

## RELATIONSHIPS BETWEEN DENNING OF POLAR BEARS AND CONDITIONS OF SEA ICE

STEVEN H. FERGUSON,\* MITCHELL K. TAYLOR, AQQALU ROSING-ASVID, ERIK W. BORN, AND FRANÇOIS MESSIER

*Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada (SHF, FM)*

*Department of Resources, Wildlife, and Economic Development, Government of the Northwest Territories, Box 1340, Iqaluit, Northwest Territories X0A 0H0, Canada (MKT)*

*Greenland Institute of Natural Resources, P.O. Box 570, DK-3900, Nuuk, Greenland (ARA, EWB)*

*Present address of SHF: Faculty of Forestry and the Forest Environment, 955 Oliver Road, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada*

We examined shelter and maternity dens used by 97 adult female polar bears (*Ursus maritimus*) in relation to conditions of sea ice. Obligate use of maternity dens for pregnancy, birth, and lactation varied little with latitude or area. In contrast, timing of facultative use of shelter dens switched from autumn in the southern area (<70°N) to winter in the northern area (>75°N). For the southern area, 13 of 16 female polar bears used shelter dens in autumn versus winter (median dates of entry and exit, 11 September and 2 November; total = 56 days), whereas in the northern area, 11 of 17 bears used shelter dens in winter versus autumn (median dates, 24 December and 2 March; total = 65 days). Difference in facultative use of shelter dens was associated with conditions of sea ice. Southern regions had no sea ice when polar bears used shelter dens. In contrast, northern areas had more constant ice conditions that included presence of ice throughout the year. Southern regions seem to have greater primary productivity and more seals as a result of a pronounced seasonal cycle of annual ice. Polar bears in northern areas responded to the more constant ice conditions and less productive environment with use of shelter dens during the period with lowest seal accessibility.

Key words: annual ice, den use, dormancy, seasonality, sheltering, *Ursus maritimus*

Adaptations to life at high latitudes include abilities to store somatic energy during periods of food availability (i.e., hyperallometric scaling of reserves—Schultz and Conover 1997) and reduce energy expenditure during periods when food is unavailable (Lyman 1963; Watts and Hansen 1987). Consequently, at high latitudes natural selection likely favors organisms that can physiologically endure protracted periods of food shortages (Conover 1992; Dunbrack and Ramsay 1993; Lindstedt and

Boyce 1985). Bears apparently evolved in high-latitude temperate regions that are characterized by variable food availability among seasons (Ferguson et al. 1996; Lyman 1963; Stirling and Derocher 1990). For bears, the physiological adaptation to highly seasonal environments is overwinter dormancy or hibernation (Lyman 1963; Ramsay et al. 1991). Nearly all brown bears (*Ursus arctos*) and black bears (*U. americanus*) hibernate over winter because of low availability of food (Pasitschniak-Arts and Messier 1999).

The polar bear (*U. maritimus*) has

\* Correspondent: Steven.Ferguson@lakeheadu.ca

evolved from the brown bear (Kurtén 1964; Stirling and Derocher 1990). In contrast to terrestrial bears, polar bears inhabit an environment with food available during winter. As a result, overwinter dormancy in polar bears is restricted to pregnant females that use maternity dens for reproduction. Maternity dens enable pregnant polar bears to conserve energy and provide protection for newborn cubs (Atkinson and Ramsay 1995; Messier et al. 1992; Watts and Hansen 1987). In contrast, polar bears of all ages and sex may use snow shelters for 0.5–4 months (Harington 1968; Koch 1930; Pedersen 1942) and fast in a manner that is physiologically similar to dormancy during periods of food shortages (Watts and Hansen 1987). Thus, use of shelter dens is a facultative strategy to reduce thermal stress and energy expenditure during periods when food is largely unavailable (Derocher and Stirling 1990; Messier et al. 1994; Ramsay et al. 1991). Polar bears are capable of entering a hibernationlike state at any time of the year within 7–10 days after food is removed (Derocher et al. 1990), an adaptation not found among terrestrial bears.

We compared use of dens by polar bears in 3 distinct zones of a larger Canada–Greenland study area. Those zones varied from more multiyear ice and less seasonal changes in amount of open water (northern zone) to more annual ice and greater seasonal changes in amount of open water (southern zone). We predicted that female polar bears would exhibit different patterns of use of shelter dens with differences in length of the ice-free period. The assumption was that food accessibility varied with conditions of sea ice because the amount of annual ice is positively associated with primary productivity and abundance of seals (Arrigo et al. 1997).

First, we compared use of maternity and autumn and winter shelter dens for differences in distance to coastline, differences due to family status, and differences in the chronology of den entry, den exit, and time in dens. We predicted greater variability in

use of autumn and winter shelter dens relative to use of maternity dens. Second, we compared use of autumn and winter shelter dens among the 3 zones. We predicted greater use of winter shelter dens and less use of autumn shelter dens by polar bears inhabiting northern areas relative to those in southern areas. Third, we compared denning behavior with ice characteristics among the 3 zones using 3 trigonometric measurements of changes in open water (amplitude, mean level, and phase). We predicted that polar bears in areas with less open water (lower amplitude, lower mean level, and later start to open water season) used winter shelter dens, whereas areas with greater open water had polar bears that used autumn shelter dens during the ice-free period.

#### MATERIALS AND METHODS

*Study area.*—Our study area ( $2.3 \times 10^6$  km<sup>2</sup>) extended from 60°N to 80°N and from 65°W to 110°W (Fig. 1). The region was dominated by a cycle of almost total ice cover in late winter and minimum ice cover in September (Collin and Dunbar 1964; Ferguson et al. 2000). The study area was divided into 3 zones defined by conditions of sea ice (Ferguson et al. 1998): a southern zone in the South Baffin Bay–Davis Strait area (<70°N), a central zone in Lancaster Sound–North Baffin Bay area (70–75°N), and a northern zone in the High Arctic area (>75°N). More open water occurred in the South Baffin Bay–Davis Strait area than in other zones. The South Baffin Bay–Davis Strait zone was dominated by extreme seasonal fluctuations in sea-ice cover (0–98% change) and consisted mostly of annual ice (80%—Ferguson et al. 2000). Annual ice formed and melted within a year whereas multi-year ice remained for greater than a year. In contrast, the northern zone was located within the Arctic Archipelago and was characterized by mostly multi-year ice (51%) and low seasonal variation in ice cover (2–20% change—Ferguson et al. 2000). The Lancaster Sound–North Baffin Bay zone was a transitional zone between the extremes of the 2 other zones.

*Seasonality of sea ice.*—Ice characteristics were derived from 12 monthly ice maps (MAN-ICE 1994) for 1993 that were digitized for a

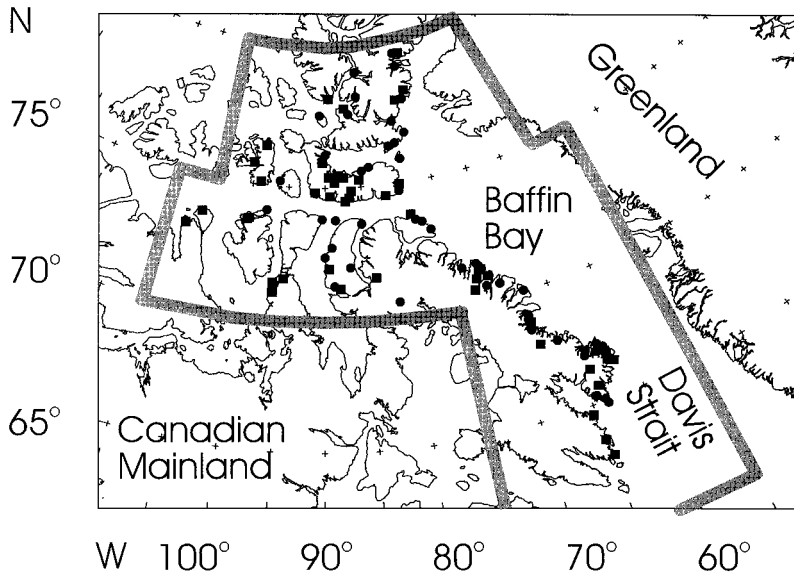


FIG. 1.—Study area with locations of adult female polar bears that used a shelter den (circle) or a maternity den (square), 1991–1997.

geographic information system. Ice-habitat maps were overlaid on annual home ranges of polar bears (adaptive kernel—Worton 1989) for polar bears with a complete year of locational data (individuals in maternity dens were excluded). We calculated the proportion of multiyear ice, annual ice, and open water in the annual home range of each polar bear for each month (Ferguson et al. 1999). To avoid data dependence, we did not use the percentage of land, and thus habitat proportions did not sum to unity (Aebischer et al. 1993). For example, percentage of open water was calculated as area of open water divided by area of sea ice and open water in a home range.

We delineated 12 monthly periods to record seasonal variation in ice phenology and used sine-wave functions to assess seasonal variations (Bowerman and O'Connell 1993; Ferguson et al. 2000). To assess seasonal variation, we used the median location of annual movements of polar bears. The amplitude increased with greater seasonal changes of sea-ice cover. The phase of each cycle was used to assess timing of the cycle in relation to the calendar year.

*Use of maternity and shelter dens.*—We used satellite telemetry to obtain locations of polar bears every 4 or 6 days (Messier et al. 1994) from a sample of 97 adult female bears that were equipped with collar-mounted transmitters in

1991–1997 (Ferguson et al. 1997). Bears were captured during spring (April–May,  $n = 54$ ) and autumn (September–November,  $n = 43$ ) each year from 1991 to 1995. In spring, 16 females with cubs of the year, 17 females with yearlings, 6 females with 2-year-olds, and 18 solitary females were radiocollared. In autumn, 17 females with cubs of the year, 9 females with yearlings, 3 females with 2-year-olds, and 14 solitary females were radiocollared. We used movement data for 97 adult female polar bears over 162 bear-years from 1991 to 1997. Thirteen bears were monitored during 1991, 31 in 1992, 53 in 1993, 49 in 1994, 17 in 1995, and 5 in 1996.

Use of maternity and shelter dens was assessed from the locational and sensor data transmitted from radiocollars. Two sensors located in the collar transmitted information on internal temperature of the collar and activity of the bear during the previous 24 h (Messier et al. 1994). To minimize the degree of dependence among data, only 1 set of sensor data and 1 location per day were kept for each bear. Denning and sheltering by a radiocollared bear was determined from a series of stationary locations, reduced levels of activity, and higher than seasonal temperatures of collars (Messier et al. 1994). We estimated date of emergence from a den as the middle date between the last location in a den and the 1st movement.

We recorded family status at the time of capture as females with cubs of the year, females with 1-year-olds, females with 2-year-olds, and solitary adult females (5+ years). We also were able to confirm subsequent family status of radiocollared bears from recaptures ( $n = 23$ ). We assumed that a recaptured female with cubs of the year was solitary the previous year. A recaptured female with yearlings was assumed to have been accompanied by cubs of the year the previous year. If maternity denning was confirmed from telemetry data, then that female was considered to have cubs of the year the following year. Females that were captured initially with cubs of the year and did not enter a maternal den were assumed to be accompanied by yearlings the following year. Those assumptions were applied to 42 bear-years of data (26% of recorded family status was determined without visual verification) and were based on the finding that female polar bears in this region tended to follow a regular 3–4-year reproductive cycle. Mature females gave birth to cubs in mid-December and nursed their young for 2–3 years before mating again during the following spring. To avoid data dependence, we ensured that family status had changed if data from >1 year was used for the same bear. For our purposes, a year began and ended in the spring (1 June).

We recognized types of denning activity. First, use of shelter dens referred to a short period (>14 days and <4 months) of confinement in a snow den or a snow pit by a bear for purposes other than reproduction (Messier et al. 1994). Second, use of maternity dens referred to occupation of a den for >5 months when pregnancy, birth, and early lactation were assumed to have occurred. Use of shelter dens also could be subdivided into 2 types. First, autumn shelter dens were used from August to January (entry date before 1 December) apparently to avoid heat stress while on land during the ice-free period. Second, winter shelter dens were used from December to March (entry date after 1 December) apparently to avoid inclement weather or reduce energy expenditure during periods of reduced food availability (e.g., thick overwinter ice characteristic of the northern zone). We excluded use of shelter dens following autumn capture in analyses because we generally captured active bears. Autumn capture may have been biased toward bears not using either shelter or maternity dens during a year. Thus, bears cap-

tured after 15 September were analyzed for denning activity only for subsequent years.

*Data analysis.*—Our data generally failed to meet the assumption of normality, and transformations did not improve the fit (Shapiro–Wilk test:  $W < 0.95$ ,  $P < 0.002$ ). Therefore, we used nonparametric tests (SAS Institute Inc. 1990). When reporting nonparametric statistics (i.e., dates), we give the median with 25% and 75% quartile values. Distance data were given as  $\bar{X} \pm 1 SE$ .

First, we described the family status of female polar bears radiotracked over time and their use of maternity and shelter dens. We used Mann–Whitney 2-sample tests ( $Z$ ) to compare distance to coastline for use of maternity and shelter dens. We used a chi-square test to test for differences in use of dens with family status. No bias in sampling of the 3 zones occurred as indicated by no significant differences in family status of polar bears with radiocollars captured among the 3 zones ( $\chi^2 = 16.4$ ,  $d.f. = 2$ ,  $P = 0.25$ ).

Second, we described the chronology of use of maternity and shelter dens. We used Spearman rank-order correlations ( $r_s$ ) to compare timing of entry and exit of dens with latitude. We used Mann–Whitney 2-sample tests to compare time spent in shelter dens in autumn and winter.

Third, we compared denning behavior and ice conditions among the 3 zones. We used Spearman rank-order correlations to compare 3 trigonometric measures of changes in the amount of open water with latitude: amplitude, as a measure of the amount of seasonal change; mean level, as a measure of the amount of open water; and phase, as a measure of changes in start of the open water season. We used a chi-square test to compare use of autumn and winter shelter dens among the 3 zones.

## RESULTS

We obtained information on use of 48 maternity dens and 45 shelter dens by 97 adult female polar bears tracked over 162 bear-years from spring 1991 to fall 1997 (Table 1). We observed 3 instances in which the same bear used a shelter and a maternity den in the same year and 3 instances in which a bear used a shelter den in both autumn and winter during the same year. Most bears were females with cubs of

TABLE 1.—Percentages ( $n$ ) of adult female polar bears in Canadian–Greenland Arctic that used shelter dens (facultative) or maternity dens (obligatory) according to family status, 1991–1997.

Family status in spring	No use of den	Use of shelter dens <sup>a</sup>		Use of maternity dens	Percentage of sample
		Autumn	Winter		
Solitary	11.1 (5)	14.4 (6.5)	14.4 (6.5)	60.0 (27)	27.8 (45)
With cubs of the year	72.5 (37)	8.8 (4.5)	19.6 (9.5)	0.0 (0)	31.5 (51)
With 1-year-olds	46.3 (19)	25.6 (10.5)	8.5 (3.5)	19.5 (8)	25.3 (41)
With 2-year-olds	32.0 (8)	0.0 (0)	16.0 (4)	52.0 (13)	15.4 (25)
Total	42.6 (69)	13.3 (21.5)	14.5 (23.5)	29.6 (48)	100.0 (162)

<sup>a</sup> For 3 female polar bears that used a shelter den in autumn and winter during the same year, we split the sample ( $n = 0.5$  for use of a shelter den in autumn and  $n = 0.5$  for use of a shelter den in winter). For 3 female polar bears that used a shelter den and a maternity den in the same year, we include their use of maternity den only.

the year (32%), followed by solitary females (28%), females with yearlings (25%), and females with 2-year-olds (15%; Table 1). Use of maternity dens never occurred for females with cubs of the year, seldom occurred for females with 1-year-old offspring in spring (20%), but was likely for females seen with 2-year-old offspring in

spring (52%) or solitary females (60%; Table 1).

The likelihood of using a shelter den differed with family status ( $\chi^2 = 8.54$ ,  $d.f. = 2$ ,  $P = 0.014$ ; Table 1). Females with cubs of the year seldom used a shelter in autumn (9%) or winter (20%). Some females with 1-year-olds used shelter dens in autumn (26%) or winter (9%). Females accompanied by yearlings over winter and solitary females were more likely to use a shelter (53%) than were females with cubs of the year (29%).

All maternity dens were located on land (Fig. 1). All shelter dens in autumn were on land, and all but 1 winter shelter, located 11 km from Cape York (Fig. 1), was on land. Maternity dens were located farther inland ( $11.9 \pm 1.5$  km,  $n = 48$ ) than were shelter dens ( $6.6 \pm 0.7$  km,  $n = 43$ ;  $Z = -2.4$ ,  $d.f. = 43, 48$ ,  $P = 0.002$ ).

*Chronology of den use.*—Timing of entry to maternity dens was variable, with median date of entry of 15 September (1 September–7 October,  $n = 48$ ). In contrast, date of exit from maternity dens was less variable with the median exit date of 20 March (15–28 March,  $n = 38$ ). Time spent in maternity dens was 180 days (range, 163–200 days;  $n = 38$ ). Bears entered maternity dens later at high latitude than at low latitude ( $r_s = 0.33$ ,  $P = 0.02$ ,  $n = 48$ ; Fig. 2). Date of exit was not related to latitude ( $r_s = 0.05$ ,  $P = 0.75$ ,  $n = 38$ ).

We found evidence of a latitudinal pat-

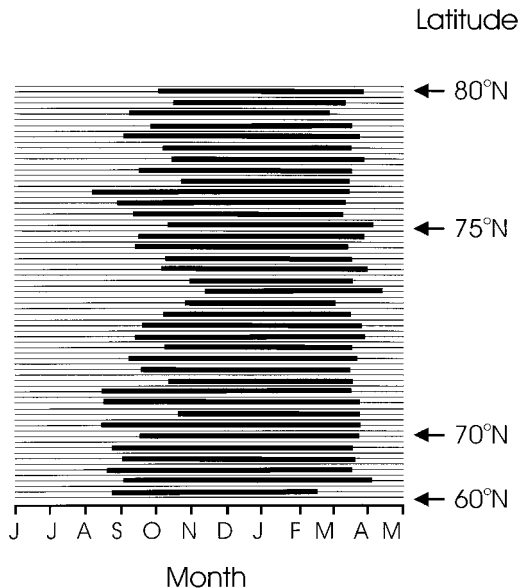


FIG. 2.—Seasonal timing of use of maternity dens by female polar bears according to latitude, 1991–1997. Median den entry date was 15 September and median exit date was 20 March. Each thin line represents a bear that was tracked for 1 year and entered a maternity den (thick horizontal line). Y-axis is sorted according to latitude.

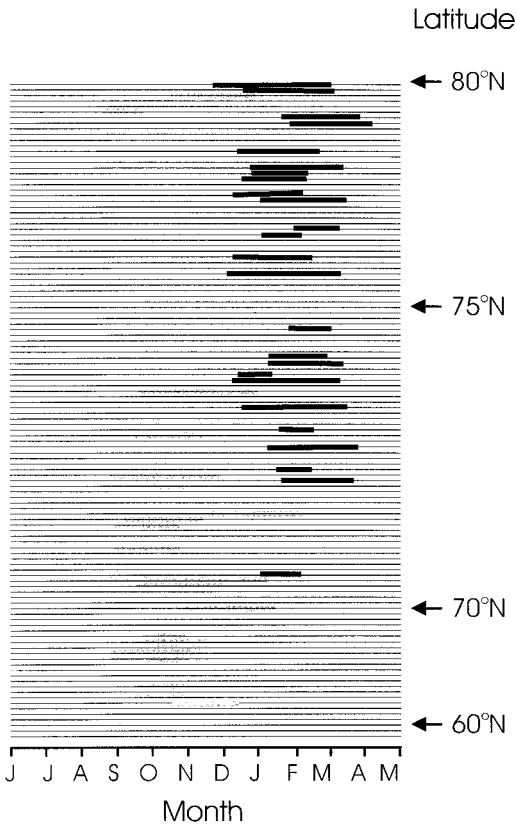


FIG. 3.—Seasonal timing of use of autumn (light shading) and winter (dark shading) shelter dens by female polar bears (thick horizontal bars) according to latitude, 1991–1997. For use of shelter dens in autumn, median entry date was 11 September, median exit date was 2 November, and entry was before 1 December. For use of shelter dens in winter, median entry date was 24 December, median exit date was 2 March, and entry was after 1 December. Each thin line represents a bear that was tracked for 1 year and excludes females that used maternity dens. Y-axis is sorted according to latitude.

tern in entry, exit, and amount of time in autumn shelter dens. For autumn sheltering, female bears in northern areas entered shelter dens later ( $r_s = 0.45$ ,  $P = 0.03$ ,  $n = 24$ ) and exited shelter dens later ( $r_s = 0.47$ ,  $P = 0.02$ ,  $n = 23$ ) than did bears in other zones. Female polar bears entered autumn shelter dens in mid-September (median date, 11 September; range, 29 August–26

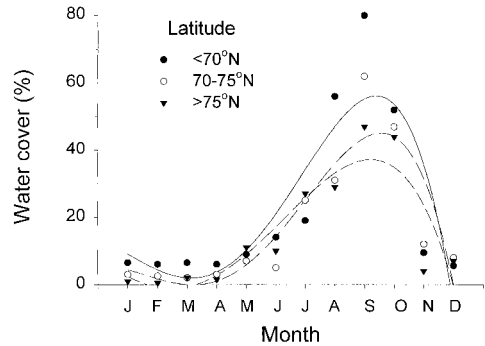


FIG. 4.—Monthly changes in percentage of open water in home ranges of polar bears for 3 zones in the Arctic. The southern zone is characterized by greater amplitude in seasonal flux of annual ice versus open water.

September;  $n = 22$ ) and exited near the beginning of November after freeze-up (median date, 2 November; range, 24 October–28 November;  $n = 21$ ; Fig. 3). Average time spent in shelter dens in autumn was 56 days (range, 50–70 days;  $n = 21$ ).

We found no evidence of a latitudinal pattern in entry, exit, and amount of time in winter shelter dens. For winter sheltering, female bears exhibited no latitudinal pattern in date of entry ( $r_s = -0.15$ ,  $P = 0.44$ ,  $n = 23$ ) or exit ( $r_s = 0.13$ ,  $P = 0.52$ ,  $n = 22$ ). Female polar bears entered winter shelter dens in late December (median date, 24 December; range, 12 December–14 January;  $n = 28$ ) and exited near the beginning of March (median date, 2 March; range, 7 February–8 March;  $n = 27$ ). Average time spent in shelter dens in winter was 65 days (range, 35–86 days;  $n = 21$ ). Time spent in shelter dens in autumn and winter did not differ ( $Z = 0.04$ ,  $d.f. = 21, 27$ ,  $P = 0.97$ ).

*Comparing ice conditions and den use.*—A cline in sea-ice conditions in home ranges of polar bears occurred over the study area, with the northern zone exhibiting less seasonal variation in ice cover (Fig. 4). Northern areas had less seasonal changes in the amplitude of open water ( $r_s = -0.30$ ,  $P = 0.02$ ,  $n = 87$ ). Northern areas had less open water throughout the year (mean level,  $>30\%$  water;  $r_s = -0.32$ ,  $P = 0.01$ ,  $n =$

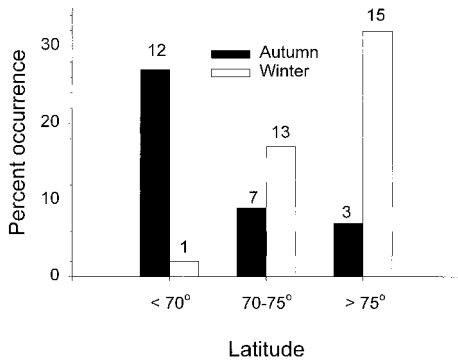


FIG. 5.—Percent occurrence of adult female polar bears that used shelter dens in autumn or winter within 3 latitudinal zones of the Arctic, 1991–1997.

87). Northern areas had a later start to the open-water season (i.e., phase  $r_s = 0.39$ ,  $P < 0.01$ ,  $n = 87$ ).

Whether female polar bears used a shelter den in autumn or winter varied with latitude (Fig. 5). Fifty-one of 120 nonpregnant females used a shelter facultatively. Comparing 3 latitudinal zones (<70°N, 70–75°N, >75°N), we found that use of shelter dens in autumn decreased with latitude but use of shelter dens in winter increased ( $\chi^2 = 21.3$ ,  $d.f. = 4$ ,  $P < 0.001$ ; Fig. 5). Thus, bears were more likely to use shelter dens in winter in the northern zone and in autumn in the southern zone.

#### DISCUSSION

Within our study area, a cline in seasonality of sea-ice conditions resulted in a cline in use of shelter dens by female polar bears. The polar bear is the most carnivorous of the bears and feeds primarily on ringed seals (*Phoca hispida*), the most available prey in the ice-covered Arctic Ocean (Stirling and McEwan 1975). In our study area, a cline occurred with higher seal densities found in the southern area of South Baffin Bay–Davis Strait, lower seal density in the central area (Lancaster Sound–North Baffin Bay), and the lowest densities recorded for the High Arctic area >75°N (Stirling and Øritsland 1995). Densities of ringed seals

vary in response to overall productivity of the ecosystem (Stirling and Lunn 1998). Regions covered with multiyear ice are considerably less productive than areas that fluctuate seasonally between annual ice and open water. Annual primary productivity in areas with 1-year ice is 27 times that of areas with multiyear ice (Arrigo et al. 1997). Areas of annual ice also have 4–8 times greater primary productivity than areas of open water at the same latitudes, indicating that the flux of seasonal ice enhances productivity (Nicol and Allison 1997; Savidge et al. 1996) and results in greater seal density (Stirling and Øritsland 1995). Density of polar bears was correlated with density of ringed seals (Stirling and Øritsland 1995). The physiological response to decreasing food availability during winter in northern areas also may influence use of shelter dens in winter by many nonpregnant female polar bears.

Polar bears exhibited physiological plasticity to accommodate changes in environmental conditions and energy availability. In northern areas, bears have responded to decreased food availability during winter with lower activity to conserve energy (Messier et al. 1992). In southern areas, bears have responded to the greater seasonal variation in ice conditions with facultative use of shelter dens during late summer–early autumn. Use of shelter dens in winter increased with latitude, as did the amount of time spent in shelter dens, possibly as a result of low seal densities in northern areas.

Polar bears adopt space-use strategies along a continuum from small home ranges when living in areas of low food availability and predictable environments to large home ranges when living in areas of high food availability but unpredictable dispersion of food (Ferguson et al. 1999). For example, in the northern zone the overall availability of seals is lower but seasonal variation is less. Polar bears living in the northern zone tended to use shelter dens in winter and have smaller home ranges. Use

of shelter dens in winter may have occurred because of the overall low seal density and the greater proportion of adult seals, which are more difficult to hunt. Polar bears also may use shelter dens in winter to take refuge from storms, although females with cubs were the least likely to use winter shelters. In contrast to polar bears in northern areas, those in southern areas move greater distances to take advantage of areas of seal pupping in spring and concentrations of juvenile seals in winter. Bears on land in autumn use shelter dens to escape heat, and they move to high elevations where precipitation falls as snow rather than rain.

In all but 1 study (Amstrup and Gardner 1994), the majority of maternity dens were discovered on land in coastal areas adjacent to areas with high seal density in spring (Harington 1968; Stirling and Andriashek 1992; Uspenski and Kistchinski 1972). Maternity dens were scattered across the study area, with the only concentration occurring along Cumberland Peninsula (Ferguson et al. 1997; Stirling et al. 1980). We found all maternity dens on land. Similarly, all maternity dens located in Viscount Melville (Messier et al. 1994), Svalbard (Wiig 1995), Hudson Bay (Ramsay and Stirling 1990), eastern Beaufort Sea (Stirling and Andriashek 1992), Baffin Island (Ferguson et al. 1997), Russian Arctic (Garner et al. 1990; Uspenski and Kistchinski 1972), and Greenland (Born et al. 1997) were on land. Our results agree with those of other studies in the Arctic ( $>60^{\circ}\text{N}$ ) in that maternity dens were located  $<20$  km from the coast (Harington 1968; Larsen 1985; Uspenski and Kistchinski 1972) and generally only a few kilometers from the coast (Born et al. 1997; Ferguson et al. 1997; I. Stirling et al., in litt.). These findings contrast with the majority of maternity dens located  $>20$  km inland along the coast of Hudson Bay (Kolenosky and Prevett 1983; Stirling and Ramsay 1986; Stirling et al. 1977). Relative to the coastline on Hudson Bay, northern Arctic coastlines generally are characterized as rugged with high elevations.

Researchers have seldom reported use of shelter dens in winter for polar bears, probably because of the difficulty of making observations during winter darkness. Only recently has satellite telemetry made observations of use of shelter dens in winter possible. For example, the Arctic Archipelago (e.g., Viscount Melville) area is characterized by mostly multiyear ice with fewer seasonal changes in ice characteristics (Ferguson et al. 2000; Messier et al. 1992). Thus, we expected female polar bears from the western Arctic Archipelago to use shelter dens in winter more often than bears from our study area. Female polar bears in our study area were less likely to use shelter dens (43%) than were bears tracked in the Viscount Melville area (60%—Messier et al. 1994). We recorded only 1 of 48 shelter dens on sea ice compared with 6 of 20 shelter dens in the Viscount Melville area (Messier et al. 1994). We found less use of shelter dens by females with cubs of the year relative to other females, whereas use of shelter dens did not differ with family status in the Viscount Melville area (Messier et al. 1994).

Polar bears probably use shelter dens in areas with reduced food availability during winter. During autumn, availability of multiyear ice at high latitudes permits continued access to seals; hence, use of shelter dens in autumn is rare. Similarly, seals are available and more abundant during winter in southern areas precluding the need to shelter in winter. In southern areas, productive waters become ice free during autumn, and bears often shelter in autumn in response to inaccessibility of food. In our study area, a trend in use of shelter dens in winter by female polar bears paralleled changes in seasonal variation of ice conditions.

#### ACKNOWLEDGMENTS

This study was supported by Heritage Canada Parks Service, Polar Continental Shelf Project, Greenland Institute of Natural Resources, Canadian Wildlife Service, Nunavut Wildlife Man-

agement Board, Nunavut and Inuvait Hunters and Trappers Organizations, and the Department of Resources, Wildlife, and Economic Development, Government of the Northwest Territories. Comments by 2 anonymous reviewers provided considerable improvements to the manuscript.

#### LITERATURE CITED

- AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- AMSTRUP, S. C., AND C. GARDNER. 1994. Polar bear maternity denning in the Beaufort Sea. *The Journal of Wildlife Management* 58:1–10.
- ARRIGO, K. R., D. L. WORTHEN, M. P. LIZOTTE, P. DIXON, AND G. DIEKMANN. 1997. Primary production in Antarctic sea ice. *Science* 276:394–397.
- ATKINSON, S. N., AND M. A. RAMSAY. 1995. The effect of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). *Functional Ecology* 9:559–567.
- BORN, E. W., O. WIIG, AND J. THOMASSEN. 1997. Seasonal and annual movements of radio-collared polar bears (*Ursus maritimus*) in northeast Greenland. *Journal of Marine Systems* 10:67–77.
- BOWERMAN, B. L., AND R. T. O'CONNELL. 1993. Forecasting and time series: an applied approach. 3rd ed. Duzbury Press, Belmont, California.
- COLLIN, A. E., AND M. J. DUNBAR. 1964. Physical oceanography in Arctic Canada. *Oceanography and Marine Biology Annual Review* 2:45–75.
- CONOVER, D. O. 1992. Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology* 41B:161–178.
- DEROCHER, A. E., R. A. NELSON, I. STIRLING, AND M. A. RAMSAY. 1990. Effects of fasting and feeding on serum urea and serum creatinine levels in polar bears. *Marine Mammal Science* 6:196–203.
- DEROCHER, A. E., AND I. STIRLING. 1990. Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. *Canadian Journal of Zoology* 68:1395–1403.
- DUNBRACK, R. L., AND R. M. RAMSAY. 1993. The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis. *Oikos* 66:336–342.
- FERGUSON, S. H., E. W. BORN, M. K. TAYLOR, AND F. MESSIER. 1998. Fractals, sea-ice landscape and spatial patterns of polar bears. *Journal of Biogeography* 25:1081–1092.
- FERGUSON, S. H., M. K. TAYLOR, AND F. MESSIER. 1997. Space-use of polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. *Canadian Journal of Zoology* 75:1585–1594.
- FERGUSON, S. H., M. K. TAYLOR, AND F. MESSIER. 2000. Influence of sea ice dynamics on habitat selection by polar bears. *Ecology* 81:761–772.
- FERGUSON, S. H., M. K. TAYLOR, A. ROSING-ASVID, E. W. BORN, AND F. MESSIER. 1999. Determinants of home range size for polar bears (*Ursus maritimus*). *Ecology Letters* 2:311–318.
- FERGUSON, S. H., J. A. VIRGL, AND S. LARIVIÈRE. 1996. Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. *Ecoscience* 3:7–17.
- GARNER, G. W., S. T. KNICK, AND D. C. DOUGLAS. 1990. Seasonal movements of adult female polar bears in the Bering and Chuckchi seas. *International Conference of Bear Research and Management* 8: 219–226.
- HARINGTON, C. R. 1968. Denning habits of the polar bear (*Ursus maritimus* Phipps). *Canadian Wildlife Service Report Series* 5:1–30.
- KOCH, L. 1930. Report on the geological expedition to east Greenland 1926–27. *Meddelelser om Grønland* 76:227–287.
- KOLENOSKY, G. B., AND J. P. PREVETT. 1983. Productivity and maternity denning of polar bears in Ontario. *International Conference of Bear Research and Management* 5:238–245.
- KURTÉN, B. 1964. The evolution of the polar bear, *U. maritimus* Phipps. *Acta Zoologica Fennica* 108:3–30.
- LARSEN, T. 1985. Polar bear denning and cub production in Svalbard, Norway. *The Journal of Wildlife Management* 49:320–326.
- LINDSTEDT, S. L., AND M. S. BOYCE. 1985. Seasonality, fasting endurance, and body size in mammals. *The American Naturalist* 125:873–878.
- LYMAN, C. P. 1963. Hibernation in mammals and birds. *American Scientist* 51:127–138.
- MANICE. 1994. Manual of standard procedures for observing and reporting ice conditions. 8th ed. Atmospheric Environment Service, Ice Services Branch, Ottawa, Ontario, Canada.
- MESSIER, F., M. K. TAYLOR, AND M. A. RAMSAY. 1992. Seasonal activity pattern of female polar bears (*Ursus maritimus*) in the Canadian Arctic as revealed by satellite telemetry. *Journal of Zoology (London)* 226:219–229.
- MESSIER, F., M. K. TAYLOR, AND M. A. RAMSAY. 1994. Denning ecology of polar bears in the Canadian Arctic archipelago. *Journal of Mammalogy* 75:420–430.
- NICOL, S., AND I. ALLISON. 1997. The frozen skin of the southern ocean. *American Scientist* 85:426–439.
- PASITSCHNIK-ARTS, M., AND F. MESSIER. 2000. Brown (grizzly) and polar bears. Pp. 409–428 in *Ecology and management of large mammals in North America* (S. Demarais and P. R. Krausman, eds.). Prentice-Hall, Upper Saddle River, New Jersey.
- PEDERSEN, A. 1942. Säugetiere und vogel [mammals and birds]. *Meddelelser om Grønland* 128:1–119.
- RAMSAY, M. A., R. A. NELSON, AND I. STIRLING. 1991. Seasonal changes in the ratio of serum urea to creatinine in feeding and fasting polar bears. *Canadian Journal of Zoology* 69:298–302.
- RAMSAY, M. A., AND I. STIRLING. 1990. Fidelity of female polar bears to winter-den sites. *Journal of Mammalogy* 71:233–236.
- SAS INSTITUTE INC. 1990. SAS/STAT user's guide. Version 6, Vol. 2, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SAVIDGE, G., ET AL. 1996. An assessment of the role

- of the marginal ice zone in the carbon cycle of the Southern Ocean. *Antarctic Science* 8:349–358.
- SCHULTZ, E. T., AND D. O. CONOVER. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). *Oecologia* 109:516–529.
- STIRLING, I., AND D. ANDRIASHEK. 1992. Terrestrial maternity denning of polar bears in the eastern Beaufort Sea area. *Arctic* 45:363–366.
- STIRLING, I., W. R. ARCHIBALD, AND D. P. DEMASTER. 1977. The distribution and abundance of seals in the eastern Beaufort Sea. *Journal of the Fisheries Research Board of Canada* 34:976–988.
- STIRLING, I., W. CALVERT, AND D. ANDRIASHEK. 1980. Population ecology studies of the polar bear in the area of southeastern Baffin Island. *Canadian Wildlife Service Occasional Papers* 44:1–33.
- STIRLING, I., AND A. E. DEROCHE. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. *International Conference of Bear Research and Management* 8:189–204.
- STIRLING, I., AND N. J. LUNN. 1998. Environmental fluctuations in Arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. Pp. 167–181 in *Ecology of Arctic environments* (S. Woodin and M. Marquiss, eds.). British Ecological Society, Blackwell Science, Oxford, United Kingdom.
- STIRLING, I., AND E. H. MCEWAN. 1975. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behaviour. *Canadian Journal of Zoology* 53:1021–1027.
- STIRLING, I., AND N. A. ØRITSLAND. 1995. Relationships between estimates of ringed seal and polar bear populations in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2594–2612.
- STIRLING, I., AND M. A. RAMSAY. 1986. Polar bears in Hudson Bay and Foxe Basin: present knowledge and research opportunities. Pp. 341–354 in *Canadian inland seas* (I. P. Martini, ed.). Elsevier Science Publications, Amsterdam, The Netherlands.
- USPENSKI, S. M., AND A. A. KISTCHINSKI. 1972. New data on the winter ecology of the polar bear (*Ursus maritimus*) on Wrangel Island. *International Conference of Bear Research and Management* 2:181–197.
- WATTS, P. D., AND S. E. HANSEN. 1987. Cyclic starvation as a reproductive strategy in the polar bear. *Symposia of the Zoological Society of London* 57:305–318.
- WIIG, O. 1995. Distribution of polar bears (*Ursus maritimus*) in the Svalbard area. *Journal of Zoology (London)* 237:515–529.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

Submitted 24 May 1999. Accepted 2 March 2000.

Associate Editor was John A. Litvaitis.