

WILEY



---

Mass Emigration of Arctic Tundra Caribou from a Traditional Winter Range: Population Dynamics and Physical Condition

Author(s): Michael A. D. Ferguson and François Messier

Source: *The Journal of Wildlife Management*, Jan., 2000, Vol. 64, No. 1 (Jan., 2000), pp. 168-178

Published by: Wiley on behalf of the Wildlife Society

Stable URL: <https://www.jstor.org/stable/3802987>

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Wiley and Wildlife Society are collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*

# MASS EMIGRATION OF ARCTIC TUNDRA CARIBOU FROM A TRADITIONAL WINTER RANGE: POPULATION DYNAMICS AND PHYSICAL CONDITION

MICHAEL A. D. FERGUSON,<sup>1</sup> Department of Sustainable Development, Government of Nunavut, Pond Inlet, Nunavut X0A 0S0, Canada

FRANÇOIS MESSIER, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada

**Abstract:** Major declines of populations of caribou and reindeer (*Rangifer tarandus*) that permanently reside on Arctic tundra have been attributed to short-term inaccessibility of forage through restrictive snow cover. Such density-independent phenomena would produce unpredictable changes in populations of Arctic tundra caribou. In 1985, Inuit correctly predicted mass emigration from the winter range of a caribou subpopulation on Foxe Peninsula (FP), southern Baffin Island, Canada. During 1982–94, we conducted aerial surveys, satellite telemetry, and physical condition studies to examine features of the predicted range shift. Between 1984 and 1992, caribou density on upland terrain on FP dropped ( $P < 0.001$ ) from 6.2 to 0.3 caribou/km<sup>2</sup>. Cows began to emigrate en masse during winter 1988–89 ( $P = 0.10$ ) toward Meta Incognita Peninsula (MIP), where caribou showed greater fidelity to that wintering area during 1988–94 ( $P = 0.005$ ). Density of caribou on upland terrain on MIP increased ( $P = 0.001$ ) from 0.2 to 5.0 caribou/km<sup>2</sup> between 1982 and 1992. In April 1992, body size did not differ ( $P \geq 0.47$ ) between FP and MIP. Cows on MIP had greater ( $P \leq 0.04$ ) fat and muscle reserves than cows on FP, while only fat reserves of MIP bulls were greater than ( $P \leq 0.03$ ) those of FP bulls. Our results support Inuit observations of declining physical condition of FP caribou in the early 1980's, and their view that the range shift was caused by cumulative annual overgrazing of the winter range during the previous 10 to 30 yr. Fewer cows on FP were pregnant (2 of 8) than on MIP (10 of 10;  $P = 0.002$ ). Calf:cow ratios were higher ( $P = 0.05$ ) on MIP than on FP in 1992. Although few caribou had occupied MIP for 50 yr before 1988–89, MIP caribou were in relatively poor condition by April 1992 compared to those on overgrazed Coats Island during mild winters. Winter range shifts and population declines by Arctic tundra caribou may be predictable. Ecological indicators may enable managers to mitigate the effects of overgrazing on caribou populations through intensive harvesting at critical stages during long-term population increases.

*JOURNAL OF WILDLIFE MANAGEMENT* 64(1):168–178

**Key words:** Baffin Island, Canada, caribou, cumulative density-dependent effects, fecundity, habitat fidelity, Northwest Territories, Nunavut, plant–herbivore interactions, range shift, *Rangifer tarandus*, winter forage depletion.

To varying degrees, predation, forage resources, forage accessibility, and other factors have limited populations of caribou and reindeer in different ecosystems (i.e., forests, forest–tundra ecotones, and Arctic tundra; Bergerud 1980, Klein 1991, Messier 1995, Ferguson 1996). For caribou permanently residing on Arctic tundra, evidence of population limitation by forage has come mainly from islands without natural predators and with little harvesting by humans (Ouellet et al. 1996). In some cases, *Rangifer* populations on Arctic tundra have experienced major declines and occasionally extinctions (Meldgaard 1986). On South Georgia, long-term depletion of lichen led to successful diet changes to other plant species (Leader-Wil-

liams et al. 1981). In several cases, long-term diet changes have been followed by population fluctuations, caused by interannual variations in accessibility of winter forage through snow (Tyler 1987, Adamczewski et al. 1988).

Miller (1982) suggested that mortality factors other than forage production (e.g., adverse snow–icing conditions) usually limits caribou populations below levels where forage could become the limiting factor. Nevertheless, Gaare (1997) has hypothesized that *Rangifer* and lichen-dominated communities have coevolved, whereby periodic overgrazing resets succession to prevent the eventual domination of tundra communities by vascular plants.

Inuit have suggested that Arctic tundra caribou periodically shift winter ranges (Ferguson et al. 1998) in response to forage depletion caused by long-term overgrazing. Overgrazing

<sup>1</sup> E-mail: BaffBio@nunanet.ca

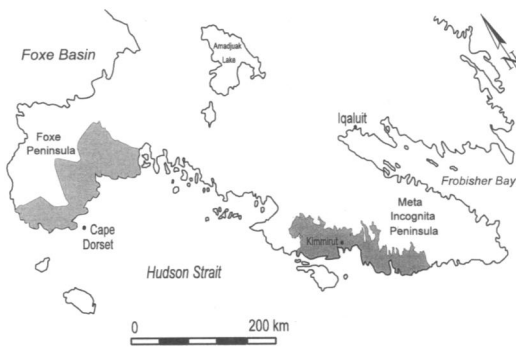


Fig. 1. Intensive study areas (shaded) on Foxe and Meta Incognita Peninsulas on southern Baffin Island, Nunavut, Canada, April 1992.

occurs when a caribou population annually consumes more biomass of winter forage than is produced on the proportion of winter range that is accessible under “prevailing snow conditions” (*sensu* Nelleman 1997). As annual overgrazing eventually depletes forage biomass that accumulated over several decades, individual caribou compete for lower quality forage (Klein 1968, Leader-Williams 1988). Despite local overgrazing, shifts of winter ranges could allow Arctic tundra caribou to maintain access to adequate forage over the long term. Before a population shifts to a new winter range, we expect that body size, physical condition, reproduction, and survival would decline. After the shift, physical condition, reproduction, and survival should quickly recover among adult caribou, while the body size of animals born after the shift should increase.

Inuit described changes in caribou winter distributions on southern Baffin Island during the 1900's (Ferguson et al. 1998). In 1985, Inuit elders in Cape Dorset (Fig. 1) predicted a range shift of caribou from FP, based on observed declines in physical condition of caribou, recent winter foraging by caribou on small offshore islands and cliff faces, delayed spring migration of females, and unusual calving on and near the wintering area. During the late 1980's, Inuit hunters in Cape Dorset and Kimmirut reported that most of the FP subpopulation apparently emigrated about 350 km to MIP. The ecological cause suggested by Inuit was cumulative density-dependent effects of caribou on their forage over the previous 10 to 30 yr (E. Peter, Aiviq Hunters and Trappers Association, personal communication).

We examined several aspects of caribou bi-

ology due to shifts in winter range on Arctic tundra. We tested whether the changes in caribou densities on FP and MIP between the early 1980's and 1992 were significant. We predicted that during the period of range shift (1988–94) adult females (cows) would show less fidelity to winter range on FP than those on MIP. Assuming that adult males (bulls) also participated in the range shift, we predicted that after the shift, bull:cow ratios on the 2 peninsulas would be similar. We also predicted that caribou remaining on FP winter range would have less fat and muscle reserves, and lower fecundity and recruitment than caribou on the MIP winter range in 1992. However, we predicted that body sizes of adult caribou on both ranges would not differ because most adults on MIP probably were born on FP.

## STUDY AREA

Baffin Island (>500,000 km<sup>2</sup>; 62° to 74°N, 62° to 90°W) forms the eastern margin of the Canadian Arctic archipelago. The South Baffin caribou population occupies approximately half of the island (Ferguson 1989), and was estimated at 60,000 to 180,000 animals in the late 1980's (Ferguson and Gauthier 1992). The South Baffin population is composed of “subpopulations”, defined as groupings of individuals within the population, each demonstrating fidelity to a distinct winter range over the short term (i.e., 10 to 30 yr), leading to distinct short-term demographic characteristics due to differing ecological conditions among winter ranges (e.g., prevailing snow cover). Over the long term (i.e., 70 to 90 yr), subpopulations interact through range shifts or mass emigrations, leading to shared long-term population trends (Ferguson et al. 1998).

South Baffin caribou exhibit 2 seasonal migratory patterns; some migrate up to 400 km to their summering areas, while others remain close to their wintering areas (Ferguson 1989, Ferguson et al. 1998). Based on Inuit knowledge, movements that we observed during May 1992 and satellite telemetry (M. A. D. Ferguson, Government of Nunavut, unpublished data), the majority of caribou in both of our study areas spent summer on the extensive coastal lowlands south and east of Foxe Basin (Fig. 1; Nettleship and Smith 1975). Some caribou in both areas may have been resident animals that summer near lakes and ponds near their wintering areas.

South Baffin caribou migrate onto their wintering areas during October–November and usually remain until late April (Ferguson et al. 1998). Satellite telemetry (M. A. D. Ferguson, Government of Nunavut, unpublished data) showed that seasonal movements are most restricted from January to March, and migratory movements were not well underway until May. Fourteen caribou that had been captured on MIP and FP and monitored for 2 years had moved out of their wintering areas only 3 of 28 times by mid-April.

In November 1978, Chowns (1979) estimated that 21,350 ( $\pm 2,230$  SE) caribou used FP. This wintering area held 60% of all caribou within 3 major winter ranges occupied by South Baffin subpopulations. In the late 1970's and early 1980's, the FP winter range moved to the west and extended onto small islands in northwestern Hudson Strait, while eastern parts of the range were abandoned (Ferguson et al. 1998). We refer to this as "range drift", expanding on one front while contracting on another. A subsequent survey in November 1984 confirmed the reported range drift and suggested that the subpopulation had increased to about 34,410 ( $\pm 4,650$ ; M. A. D. Ferguson, Government of Nunavut, unpublished data).

In November 1988, J. Ikkidluak (Qikiqtaaluk Wildlife Board, personal communication) observed a massive immigration of caribou onto MIP. No population estimates were available for caribou wintering on MIP before the 1980's. Chowns (1979) did not recognize it as a major wintering area in 1978. Although caribou had been increasing and expanding their winter range on MIP since the 1950's, abundance remained relatively low into the 1980's (Ferguson et al. 1998). In March 1982, 1,600 ( $\pm 335$ ) caribou were estimated to occur on MIP (M. A. D. Ferguson, Government of Nunavut, unpublished data).

Since muskoxen (*Ovibos moschatus*) do not occupy Baffin Island, and Arctic hares (*Lepus arcticus*) are not known to occur in high densities, caribou are the primary prey of wolves (*Canis lupus*; Clark 1971). Subsistence harvesting of caribou by Inuit has been unrestricted during the past 40 years. In 1982, Inuit in Cape Dorset and Kimmirut (Fig. 1) harvested 2,260 and 550 caribou from the FP and MIP subpopulations, respectively (Donaldson 1988).

The terrain on the FP wintering area consists of rugged uplands  $\leq 410$  m above sea level

(ASL). During winter, caribou largely abandon the northern coastal lowlands (25% of FP). Caribou occupy 2 terrain types on MIP: rugged coastal uplands  $\leq 305$  m ASL and rugged plateau 305–850 m ASL. Vegetation on most of FP and MIP is characterized by dwarf and prostrate shrub tundra, while some areas are in the low, erect shrub zone (Edlund 1990). Climatic conditions and plant communities on the plateau of MIP resemble those at higher latitudes. Consequently, only uplands  $\leq 305$  m ASL on both peninsulas were included for aerial surveys and caribou sampling.

## METHODS

### Caribou Distribution and Demography

To examine the predicted changes in caribou distribution and density, we used data from 2 aerial surveys of each peninsula conducted during winter. In late March 1982, caribou were surveyed on about 60% of MIP (18,350 km<sup>2</sup>) where caribou were suspected to occur, and on all of FP (11,650 km<sup>2</sup>) in early November 1984. Parallel transects were 6.4 km apart on MIP and 5.5 km apart on FP, and oriented approximately perpendicular to major river valleys. In both surveys, caribou were counted within 400-m wide strips on each side of a fixed-wing Cessna 337 flown about 122 m above ground at 140–195 km/hr. We subsampled 20 random 7.5-km segments of transects from each of the 1982 MIP and 1984 FP surveys to compare between the 2 areas and with subsequent surveys (see below).

Surveys of FP and MIP were also conducted in April 1992 after the winter range shift was observed by Inuit (Ferguson et al. 1998). To assess differences in density, recruitment, and sex–age ratios, study areas of 6,540 km<sup>2</sup> on FP and 5,210 km<sup>2</sup> on MIP were established based on the knowledge of Inuit hunters (Ferguson et al. 1998) and satellite telemetry data (M. A. D. Ferguson, Government of Nunavut, unpublished data). Within each of the 2 study areas, caribou were counted along 20 7.5-km transects located randomly, with no transect being closer than 5.5 km to another. The transects were flown in a Bell 206L helicopter about 75 m above ground at 60–130 km/hr, with a strip width of 400 m to each side of the aircraft (Miller 1991).

We tested for differences between the 4 surveys using Kruskal-Wallis 1-way analysis of var-

iance by ranks (Mehta and Patel 1997), followed by multiple comparisons between pairs of surveys (Siegel and Castellan 1988). Although the statistical tests were based on the actual number of caribou counted along each 7.5-km transect, mean densities are presented as caribou/km<sup>2</sup>.

In 1992, after surveying each transect, we classified caribou by sex and age as the helicopter crisscrossed along the transect, staying within 2.5 km of the transect. Caribou were initially categorized as calves (i.e., 10 months old), yearlings, and adults. As large yearlings may have been mistakenly classified as adults, all yearlings were treated as adults in data analyses. The presence or absence of a vulva was used for sex determination. We attempted to classify at least 25 caribou along each transect. Because of low caribou density, this objective was not met for any of the 20 transects on FP, so caribou groups encountered incidentally while off transects were also classified. On MIP, the objective of at least 25 caribou per transect was met for all but 1 transect ( $n = 11$  for that transect). The proportions of calves and bulls per 100 cows were compared between the 2 peninsulas using the  $z$  test (Zar 1984). Calf:cow and bull:cow ratios are presented with 90% confidence intervals (Czaplewski et al. 1983).

### Winter Range Fidelity and Emigration

During 7 to 22 April 1987–92, satellite telemetry collars (Telonics, Mesa, Arizona, USA) were placed on 8 cows on FP (5 in 1987, and 1 in each of 1988, 1989 and 1992) and 6 on MIP (4 in 1988 and 2 in 1989). The majority of collars were deployed before the range shift of autumn 1988, while some collars were deployed later to assess if FP cows continued to emigrate in subsequent years. Collars were distributed throughout occupied portions of the peninsulas. Caribou were captured using a gun net from a Bell 206 B or L helicopter. The collars transmitted data to satellites for 6–7 hr every 4 days for 2 years, and locations were determined by Service Argos, (Landover, Maryland, USA) based on the Doppler shift in signal frequency (Fancy et al. 1988). We used locations of the collars that were usually accurate to within 1 km.

To assess the fidelity of cows to wintering ranges on FP and MIP, we assumed each animal represented the peninsula where it was initially captured. Cows were considered to show strong fidelity to a given wintering area if found there during at least 75% of subsequent win-

ters, while those with little fidelity wintered elsewhere in at least 50% of subsequent winters. To test for differences in fidelity to the 2 wintering areas, we grouped animals by the peninsula that they were assumed to represent, and compared the 2 groups by the wintering area occupied in each of 2 subsequent years, based on mid-February locations. These data were analysed using a chi-square likelihood-ratio test (Mehta and Patel 1997). We also determined the distances from the capture location to relocations in the subsequent 2 years during mid-February for each animal. These distances were compared between the 2 peninsulas using the Wilcoxon-Mann-Whitney test (Mehta and Patel 1997). To examine the timing of the emigration from FP as reported by Inuit, we used the Fisher exact test (Mehta and Patel 1997) to compare the fidelity of FP caribou during winter 1987–88 to that during subsequent winters.

### Body Size, Physical Condition, and Fecundity

In April 1992, we collected samples and measurements from adult caribou on FP and MIP. Each study area was divided into thirds along its longest side, and 3 cows and 2 bulls were to be randomly sampled from each third. This distribution was accomplished on MIP, with 10 females and 5 males sampled. The ground crew on FP could not locate animals in two-thirds of the study area, resulting in the collection of 8 cows and 6 bulls from 5 different groups in the remaining third.

The age of each animal was determined from cementum annuli counts of incisors at Matson's Laboratory (Milltown, Montana, USA). The age of 1 female from MIP was not determined due to a shipping error. The following data were recorded from each caribou: body length (nose to base of the tail; Langvatn 1977), femur length (Langvatn 1977), carcass weight (with metacari and metatarsi removed; Adamczewski et al. 1987a), gastrocnemius muscle weight (fresh, towel-dried, fat and tendons removed), back fat depth (Riney 1955), trimmed kidney fat weight (Dauphiné 1976), and fat content of femur marrow (by oven drying at 60°C for  $\geq 5$  days; Neiland 1970). The left femur, gastrocnemius muscle, and kidney with fat were collected from each animal. If a specimen on the left side was damaged by a gun shot, the specimen was collected from the right side. The presence or absence of a gravid uterus was recorded for each



cow. Amount of dissectible muscle and fat was estimated from the gastrocnemius muscle weight, and the back fat depth and weight of trimmed kidney fat, respectively (Adamczewski et al. 1987a).

Data on age, body size, and physical condition of each sex were compared between the 2 study areas using the Wilcoxon-Mann-Whitney test (Mehta and Patel 1997). Pregnancy rates of cows was compared using Fisher's exact test (Mehta and Patel 1997). All statistical results are presented with 2-tailed probability levels unless otherwise stated.

## RESULTS

### Caribou Densities

Densities of caribou differed among the 4 aerial surveys ( $X^2_3 = 43.0$ ,  $P < 0.001$ ), allowing multiple comparisons between pairs of surveys. In the early 1980's, the density of caribou on FP ( $6.2 \pm 1.6$  [SE]) was higher ( $P < 0.001$ ) than that on MIP ( $0.23 \pm 0.10$  caribou/km<sup>2</sup>). Between 1984 and 1992, caribou density on FP decreased ( $P < 0.001$ ) to  $0.28 \pm 0.12$ , while the density of caribou on MIP increased ( $P < 0.001$ ) to  $5.0 \pm 1.0$  caribou/km<sup>2</sup> between 1982 and 1992. In April 1992, caribou densities were less ( $P < 0.001$ ) on FP than on MIP.

### Winter Range Fidelity and Emigration

Cows collared initially on FP demonstrated less fidelity ( $X^2_2 = 11.3$ ,  $P = 0.005$ ) to that area than those collared on MIP. Cows from FP were found in the same area 7 of 16 times (44%) in subsequent winters, compared to 12 out of 12 times for MIP cows (100%). During mid-February, FP females were found  $216 \pm 34$  km from their initial capture location, farther

than MIP females ( $71 \pm 10$  km,  $U_{12,16} = 150$ ,  $P = 0.01$ ). When FP females did return to their initial wintering area, the distance from their capture location ( $82 \pm 23$  km,  $n = 7$ ) was comparable to that of MIP females. When they wintered on MIP, they were  $327 \pm 25$  km ( $n = 8$ ) from their capture location. The female that wintered elsewhere moved 279 km to a wintering area north of Amadjuak Lake (Fig. 1) previously identified by Chowns (1979).

Telemetry data corroborated Inuit reports of the timing of the initial emigration from FP (autumn 1988), with more cows returning to FP during winter 1987–88 than in subsequent winters (Fisher exact test,  $P = 0.10$ ). Overall, the fidelity of all collared FP cows decreased from 80% (4 out of 5 relocations on FP) during winter 1987–88, to 33% (2 out of 6) during winter 1988–89 and 20% (1 out of 5) during winters from 1989–90 to 1992–93. Of 4 FP cows that emigrated to MIP in the first winter after capture, 3 returned to MIP again in the second winter, suggesting that they adopted it as a new wintering area (based on our threshold of 75% for strong fidelity). All MIP cows remained faithful to their wintering area throughout these years.

Because bulls were not radiocollared, we had no direct evidence whether they emigrated from FP at the same time as females. Assuming that both males and females emigrated from FP to the same extent, and that they both emigrated largely to MIP, the proportion of bulls among adult caribou should not have differed between the 2 peninsulas in April 1992. The relative proportion of bulls on FP ( $117 \pm 33$ : 100,  $n = 127$ ) was similar ( $z = 1.53$ ,  $P = 0.13$ ) to MIP ( $86 \pm 9$ : 100,  $n = 894$ ).

Table 1. Mean ( $\pm$ SE) age, body size, and carcass weight of adult caribou ( $>1$  yr old) on historically grazed (Foxy Peninsula, FP) and recently occupied (Meta Incognita Peninsula, MIP) winter range on southern Baffin Island in April 1992.

Study area and <i>U</i> , <i>P</i> <sup>a</sup>	Age (yr)	Body length (cm)	Femur length (mm)	Carcass weight (kg)
<b>Female</b>				
FP ( $n = 8$ )	$4.9 \pm 1.0$	$159 \pm 3$	$267 \pm 4$	$33 \pm 1$
MIP ( $n = 10$ ) <sup>b</sup>	$3.9 \pm 0.6$	$158 \pm 2$	$265 \pm 2$	$37 \pm 1$
<i>U</i> , <i>P</i>	41, 0.67	40, 1.0	48.5, 0.47	69, 0.008
<b>Male</b>				
FP ( $n = 6$ )	$2.8 \pm 0.5$	$166 \pm 3$	$282 \pm 7$	$41 \pm 4$
MIP ( $n = 5$ )	$3.8 \pm 0.8$	$167 \pm 6$	$277 \pm 7$	$45 \pm 4$
<i>U</i> , <i>P</i>	21.5, 0.26	17.5, 0.70	17.5, 0.67	20.5, 0.35

<sup>a</sup> Wilcoxon-Mann-Whitney test.

<sup>b</sup> Except for age, for which  $n = 9$ .

Table 2. Mean body condition ( $\pm$ SE) of adult caribou ( $>1$  yr old) on historically grazed (Foxy Peninsula, FP) and recently occupied (Meta Incognita Peninsula, MIP) winter range on southern Baffin Island in April 1992.

Study area and <i>U, P</i> <sup>a</sup>	Gastrocnemius muscle (g)	Back fat (mm)	Kidney fat (g)	Femur marrow fat (%)	Dissectible muscle (kg)	Dissectible fat (kg)
<b>Female</b>						
FP ( <i>n</i> = 8)	252 $\pm$ 9	0 $\pm$ 0	5 $\pm$ 1	26 $\pm$ 1	23 $\pm$ 1	0.0 $\pm$ 0.04
MIP ( <i>n</i> = 10) <sup>b</sup>	276 $\pm$ 7	13 $\pm$ 2	31 $\pm$ 4	89 $\pm$ 1	25 $\pm$ 1	2.8 $\pm$ 0.4
<i>U, P</i>	63, 0.04	72, <0.001	72, <0.001	72, <0.001	63, 0.04	72, <0.001
<b>Male</b>						
FP ( <i>n</i> = 6)	332 $\pm$ 29	0 $\pm$ 0	7 $\pm$ 1	31 $\pm$ 0.03	31 $\pm$ 3	0.1 $\pm$ 0.04
MIP ( <i>n</i> = 5)	326 $\pm$ 28	2 $\pm$ 1	33 $\pm$ 6	89 $\pm$ 0.3	30 $\pm$ 3	1.7 $\pm$ 0.4
<i>U, P</i>	15, 1.0	27, 0.03	30, 0.004	30, 0.004	15.0, 1.0	30, 0.004

<sup>a</sup> Wilcoxon-Mann-Whitney test.

<sup>b</sup> Except for kidney fat and dissectible fat weight, for which *n* = 9.

### Body Size, Physical Condition, Fecundity, and Recruitment

Body and femur lengths did not differ ( $P \geq 0.47$ ) between the 2 peninsulas for either sex (Table 1). The ages of females and males did not differ significantly between the 2 peninsulas ( $P \geq 0.26$ ), although cows on FP were 1 year older than on MIP on average, and bulls on FP averaged 1 year younger. Carcass weights of cows were lower ( $P = 0.008$ ) on FP than on MIP (Table 1).

Gastrocnemius muscles of females on FP weighed less ( $P = 0.04$ ) than on MIP (Table 2). However, gastrocnemius muscle weight of males did not differ between the 2 peninsulas ( $P = 1.0$ ). Back, kidney, and femur marrow fat indicated that both cows ( $P \leq 0.001$ ) and bulls ( $P \leq 0.03$ ) were in better physical condition on MIP than on FP. Both cows and bulls on FP had negligible amounts of dissectible fat, which was lower than in animals from MIP ( $P \leq 0.004$ ).

The number of calves per 100 cows was  $42 \pm 16$  on FP (*n* = 84) compared to  $64 \pm 7$  on MIP (*n* = 789;  $z = 1.68$ , 1-tailed  $P = 0.05$ ). Only 2 of 8 sampled cows were pregnant on FP, while all 10 sampled cows were pregnant on MIP (Fisher exact test,  $P = 0.002$ ).

### DISCUSSION

Caribou returned to FP in the 1950's after a virtual absence of 30 years (Ferguson et al. 1998). The abundance of caribou on FP during winter gradually increased until a sudden decline in the late 1980's. After an absence of 40 years, caribou on MIP increased slowly from the late 1950's until the mid-1980's (Ferguson et al. 1998). In November 1988, hunters saw more caribou on MIP than seen previously in

living memory. Our aerial surveys showed that during winter, caribou densities declined by about 95% on FP between 1984 and 1992, and those on MIP increased 2,000% between 1982 and 1992.

Inuit suggested that shifts in caribou winter distributions are predictable and caused by cumulative density-dependent effects of caribou on forage resources (Ferguson et al. 1998). Given the slow recovery of lichen forage (Klein 1987), annual overgrazing of winter forage would lead to such effects on Arctic tundra if caribou show fidelity to specific wintering areas for several years or decades. Inuit knowledge suggested that caribou returned annually to the FP winter range for about 30 years (Ferguson et al. 1998). During 1988–94, caribou captured on MIP surpassed our threshold of 75% for showing strong fidelity, returning to that wintering area 100% of the time. Caribou that emigrated from FP to MIP also showed strong fidelity to their new winter range.

Although fidelity to winter range by Arctic tundra caribou has not been described in the scientific literature, fidelity to tundra calving grounds is well known among migratory ecotypes that winter in forested habitats (Gunn and Miller 1986). Winter range fidelity among Arctic tundra caribou may occur because areas with rugged terrain provide predictable access to winter forage (Nelleman 1997), and caribou that develop traditional movements to such habitats would have a selective advantage. This argument parallels Skoog's (1968) rationale for calving-ground fidelity among Alaskan caribou because tundra habitats needed for calving are spatially limited to alpine and arctic coastal areas within Alaska. Tundra habitats for calving would not be spatially limited for caribou residing on Arctic tundra because availability of

snow-free tundra, and the quality and quantity of tundra forage, increases as snow melts within the same habitats occupied during winter.

As population density increases on a traditional winter range, annual overgrazing may lead to severe nutritional stress and eventually to a selective advantage for abandonment of that winter range. Traditional use of specific areas is not necessarily permanent (Gunn and Miller 1986). During 1988–94, cows from FP returned to that wintering area only 44% of the time, less than our threshold of 50% for weak fidelity. On average, collared cows from FP were about 3 times farther from their capture locations than MIP cows in subsequent winters. This change in winter range fidelity was predicted by Inuit in 1985, when the early signs included redistribution of wintering caribou onto small islands, foraging on cliff faces, and delayed spring migrations (Ferguson et al. 1998). Although some animals emigrated to other wintering areas, most FP caribou apparently emigrated to MIP.

The similarity of bull:cow ratios on FP and MIP in 1992 indicated that both sexes participated in the range shift. The subsistence harvest of FP caribou by Inuit may have skewed the late winter bull:cow ratio on FP because of their 2:1 preference for cows over bulls during winter (Pattimore 1986) and the potential effects of high subsistence demand (Donaldson 1988) on this small subpopulation. Such sex-biased harvesting would not have similar effects on the larger population on MIP. Despite these potential effects on FP, sex ratios were similar with those on MIP ( $P = 0.13$ ).

We believe that summer habitats did not substantively influence either the emigration of caribou from FP to MIP or the differences in physical condition and recruitment between the 2 peninsulas during late winter, although summer range quality has not been studied. All caribou that were monitored via satellite telemetry showed 100% fidelity to their summering areas (M. A. D. Ferguson, Government of Nunavut, unpublished data). Inuit knowledge and our aerial observations during spring migration suggested that most caribou wintering on the coastal uplands on both FP and MIP summered in the same area south and east of Foxe Basin (Fig. 1). The majority of satellite-collared cows that wintered on FP occurred in this area during summer, and FP cows that shifted their wintering area to MIP subsequently returned to the

same summering area near Foxe Basin. During 1987–92, the distance between 2 subsequent mid-July locations for collared FP and MIP caribou averaged only  $27 \pm 30$  km ( $n = 14$ ) compared to mean interannual differences in winter locations of 71 km for MIP caribou, 82 km for non-emigrating FP caribou, and 327 km for emigrating FP caribou.

Comparable shifts in the winter ranges of Arctic tundra caribou have not been well documented, possibly due to the perception that mass emigrations of caribou are neither predictable nor of known cause (Miller 1982). Nevertheless, range shifts by Arctic tundra caribou may have occurred on the Queen Elizabeth Islands and northwestern Greenland during the 1980's and 1990's (Ferguson and Gauthier 1992). Freeman (1975) documented evidence of emigration of caribou from Bathurst Island on the Queen Elizabeth Islands during the early 1970's, reportedly in response to seismic exploration. Interannual changes in winter distribution have also been attributed to severe snow and icing conditions (Miller 1982). Inuit did not implicate either human disturbance or snow conditions in the winter range shift of caribou from FP to MIP (Ferguson et al. 1998).

If mass emigration of Arctic tundra caribou from traditional winter ranges is caused by cumulative density-dependent effects of grazing, caribou on older traditional ranges should be in poor physical condition during winters before emigration. Declining physical condition in the early 1980's was one reason Inuit predicted the impending range shift (Ferguson et al. 1998). In April 1992, indices of both fat and muscle reserves showed that emigrating from FP to MIP was advantageous for cows. Bulls on MIP also had greater fat reserves than bulls on FP, but not greater muscle mass. Use of non-parametric statistical tests and our small sample sizes, especially for bulls, limited our power to detect differences between caribou in the 2 study areas. This low statistical power, coupled with supporting observations by Inuit hunters, makes us confident that the detected statistical differences are biologically significant.

We expected that caribou wintering on FP would have similar fat and muscle masses to other Arctic tundra caribou on overgrazed range. Mean fat reserves among FP cows were lower than among female adults isolated on overgrazed Coats Island (Adamczewski et al. 1988), about 250 km southwest of FP, during



both mild and severe winters (Adamczewski et al. 1987b), indicating that forage on FP was more overgrazed than on Coats Island. Differences in previous maximum densities may explain this difference (highest density recorded on Coats Island =  $0.7/\text{km}^2$  compared to  $6.2/\text{km}^2$  on FP; Gates et al. 1986). Caribou on Coats Island experienced high mortality during severe winters, but not in other years (Gates et al. 1986). We found no evidence of similar mortality on FP during 1984–94.

Because the coastal uplands of MIP had been occupied by few caribou for >50 years prior to winter 1988–89 (Ferguson et al. 1998), the condition of MIP caribou was expected to be comparable to that of caribou on Southampton Island, about 500 km to the west. Caribou disappeared from Southampton Island in 1953, and 48 caribou were reintroduced in 1967 (Ouellet 1992). Late winter fat and muscle indices in MIP caribou were much less than those of Southampton caribou (Ouellet et al. 1997). In fact, cows on MIP were in poorer condition than those using overgrazed winter range on Coats Island during the mild winter of 1982–83 (Adamczewski et al. 1987b). The caribou density of  $5/\text{km}^2$  on MIP in April 1992 was greater than the highest densities on Southampton Island ( $2.1$  caribou/ $\text{km}^2$ ; Heard and Ouellet 1994). We suspect that the immigration of caribou to MIP may have already affected forage resources on MIP during the 4 years prior to sample collections. Caribou winter range on MIP was already drifting southeast by 1994 (Ferguson et al. 1998). In 1994, J. Arlooktoo predicted that caribou would have to leave MIP in  $\leq 10$  years (Ferguson et al. 1998). Arctic tundra caribou that can emigrate en masse from overgrazed to relatively ungrazed winter ranges should not only improve their body condition, but also benefit from higher productivity and survival, as was observed in this study. Thomas (1982) found that pregnancy rates increase with fat reserves among Peary caribou.

On smaller tundra islands and overgrazed portions of large islands, current dynamics of caribou populations (e.g., die-offs during a single severe winter) may appear density-independent, although long-term density-dependent processes probably are the underlying causes (Tyler 1987). Because density-dependent effects of grazing could persist during the entire period required for forage to fully recover (e.g., 20 to 40 yr), current dynamics of Arctic tundra

caribou may be dependent on the densities of subpopulations that were present more than a decade earlier. During the next 20 or more years, dynamics of the remnant caribou wintering on FP and their potential recovery will be dominated by grazing pressure exerted during 1960–88. Inuit have predicted the complete disappearance of caribou from FP (Ferguson et al. 1998).

Winter range shifts by subpopulations of Arctic tundra caribou on large islands and archipelagos could delay the regulatory effects of density-dependent food limitation at the population level. Messier et al. (1988) suggested that caribou can overshoot carrying capacity because of a time lag of at least 20 years between food availability and food limitation. This lag could be accentuated by the processes of range expansion, drift, and shift by caribou. During periods of population increase, more winter ranges become overgrazed as subpopulations shift their winter ranges and eventually converge on the same range. At that point, the entire population would enter a period of decline, perhaps lasting several decades. Inuit from across southern Baffin Island have provided evidence of such a process, leading to population cycles lasting 70 to 90 years (Ferguson et al. 1998). Cumulative density-dependent effects of grazing on accessible winter forage may produce a decline of the South Baffin population in the future, lasting several decades, as apparently occurred during 1920–55 (Ferguson et al. 1998).

## MANAGEMENT IMPLICATIONS

Expanding, drifting, and shifting winter ranges of Arctic tundra caribou (Ferguson et al. 1998) poses a paradigm conflict in the conventional application of caribou management options. Most definitions of animal populations and metapopulations are often based on static geographic areas (Wells and Richmond 1995), often resulting in geographically static management regimes (e.g., wildlife management zones, ecological reserves). Inuit apparently view caribou populations as biological units that use space in an adaptive manner over several decades (Ferguson et al. 1998). While our definition of a population recognizes the need for long-term management of caribou at regional scales, the definition of transitory subpopulations (with delineation of new boundaries as required) allows short-term management regimes

for local areas as biological units move through space.

In the future, intensive harvesting of Arctic tundra caribou may reduce growth of selected subpopulations, and potentially limit forage depletion on winter ranges during the increase phase of long-term cycles. Reduction of caribou population growth rates may delay effects of cumulative overgrazing and allow recovery of previously abandoned ranges, avoiding overall population declines in the long term. Given lag effects lasting 2 or more decades, robust predictive indicators and population models may enable such proactive management of Arctic tundra caribou. Baffin Inuit identified specific indicators giving about a 5-year lead time before mass emigration (Ferguson et al. 1998). Inuit elders have also made predictions several decades in advance of population changes; further understanding of their rationale may support refinement of both conceptual and mathematical models.

The process of range drift may allow sufficient lead time for management experiments since the distribution of FP caribou began to drift 10 to 15 years before the shift occurred (Ferguson et al. 1998). Intensive harvesting on FP in the 1970's may have maintained the subpopulation at 50–60% of its 1984 density, and thereby reduced cumulative overgrazing during the intervening period. However, stabilization of 20,000 caribou would be logistically difficult, so actions to reduce growth must be attempted before population size becomes too large.

The current management dilemma for FP is the maintenance of subsistence harvesting of caribou, given the subpopulation's low density and productivity. Assuming that forage resources have been largely depleted, disappearance of wintering caribou from FP appears inevitable, as happened in the mid-1900's (Ferguson et al. 1998). Since the South Baffin caribou population as a whole apparently is not in decline, we suggest that management of caribou harvesting on FP should preserve the reproductive potential of the remnant subpopulation through male-only harvesting.

When the South Baffin caribou population as a whole enters the next anticipated phase of long-term decline, intensive management options will be needed to deal with an estimated subsistence demand of about 8,000–10,000 caribou annually (based on per capita harvest rates; Donaldson 1988).

## ACKNOWLEDGMENTS

Special thanks goes to the Aiviq Hunters and Trappers Association of Cape Dorset, the Mavukalik Hunters and Trappers Association of Kimmirut, and the Qikiqtaaluk Wildlife Board for their support and assistance throughout this study. In April 1992, the caribou sampling crews on MIP and FP were led by B. Elkin and J. Obst of Resources, Wildlife and Economic Development, Government of the Northwest Territories, Yellowknife, Northwest Territories, respectively. Many individuals provided assistance in the field and laboratory and in related activities; thanks goes to: L. Gauthier, M. Kolola, O. Ashuna, I. Ikkidluak, S. Akavak, J. Ikkidluak, T. Ellsworth, P. Kilabuk, M. Labine, G. Arlooktoo, R. Walker, J. Arlooktoo, M. Saveakjuk, M. Lyta, A. Allasuaq, B. Wooley, J. Noble, J. Tongak, L. Aglak, R. Nutarak, P. Melia, M. Qiliqpalik, K. Faddegan, L. Buckmaster, G. Goodyear, T. Akavak, T. Alareaq, R. Bourget, G. Baird, Q. Nunqusuituq, K. Parr, S. Appik, M. Paddon, R. Portlock, R. Meszaros, S. Pee and J. Akearok. We appreciate the constructive comments on this manuscript by M. A. Ferguson and 2 anonymous reviewers.

## LITERATURE CITED

- ADAMCZEWSKI, J. Z., C. C. GATES, AND R. J. HUDSON. 1987a. Fat distribution and indices of carcass composition in Coats Island caribou (*Rangifer tarandus groenlandicus*). Canadian Journal of Zoology 65:368–374.
- , ———, R. J. HUDSON, AND M. A. PRICE. 1987b. Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. Canadian Journal of Zoology 65:1149–1157.
- , ———, B. M. SOUTAR, AND R. J. HUDSON. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology 66: 1986–1996.
- 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. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway.
- CHOWNS, T. 1979. Wintering ground survey, South Baffin caribou herd, November 1978. Unpublished reports, Department of Sustainable Development, Government of Nunavut, Iqaluit, Nunavut.
- CLARK, K. R. F. 1971. Food habits and behaviour of

- the tundra wolf on central Baffin Island. Dissertation, University of Toronto, Toronto, Canada.
- CZAPLEWSKI, R. L., D. M. CROWE, AND L. L. McDONALD. 1983. Sample sizes and confidence intervals for wildlife population ratios. *Wildlife Society Bulletin* 11:121–128.
- DAUPHINÉ, T. C., Jr. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction and energy reserves. *Canadian Wildlife Service Report Series No. 38*.
- DONALDSON, J. L. 1988. The economic ecology of hunting: A case study of the Canadian Inuit. Dissertation, Harvard University, Cambridge, Massachusetts, USA.
- EDLUND, S. 1990. Bioclimatic zones in the Canadian Arctic archipelago. Pages 421–441 in C. R. Harrington, editor. *Canada's missing dimension: science and history in the Canadian arctic islands*. Canadian Museum of Nature, Ottawa, Canada.
- FANCY, S. G., L. F. PANK, D. C. DOUGLAS, C. H. CURLEY, G. W. GARNER, S. C. AMSTRUP, AND W. L. REGELIN. 1988. Satellite telemetry: a new tool for wildlife research and management. U.S. Fish and Wildlife Service Resource Publication 172.
- FERGUSON, M. A. D. 1989. Baffin Island. Pages 141–149 in E. Hall, editor. *People and caribou in the Northwest Territories*. Department of Renewable Resources, Government of the Northwest Territories, Yellowknife.
- . 1996. Arctic tundra caribou and climatic change: questions of temporal and spatial scales. *Geoscience Canada* 23:245–252.
- , AND L. GAUTHIER. 1992. Status and trends of *Rangifer tarandus* and *Ovibos moschatus* populations in Canada. *Rangifer* 12:127–141.
- , R. G. WILLIAMSON, AND F. MESSIER. 1998. Inuit knowledge of long-term changes in a population of Arctic tundra caribou. *Arctic* 51:201–219.
- FREEMAN, M. M. R. 1975. Assessing movement in an Arctic caribou population. *Journal of Environmental Management* 3:251–257.
- GAARE, E. 1997. A hypothesis to explain lichen-*Rangifer* dynamic relationships. *Rangifer* 17:3–7.
- GATES, C. C., J. ADAMCZEWSKI, AND R. MULDER. 1986. Population dynamics, winter ecology and social organization of Coats Island caribou. *Arctic* 39:216–222.
- GUNN, A., AND F. L. MILLER. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. *Rangifer, Special Issue 1*: 151–158.
- HEARD, D. C., AND J.-P. OUELLET. 1994. Dynamics of an introduced caribou population. *Arctic* 47: 88–95.
- KLEIN, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management* 32:350–367.
- . 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. *Journal of Range Management* 40:336–338.
- . 1991. Limiting factors in caribou population theory. *Rangifer, Special Issue 7*:30–35.
- LANGVATN, R., editor. 1977. Criteria of physical condition, growth and development in Cervidae—Suitable for routine studies. Nordic Council for Wildlife Research, Stockholm, Sweden.
- LEADER-WILLIAMS, N. 1988. Reindeer on South Georgia: the ecology of an introduced population. Cambridge University Press, Cambridge, United Kingdom.
- , T. A. SCOTT, AND R. M. PRATT. 1981. Forage selection by introduced reindeer on South Georgia, and its consequences for the flora. *Journal of Applied Ecology* 18:83–106.
- MEHTA, C., AND N. PATEL. 1997. StatXact 3 for Windows: statistical software for exact nonparametric inference, user manual. Cytel Software, Cambridge, Massachusetts, USA.
- MELDGAARD, M. 1986. The Greenland caribou—zoogeography, taxonomy, and population dynamics. *Meddelelser on Grønland, Bioscience* 20:1–88.
- MESSIER, F. 1995. Trophic interactions in two northern wolf-ungulate systems. *Wildlife Research* 22: 131–146.
- , J. HUOT, D. LE HENAFF, AND S. LUTTICH. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. *Arctic* 41:279–287.
- MILLER, F. L. 1982. Caribou *Rangifer tarandus*. Pages 923–959 in J. A. Chapman and G. A. Feldhamer, editors. *Wild mammals of North America: biology, management, and economics*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- . 1991. Estimating Bathurst Island Peary caribou and muskox populations. *Arctic* 44:57–62.
- NEILAND, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. *Journal of Wildlife Management* 34:904–907.
- NELLEMAN, C. 1997. Range ecology of the Arctic ungulates during winter and spring: relations to terrain structure and anthropogenic disturbance. Dissertation, Agricultural University of Norway, Ås, Norway.
- NETTLESHIP, D. N., AND P. A. SMITH, editors. 1975. Ecological sites in northern Canada. Canadian Committee for the International Biological Programme, Ottawa, Canada.
- OUELLET, J.-P. 1992. Ecology of an introduced caribou population on Southampton Island, N.W.T., Canada. Dissertation, University of Alberta, Edmonton, Canada.
- , D. C. HEARD, S. BOUTIN, AND R. MULDER. 1997. A comparison of body condition and reproduction of caribou on two predator-free arctic islands. *Canadian Journal of Zoology* 75:11–17.
- , D. C. HEARD, AND R. MULDER. 1996. Population ecology of caribou populations without predators: Southampton and Coats Island herds. *Rangifer, Special Issue 9*:17–25.
- PATTIMORE, J. H. 1986. Baffin Region wildlife harvesting study: five year summary report, 1980–1984. Unpublished report, Baffin Region Inuit Association (Qikiqtani Inuit Association), Iqaluit, Nunavut, Canada.
- RINEY, T. N. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*) with special reference to New Zealand. *New Zealand Journal of Science and Technology* 36B:429–463.
- SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. Non-

- parametric statistics for the behavioral sciences. Second edition. McGraw-Hill, New York, New York, USA.
- SKOOG, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Dissertation, University of California, Berkeley, California, USA.
- THOMAS, D. C. 1982. The relationship between fertility and fat reserves of Peary caribou. *Canadian Journal of Zoology* 60:597–602.
- TYLER, N. J. C. 1987. Natural limitation of the abundance of the High Arctic Svalbard reindeer. Dissertation, University of Cambridge, Cambridge, United Kingdom.
- WELLS, J. V., AND M. E. RICHMOND. 1995. Populations, metapopulations, and species populations: What are they and who should care? *Wildlife Society Bulletin* 23:458–462.
- ZAR, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Received 11 December 1998.

Accepted 11 May 1999.

Associate Editor: Merrill.

## EFFECT OF HIBERNATION AND REPRODUCTIVE STATUS ON BODY MASS AND CONDITION OF COASTAL BROWN BEARS

GRANT V. HILDERBRAND, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518, USA

CHARLES C. SCHWARTZ,<sup>1</sup> Alaska Department of Fish and Game, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, USA

CHARLES T. ROBBINS, Departments of Natural Resource Sciences and Zoology, Washington State University, Pullman, WA 99164, USA

THOMAS A. HANLEY, United States Forest Service, Pacific Northwest Research Station, 2700 Sherwood Lane, Suite 2A, Juneau, AK 99801, USA

**Abstract:** We investigated the effect of hibernation and reproductive status on changes in body mass and composition of adult female brown bears (*Ursus arctos*) on the Kenai Peninsula, Alaska. This information is fundamental to understanding nutritional ecology of wild brown bear populations. Six adult females handled in the fall and following spring (paired samples) lost  $73 \pm 22$  kg ( $\bar{x} \pm$  SD;  $32 \pm 10\%$ ) of fall body mass over  $208 \pm 19$  days. Of this mass loss,  $56 \pm 22\%$  ( $55 \pm 22$  kg) was lipid and  $44 \pm 22\%$  ( $43 \pm 21$  kg) was lean body mass. Catabolism of lipid stores accounted for  $88.4 \pm 8.1\%$  of the body energy used to meet maintenance demands. Overwinter differences in body composition of adult females assessed only once in either the fall ( $n = 21$ ) or spring ( $n = 32$ ) were similar to those of paired samples. Relative fatness of bears entering the den was positively related to the contribution of fat (%) to body mass ( $P < 0.01$ ) and body energy ( $P < 0.01$ ) losses during hibernation. Thus, relative fatness at the onset of fasting influences the relative proportion of lipid stores and lean body mass catabolized to meet protein and energy demands during hibernation. In the spring, lone females had greater body and lean masses than females with cubs of the year or yearlings. Lipid content was greatest in lone females in the fall. Studies using body mass and composition as indices of population health should consider season or reproductive class.

*JOURNAL OF WILDLIFE MANAGEMENT* 64(1):178–183

**Key words:** body composition, body condition, brown bear, hibernation, Kenai Peninsula, reproductive class, *Ursus arctos*.

Knowledge of seasonal changes in body mass and composition provides important insights into the nutritional ecology of bears. Female brown bears fast during hibernation, give birth during this winter dormancy, and lactate for 2 to 3 months before den emergence (Farley and Robbins 1995). Additionally, the cubs may stay

with the mother, who continues to lactate, for up to 3 years. These life-history traits create significant energy demands for the female. Female body mass and body fat content are positively related to reproductive success of individuals and, thus, to parameters of population productivity such as litter size, interval between litters, and age of first reproduction (Rogers 1976, 1987; Bunnell and Tait 1981; Blanchard 1987; Stringham 1990; Noyce and Garshelis 1994; Atkinson and Ramsay 1995; Samson and Huot

<sup>1</sup> Present Address: Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717, USA.