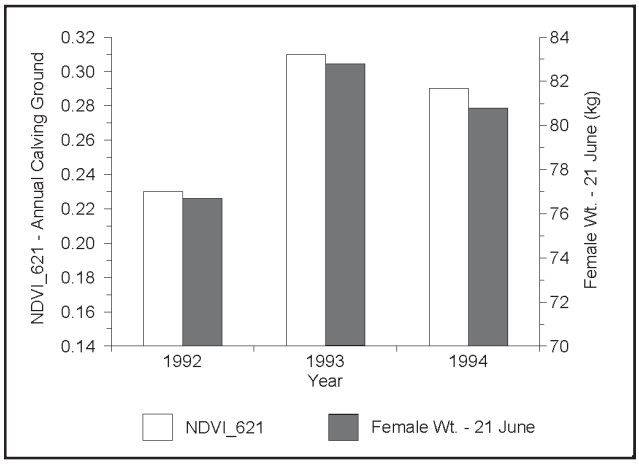

Figure 3.25. Median Normalized Difference Vegetation Index on 21 June (NDVI_621) within the annual calving grounds of the Porcupine caribou herd and weights of parturient female caribou when captured within the annual calving ground on 21 June, 1992-1994.

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 * NDVI_621 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

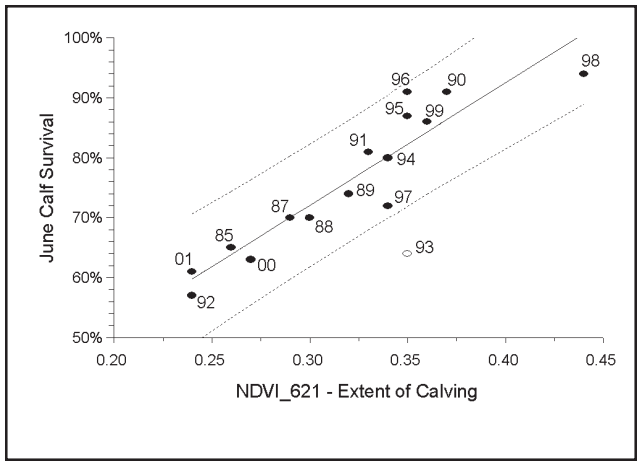

Figure 3.26. Calf survival through June for the Porcupine caribou herd, 1985-2001, in relation to median Normalized Difference Vegetation Index on 21 June (NDVI_621) within the aggregate extent of calving (EC). Legends identify the year of the estimate. Calf survival was not estimated in 1986 because 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 carry-over 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 radio-collared 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 predation on calf survival, it is imperative to specify the scale of analysis, and assess multiple scales simultaneously.

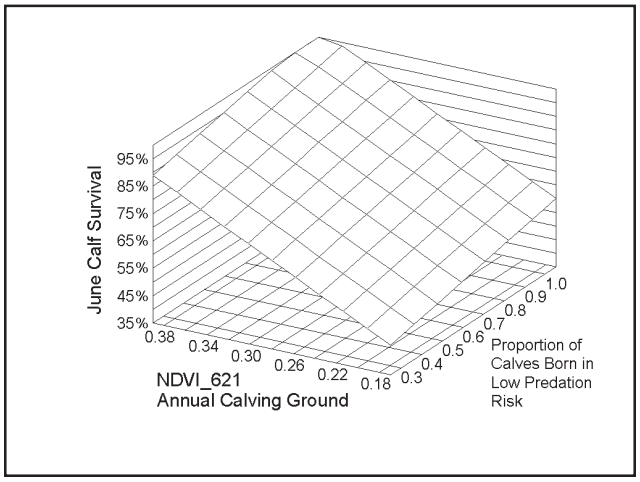

Figure 3.27. Predicted calf survival for the Porcupine caribou herd, 1985-2001, in relation to median Normalized Difference Vegetation Index on 21 June (NDVI_621) within the annual calving ground and to the proportion of calves born on the Arctic National Wildlife Refuge coastal plain physiographic zone 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.

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 post-calving 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 uni-directional 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 barren-ground 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 habitat-demography 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 * median NDVI_621 in the annual calving ground) + (0.00283 * proportion of calves born in low predation risk)] * 100, ($r^2 = 0.70$; $P < 0.001$). 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.

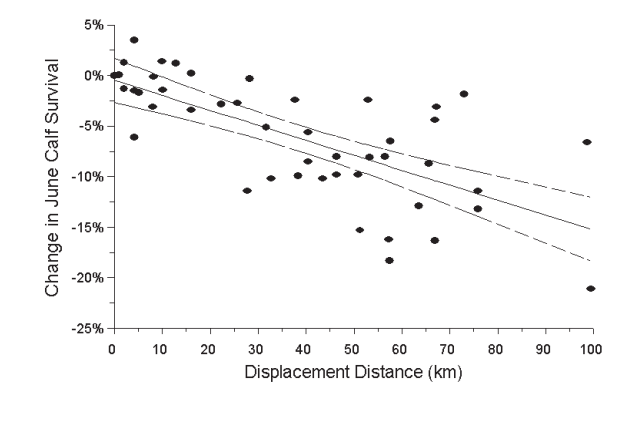

Figure 3.28. Estimated change in calf survival during June for the Porcupine caribou herd, 1985-2001, as a function of the distance of displacement of the annual calving ground and associated concentrated calving area and calving sites. Upper and lower dashed lines indicate 95% confidence intervals on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

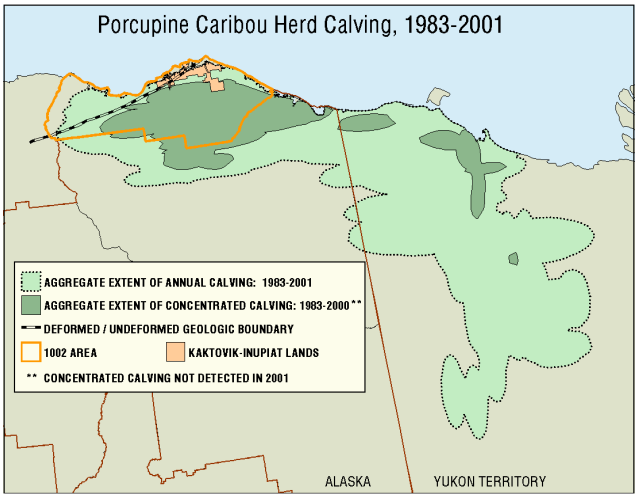

Figure 3.29. Aggregate extent of annual calving (light green shading) and aggregate extent of concentrated calving (dark green shading) for the Porcupine caribou herd, 1983-2001. The deformed/undeformed geological boundary is discussed in USGS Fact Sheet FS-028-01 (U.S. Geological Survey 2001).

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 weight-gain 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 freeze-thaw 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. 3.7*a,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).

References

Akaike, H. 1973. Information theory, an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kaidi, Budapest, Hungary.

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

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

Bergerud, A. T. 1980. A review of the population dynamics of caribou and wild reindeer in North America. Pages 556-581 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/Caribou Symposium, Roros, Norway, 1979. Directoratet for vilt og ferskvannsfisk, Trondheim, Norway.

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

Billings, W. D., and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biological Review 43:481-529.

Bliss, L. C. 1971. Arctic and alpine life cycles. Annual Review of Ecology and Systematics 2:405-438.

Brown, R. D., and R. O. Braaten. 1998. Spatial and temporal variability of monthly Canadian snow depths, 1946-1995. Atmosphere and Ocean 36:37-54.

Cameron, R. D. 1983. Issue: caribou and petroleum development in arctic Alaska. Arctic. 36:227-231.

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

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

_____, and J. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58:674-678.

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

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

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

_____, _____, and D. E. Russell. 1999. Comparative body composition strategies of breeding and non-breeding female caribou. Canadian Journal of Zoology 77:1901-1907.

Chapman, W. L., and J. E. Walsh. 1993. Recent variations of sea ice and air temperatures in high latitudes. Bulletin of the American Meteorological Society 74:33-47.

Clough, N. K., P. C. Patton, and A. C. Christensen, editors. 1987. Arctic National Wildlife Refuge, Alaska, coastal plain resource assessment - report and recommendation to the Congress of the United States and final legislative environmental impact statement. U.S. Fish and Wildlife Service, U.S. Geological Survey, and Bureau of Land Management, Washington D.C., USA.

Cronin, M. A., S. C. Amstrup, G. M. Durner, L. E. Noel, T. L. McDonald, and W. B. Ballard. 1998. Caribou distribution during the post-calving period in relation to infrastructure in the Prudhoe Bay oil field, Alaska. Arctic 51:85-93.

_____, W. B. Ballard, J. D. Bryan, B. J. Pierson, and J. D. McKendrick. 1998. Northern Alaska oil fields and caribou: a commentary. Biological Conservation 83:195-208.

Curatolo, J. A., and S. M. Murphy. 1986. The effects of pipelines, roads, and traffic on the movements of caribou, *Rangifer tarandus*. Canadian Field-Naturalist 100:218-224.

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

Duquette, L. S. 1984. Patterns of activity and their implications to the energy budget of migrating caribou. Thesis, University of Alaska, Fairbanks, Alaska, USA.

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

_____, and R. G. White. 1987. Energy expenditures for locomotion by barren ground caribou. Canadian Journal of Zoology 65:122-128.

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

_____, _____, and D. E. Russell. 1994. Demography of the Porcupine caribou herd, 1983-1992. Canadian Journal of Zoology 72:840-846.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist 138:478-498.

_____. 1995. Aggregation and migration by grazing ungulates in relation to resources and predators. Pages 257-273 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.

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

Groisman, P. A., T. R. Karl, and R. W. Knight. 1994. Observed impact of snow cover on the heat balance and rise of continental spring temperatures. Science 263:198-200.

Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993. Functional response of herbivores in food-concentrated patches - tests of a mechanistic model. Ecology 74:778-791.

Hamilton, W. D. 1971. Geometry for the selfish herd. Journal of Theoretical Biology 31:295-311.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-145.

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

Helle, T., and L. Tarvainen. 1984. Effects of insect harassment on weight gain and survival in reindeer calves. Rangifer 4:24-27.

Holben, B. N. 1986. Characteristics of maximum-value composite images from temporal AVHRR data. International Journal of Remote Sensing 7:1417.

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

Houghton, J. T., L. G. Meira Fihlo, B. A. Callender, N. Harri, A. Kattenberg, and K. Maskell. 1996. Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, England, United Kingdom.

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

Jorgenson, J. C., P. E. Joria, T. R. McCabe, B. R. Reitz, M. K. Raynolds, M. Emers, M. A. Wilms. 1994. Users guide for the land-cover map of the coastal plain of the Arctic National Wildlife Refuge. U.S. Fish and Wildlife Service, Fairbanks, Alaska, USA.

Kelleyhouse, R. A. 2001. Calving ground selection and fidelity: Western Arctic and Teshekpuk Lake herds. Thesis, University of Alaska, Fairbanks, Alaska, USA.

Kuropat, P. J. 1984. Foraging behavior of caribou on a calving ground in Northwestern Alaska. Thesis, University of Alaska, Fairbanks, Alaska, USA.

Langvatn, R., and T. A. Hanley. 1993. Feeding-patch choice by red deer in relation to foraging efficiency - an experiment. Oecologia 95:164-170.

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

_____, L. C. Byrne, and C. B. Johnson. 1993. Caribou Synthesis: 1987-90 Endicott environmental monitoring program. Unpublished report sponsored by U.S. Army Corps of Engineers, Alaska District, Anchorage, Alaska, USA.

_____, and A. K. Prichard, 2001. Surveys of caribou and muskoxen in the Kuparuk-Colville region, Alaska, 2000. Final Report for Phillips Alaska, Inc., prepared by ABR, Inc., Fairbanks, Alaska, USA.

Malingreau, J. P., and A. S. Belward. 1992. Scale considerations in vegetation monitoring using AVHRR data. International Journal of Remote Sensing 13:2289-2307.

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

Maxwell, B. 1996. Recent climate patterns in the Arctic. Pages 21-46 *in* W. C. Oechel, T. Callaghan, T. Gilmanov, J. I. Holten, B. Maxwell, U. Molau, and B. Sveinbjornsson, editors. Global change and arctic terrestrial ecosystems. Ecological Studies 124, Springer Verlag, New York, USA.

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

Minnis, P., E. F. Harrison, L. L. Stowe, G. G. Gibson, F. M. Denn, D. R. Doelling, and W. L. Smith, Jr. 1993. Radiative climate forcing by the Mount Pinatubo eruption. Science 259:1411-1415.

Murphy, S. M., and J. A. Curatolo. 1987. Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. Canadian Journal of Zoology 65:2483-2490.

_____, and B. E. Lawhead. 2001. Caribou. Pages 59-84 *in* J. C. Truett and S. R. Johnson, editors. The natural history of an Arctic oil field: development and the biota. Academic Press, San Diego, California, USA.

Myneni, R. B., C. J. Tucker, G. Asrar, and C. D. Keeling. 1998. Interannual variations in satellite-based vegetation index data from 1981 to 1991. Journal of Geophysical Research D6 103:6145-6160.

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

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

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

Nixon, W. A. C. 1990. Group dynamics and behavior of the Porcupine caribou herd during the insect season. Thesis, University of Alaska, Fairbanks, Alaska, USA.

O'Neill, R. V., and A. W. King. 1998. Homage to St. Michael: or, why are there so many books on scale. Pages 3-16 *in* D. L. Peterson and V. T. Parker, editors. Ecological scale: theory and applications. Columbia University Press, New York, New York, USA.

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

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

Pollard, R. H., W. B. Ballard, L. E. Noel, and M. A. Cronin. 1996. Summer distribution of caribou, *Rangifer tarandus granti*, in the area of the Prudhoe Bay oil field, Alaska, 1990-1994. Canadian Field-Naturalist 110: 659-674.

Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322-1339.

_____, _____, R. Langvatn, and J. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. Proceedings of the Royal Society of London, Series B 264:1317-1324.

Rexstad, E. A., and E. Debevec. 2001. Hueristic metric for ecological monitoring. Paper presented at the Annual Meeting of The Wildlife Society, 28 September, 2001, Reno, Nevada, USA.

Roffe, T. J. 1993. Perinatal mortality in caribou from the Porcupine herd, Alaska. Journal of Wildlife Diseases 29:295-303.

Russell, D. E., K. L. Gerhart, R. G. White, and D. van de Wetering. 1998. Detection of early pregnancy in caribou: evidence for lactational infertility. Journal of Wildlife Management 62:1066-1075.

_____, A. M. Martell, and W. A. C. Nixon. 1993. Range ecology of the Porcupine caribou herd in Canada. Rangifer Special Issue 8.

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

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criteria statistics. KTK Scientific, Tokyo, Japan.

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

_____, J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

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

Serreze, M. C., J. E. Walsh, F. S. Chapin III, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high latitude environment. Climatic Change 46:159-207.

Shipley, L. A., and D. E. Spalinger. 1992. Mechanics of browsing in dense food patches - effects of plant and animal morphology on intake rate. Canadian Journal of Zoology 70:1743-1752.

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

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, England, United Kingdom.

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

Spalinger, D. E., T. A. Hanley, and C. T. Robbins. 1988. Analysis of the functional response in foraging in the Sitka black tailed deer. Ecology 69:1166-1175.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21:264-265.

Stone, R. S., J. R. Key, and E. G. Dutton. 1993. Properties and decay of stratospheric aerosols in the Arctic following the 1991 eruptions of Mount Pinatubo. Geophysical Research Letters 20:2359-2362.

Thompson, D. C., and K. H. McCourt. 1981. Seasonal diets of the Porcupine Caribou herd. American Midland Naturalist 105:70-76.

_____, and J. M. Wallace. 1998. The Arctic Oscillation signature in wintertime geopotential height and temperature fields. Geophysical Research Letters 25:1297-1300.

_____, and _____. 2001. Regional climate impacts of the Northern Hemisphere Annular Mode and associated climate trends. Science 293:85-89.

Toupin, B., J. Huot, and M. Manseau. 1996. Effect of insect harassment on the behaviour of the Riviere George caribou. Arctic 49:375-382.

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

Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of the Environment 8:127-150.

_____, I. Y. Fung, C. D. Keeling, and R. H. Gammon. 1986. Relationship between atmospheric CO_2 variations and a satellite-derived vegetation index. Nature 319:195-199.

_____, and P. J. Sellars. 1986. Satellite remote sensing of primary production. International Journal of Remote Sensing 7:1395-1416.

Tussing, A. R., and S. Haley. 1999. Drainage pierces ANWR in Alaska study scenario. Oil and Gas Journal 97:71-84.

U.S. Geological Survey. 2001. Arctic National Wildlife Refuge, 1002 Area, petroleum assessment, 1998, including economic analysis. U.S. Geological Survey Fact Sheet FS-028-01 (Supercedes FS-040-98) April 2001.

Walsh, N. E., S. G. Fancy, T. R. McCabe, and L. F. Pank. 1992. Habitat use by the Porcupine caribou herd during predicted insect harassment. Journal of Wildlife Management 56:465-473.

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

_____, T. R. McCabe, J. M. Welker, and A. N. Parsons. 1997. Experimental manipulations of snow-depth: effects on nutrient content of caribou forage. Global Change Biology 3 (Supplement 1):158-164.

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377-384.

_____. 1992. Nutrition in relation to season, lactation, and growth of north temperate deer. Pages 407-417 *in* R. D. Brown, editor. The biology of deer. Springer-Verlag, New York, New York, USA.

_____, F. L. Bunnell, E. Gaare, T. Skogland, and B. Hubert. 1981. Ungulates on arctic ranges. Pages 397-483 *in* L.C. Bliss, O. W. Heal, and J. J. Moore, editors. Tundra ecosystems: a comparative analysis. International Biological Program 25. Cambridge University Press, Cambridge, England, United Kingdom.

_____, and J. R. Luick. 1984. Plasticity and constraints in the lactational strategy of reindeer and caribou. Symposium of the Zoological Society of London 51:215-232.

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

_____, and J. Trudell. 1980*a*. Patterns of herbivory and nutrient intake of reindeer grazing tundra vegetation. Pages 180-195 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/Caribou Symposium, Roros, Norway, 1979. Directoratet for vilt og ferskvannsfisk, Trondheim, Norway.

_____, and _____. 1980*b*. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research 12:511-529.

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

_____, and _____. 1985. Distribution of caribou calving in relation to the Prudhoe Bay oil field. Pages. 35-39 *in* A. M. Martell and D.E. Russell, editors. Caribou and human activity: proceedings of the First North American Caribou Workshop, Whitehorse, Yukon Territory, 1983. Canadian Wildlife Service Special Publications, Ottawa, Ontario, Canada.

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

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wilmshurst, J. and J. Fryxell. 1995. Patch selection by red deer in relation to energy and protein intake: a re-evaluation of Langvatn and Hanley's (1993) results. Oecologia 104:297-300.

Wolfe, S. A. 2000. Habitat selection by calving caribou of the Central Arctic herd, 1980-95. Thesis, University of Alaska, Fairbanks, Alaska, USA.

_____, B. Griffith, and C. A. Gray Wolfe. 2000. Response of reindeer and caribou to human activities. Polar Research 19:63-73.

Young, D. J., and T. R. McCabe. 1997. Grizzly bear predation rates on caribou calves in northeastern Alaska. Journal of Wildlife Management 61:1056-1066.

Zhou, L., C. J. Tucker, R. K. Kaufmann, D. Slayback, N. V. Shabanov, and R. B. Myneni. 2001. Variation in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. Journal of Geophysical Research-Atmospheres 106 (D17):20069-20083.