

DENNING ECOLOGY OF BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL ARCTIC

PHILIP D. McLOUGHLIN,* H. DEAN CLUFF, AND FRANÇOIS MESSIER

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

Department of Resources, Wildlife, and Economic Development, Government of the Northwest Territories, North Slave Region, P.O. Box 2668, Yellowknife, Northwest Territories X1A 2P6, Canada (HDC)

Present address of PDM: Department of Biological Sciences, CW-405 Biological Sciences Centre, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Between May 1995 and June 1999, we studied denning ecology of 81 barren-ground grizzly bears (*Ursus arctos*) equipped with satellite radio-collars within a study area of 235,000 km², centered 400 km northeast of Yellowknife, Northwest Territories, Canada. All dens were located on well-drained slopes ($\bar{X} = 25.3^\circ$, $SE = 1.20$, $n = 55$). Choice of den aspect was nonrandom ($\chi^2 = 12.4$, $d.f. = 3$, $P < 0.01$, $n = 56$); the majority of dens faced south (25), followed by west (13), east (10), and north (8). Most dens were constructed under cover of tall (>0.5 m) shrubs (*Betula glandulosa* and *Salix*), the root structures of which supported ceilings of dens. Selection of denning habitat by bears was significantly different from random ($G = 127.67$, $d.f. = 6$, $P < 0.0001$). Bonferroni confidence intervals indicated that esker habitat was selected more than expected by chance ($P < 0.10$). Den entrance occurred primarily in last 2 weeks of October. The majority of bears emerged from dens in the 1st week of May.

Key words: Arctic, den ecology, grizzly bear, habitat use, Northwest Territories, Nunavut, radio telemetry, resource development, Tundra

Although most grizzly bear (*Ursus arctos*) populations in North America have undergone some degree of decline or range reduction subsequent to the arrival of Europeans, populations of barren-ground grizzly bears inhabiting Arctic regions have remained relatively undisturbed. Far removed from human habitation, barren-ground grizzly bears have not been subjected to the exploitation and habitat changes that led to the extirpation of grizzly bears from much of their former range. Nonetheless, all populations of grizzly bears in Canada, including barren-ground populations, are classified as vulnerable and considered susceptible to population decline (Committee on the Sta-

tus of Endangered Wildlife in Canada 1991).

Barren-ground grizzly bears in Canada's central Arctic (Fig. 1) may be at particular risk to population decline for several reasons: they have limited continuity with other grizzly bear populations because they are near the northern and easternmost limit of the species' North American range; bears in tundra habitats are more likely than bears in forested areas to be displaced by nearby human activity because of reduced cover (McLellan 1990); populations of grizzly bears in tundra habitat exist at the lowest recorded densities of all extant North American grizzly bear populations (McLellan 1994); and they likely have very large spatial requirements (Ballard et al.

* Correspondent: pdm5@ualberta.ca

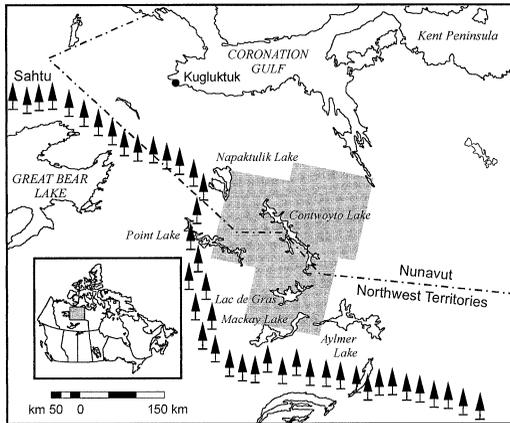


FIG. 1.—Study area in Canada's central Arctic. Shaded region indicates portions of the study area classified with Landsat TM images (75,000 km²) and used for estimating proportional habitat availability. Treeline (tree symbols) indicates the northernmost extent of coniferous forest in the study area.

1993; Clarkson and Liepins 1989; Nagy et al. 1983; Reynolds 1980) which could put individual bears in contact with humans even when developments are at considerable distances from core home ranges of bears.

Recent discoveries of diamonds, gold, and base metals in the central Arctic have only added to concerns regarding conservation of barren-ground grizzly bears in the region. Future plans for mining include construction of all-weather roads and infrastructures requiring granular materials from eskers and related surface expressions. Composed mainly of sand and gravel, eskers are prominent topographic features that trace the path of collapsed depositional landforms such as glacial rivers formed by melting of supporting ice (Soil Classification Working Group 1998). Previous studies in the central Arctic (Banci and Moore 1997; Mueller 1995) suggested that esker habitat was extremely important to grizzly bears, wolves (*Canis lupus*), Arctic ground squirrels (*Spermophilus parryi*), and foxes (*Vulpes vulpes*, *Alopex lagopus*) for denning. The use of granular materials by in-

dustry may therefore present a problem for the conservation of wildlife reliant upon glacio-fluvial habitats for denning, including barren-ground grizzly bears.

To mitigate possible conflicts between industry and the grizzly bear population in the central Arctic, the extent to which bears rely on eskers and related features for denning needs to be established. The objective of this study was to evaluate the importance of eskers and other habitats as denning habitat for barren-ground grizzly bears in the central Arctic. We documented denning habits of grizzly bears by following satellite and VHF radio-collared bears to their dens. We quantified the importance of esker habitat and other habitats for denning by bears and documented characteristics of recently excavated dens. Further, telemetry data allowed us to examine times at which grizzly bears entered and exited dens.

MATERIALS AND METHODS

Study area.—The study area was located in Canada's central Arctic, encompassing approximately 235,000 km² of mainland Nunavut and the Northwest Territories (Fig. 1). The study area was delineated by the community of Kugluktuk, the Kent Peninsula, Aylmer Lake, Mackay Lake, and Great Bear Lake. The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C and winter temperatures are commonly below -30°C. The area is semiarid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc. 1995). Drainages support willow (*Salix*) and dwarf birch (*Betula glandulosa*) shrubs as tall as 3 m, and birch shrublands (<0.5 m in height) dominate uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*V. vitis-idaea*), and crowberry (*Empetrum nigrum*) are common and their berries are important food for grizzly bears (Gau 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below treeline in April, travels to calving grounds near Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000 adult caribou in 1996 (A. Gunn et al., in litt.). Musk

ox (*Ovibos moschatus*) occur sporadically in the northern half of the study area. Much of the study area is a part of a well-drained plain with lakes in hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

Animal capture and telemetry.—Between May 1995 and June 1999, helicopters were used to search for and capture 81 grizzly bears ($n = 38$ adult females, $n = 4$ subadult females, $n = 35$ adult males, $n = 4$ subadult males). Fixed-wing aircraft equipped with skis or floats were sometimes used for more intensive searches of study area. We captured most bears in spring during snow melt (15 May–5 June) by following tracks in snow. We immobilized bears with tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected dart. Bears weighing >110 kg (males) and >90 kg (females) were fitted with tracking devices.

Satellite (Service Argos Inc., Landover, Maryland) and conventional VHF radio-telemetry (Telonics Ltd., Mesa, Arizona) were used to obtain denning information on barren-ground grizzly bears. Satellite telemetry provides continuous information on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars were equipped with a VHF beacon to permit locations of radio-marked animals from an aircraft and, eventually, for retrieval of collars. Most collars were designed to transmit approximately 2–5 latitude–longitude locations every 2 days (8-h duty cycle) from 1 May to 1 November. During other months, collars were programmed to transmit locations every 8 days to conserve battery power. We obtained an additional den location for 23 bears (mostly females) by deploying break-away VHF radio-collars after satellite collars were removed.

Denning chronology.—We determined dates of den entry and emergence for bears from dates on which radio-transmissions to satellites ceased to be received in autumn (den entry estimates) and the dates on which satellites resumed receiving transmissions in spring (den emergence estimates). However, radio telemetry transmissions to receiving satellites were entirely blocked while bears were in dens.

Den characteristics.—Satellite radio transmissions prior to den entrance in autumn allowed

us to determine the general location of most bear dens (often to <500 m). Then, using aerial VHF telemetry later in winter (October or March), we determined the exact location of dens using a global positioning system. We returned to these locations the following July to investigate den characteristics.

We measured dimensions of dens wherever possible (entrance width and height, cavity width, height, and length). We recorded the aspect of den entrances using a compass. Aspect of den entrances were coded into 1 of 4 categories: north (315 – 44.9°), east (45 – 134.9°), south (135 – 224.9°), and west (225 – 314.9°). A clinometer was used to measure the slope of the immediate area in which dens were excavated. We recorded presence or absence and percentage cover of plant species (Porsild and Cody 1980) within a radius of 1 m from den entrances, and estimated percentage soil composition by volume of denning habitat (percentage boulder, cobble, gravel, sand, silt-clay, organic) from visual examination of soil piles from den excavation. If more than 1 category of fine soil was observed to exist in a soil pile, a bulk soil sample was collected from the site and frozen. Samples were later thawed, oven-dried, and screened to determine relative proportions of fine soils in den soil piles.

Denning habitat.—We recorded the type of habitat in which dens were excavated for comparison with availability of habitats in the study area. Availability of habitats was assessed from 3 Landsat Thematic Mapper (TM) scenes classified by the Northwest Territories Centre for Remote Sensing in a representative 75,000 km² portion of the study area (Epp and Matthews 1998). Twelve discrete habitat types excluding water and ice were represented in the classified Landsat TM scenes: esker habitat, wetlands, tussock–hummock successional tundra, lichen veneer, spruce forest, boulder fields, exposed bedrock, riparian tall shrub habitat, birch seep, typical heath tundra, heath tundra with $>30\%$ boulder content, and heath tundra with $>30\%$ bedrock content (Epp and Matthews 1998).

Statistical analyses.—Dates of den entrance and emergence were converted to Julian dates for use in calculations. Mean dates of den entrance and emergence were compared across years and sexes using a 2-way analysis of variance (ANOVA; SigmaStat, Version 2.01, Jandel Corporation, San Rafael, California). A prelim-

inary ANOVA was conducted to determine whether dates of den emergence were similar for females of differing family status (lone females versus females with cubs; females with cubs-of-the-year versus females with yearlings and 2-year-olds). Following significant ANOVAs, Tukey's HSD test (Zar 1984) was used to compare individual mean values. Mean duration of denning (days) was calculated for those bears in which both dates of den entrance and emergence were available for any given winter. Mean duration of denning was compared between sexes using a *t*-test.

We calculated mean values ($\pm SE$) for all den dimensions, estimates of den aspect, slope, percentage vegetation coverage around den entrances (excluding excavation piles and caved-in portions of dens), and percentage soil particle size in excavation piles. Frequencies of aspect of den entrances were compared to what was expected from random using a chi-square goodness-of-fit test (Sokal and Rohlf 1995; Zar 1984).

The use of habitats for denning was compared to proportional availability of habitats in the study area using a log-likelihood ratio goodness-of-fit test (Zar 1984). Only those habitats in which dens were located were included for analyses, as zero values in frequency of use cannot be used in a log-likelihood ratio test. Thus, the null hypothesis tested was of no preference for those habitats in which dens were found to occur. For habitats in which dens were not known to occur, avoidance of those habitats for denning was assumed. Following rejection of the null hypothesis, 90% Bonferroni confidence intervals were constructed for the proportion of times animals denned in each available habitat type (Neu et al. 1974). Comparison of overlap of confidence intervals to habitat availability was used to determine which habitat types were being preferred or avoided for denning (Byers et al. 1984; Neu et al. 1974; White and Garrot 1990).

RESULTS

Denning chronology.—No effect of year was detected in the comparison of female and male (including subadult) dates of den entry for years 1995–1998 ($F = 0.50$, $d.f. = 3, 71$, $P > 0.60$). However, females entered dens ($\bar{X} = 16$ October, $SE = 1.5$ days, $n = 40$) significantly earlier ($F = 15.2$, $d.f. = 1, 71$, $P < 0.001$) than males ($\bar{X} = 24$

October, $SE = 1.5$ days, $n = 39$). Mean values include data from 5 subadult females and 6 subadult males. An interaction between year and sex was detected when comparing dates of den entry ($F = 2.31$, $d.f. = 3, 71$, $P = 0.08$).

A two-way ANOVA revealed no difference in mean dates of den emergence for females with cubs-of-the-year, yearlings, or cubs ≥ 2 years ($F = 1.77$, $d.f. = 2, 15$, $P > 0.20$). Further, dates of den emergence for these females were similar across years of study ($F = 1.60$, $d.f. = 3, 15$, $P > 0.20$). No difference was detected between dates of den emergence for females with and without accompanying young, including subadults ($F = 0.34$, $d.f. = 1, 32$, $P > 0.50$), although year was a significant factor in the model ($F = 2.73$, $d.f. = 3, 32$, $P = 0.06$). Females emerged from dens significantly earlier in 1997 ($\bar{X} = 27$ April, $SE = 2.7$ days, $n = 12$) than in 1996 ($\bar{X} = 8$ May, $SE = 2.8$ days, $n = 13$; Tukey's HSD test, $p = 4$, $q = 3.95$, $P = 0.04$). Dates of den emergence for females with and without cubs were independent of year of study ($F = 0.37$, $d.f. = 3, 32$, $P > 0.70$).

Females pooled across family status emerged, on an average, significantly later from dens than did males ($F = 3.11$, $d.f. = 1, 60$, $P < 0.10$). Mean date of den emergence for females was 3 May ($SE = 1.9$ days, $n = 41$) versus 27 April ($SE = 2.4$ days, $n = 27$) for males. Mean values include data from 3 subadult females and 3 subadult males. Mean dates of den emergence for all bears pooled across sex differed among years ($F = 3.26$, $d.f. = 3, 60$, $P = 0.03$). As within females, both male and female bears emerged from dens significantly earlier in 1997 ($\bar{X} = 26$ April, $SE = 2.6$ days, $n = 21$) compared with 1996 ($\bar{X} = 7$ May, $SE = 2.7$ days, $n = 20$; Tukey's HSD test, $p = 4$, $q = 3.86$, $P = 0.04$). There was no interaction between year and sex ($F = 0.09$, $d.f. = 3, 60$, $P > 0.90$); females and males adjusted their den emergence patterns similarly between years 1996 and 1997.

TABLE 1.—Plant species recorded at dens ($n = 52$) of grizzly bears in the central Arctic, Northwest Territories, and Nunavut, Canada, 1995–1999.

	Proportion of dens containing species	Proportional coverage of plant species	
		Mean ^a	SE
Dwarf birch (<i>Betula glandulosa</i>)	0.84	0.34	0.04
Willow (<i>Salix</i>)	0.35	0.09	0.03
Crowberry (<i>Empetrum nigrum</i>)	0.72	0.16	0.02
Cranberry (<i>Vaccinium vitis-idaea</i>)	0.84	0.07	0.01
Blueberry (<i>Vaccinium uliginosum</i>)	0.59	0.04	0.01
Bearberry (<i>Arctostaphylos</i>)	0.47	0.04	0.01
Labrador tea (<i>Ledum decumbens</i>)	0.57	0.03	0.06
Alpine azalea (<i>Loiseleuria procumbens</i>)	0.12	<0.01	<0.01
Saxifrage (<i>Saxifraga tricuspidata</i>)	0.06	<0.01	<0.01
Grass/sedge	0.80	0.11	0.02
Moss	0.18	0.01	<0.01
Lichen	0.06	<0.01	<0.01
Other ^b	0.60	0.10	0.03

^a Standardized to exclude proportional cover of excavation pile and caved-in portions of den.

^b Includes exposed soil and rare occurrences of identified and unidentified plant species.

Duration of denning of males ($\bar{X} = 184.6$ days, $SE = 3.8$, $n = 26$) was significantly less (t -test, $t = 3.3$, $d.f. = 61$, $P < 0.001$) than that of females ($\bar{X} = 198.6$ days, $SE = 2.3$, $n = 37$). Mean values include data from 4 subadult females and 3 subadult males.

Den characteristics.—We investigated 56 dens of barren-ground grizzly bears, all of which were excavated by bears. No snow dens, surface dens, or natural cavities were constructed or used. Further, no dens were thought to be revisited or reused by bears; all excavations were new. Most dens were composed of a single entrance, which widened after a short distance (<50 cm) into a large, circular den cavity or chamber. Two of 56 dens possessed long tunnels (>1 m in length) prior to widening into den cavities. By mid-summer, 44 of the dens had partially or fully collapsed, precluding measurements of some dimensions. Mean dimensions for grizzly bear dens were the following: entrance width = 60.4 cm ($SE = 2.1$, $n = 27$), entrance height = 55.2 cm ($SE = 2.4$, $n = 24$), cavity width = 140.3 cm ($SE = 6.3$, $n = 26$), cavity height = 82.2 cm ($SE = 3.3$, $n = 13$), den length = 261.4 cm ($SE = 13.0$, $n = 29$). Choice of

den aspect was nonrandom ($\chi^2 = 12.4$, $d.f. = 3$, $P < 0.01$, $n = 56$), with majority of dens facing south (25), followed by west (13), east (10), and north (8). All dens were located on steep slopes ($\bar{X} = 25.3^\circ$, $SE = 1.2$, $n = 55$).

Dens were constructed under cover of dwarf birch more than any other plant species. Dwarf birch was present at 84% of 52 den sites for which vegetation characteristics were recorded, and it was highest in mean percentage coverage around den entrances (Table 1). The roots of dwarf birch were observed to form ceilings of several den entrances and were sometimes visible in ceilings of cavity chambers. Other common species near den entrances included tundra berry shrubs (crowberry, cranberry, and blueberry) and several species of grasses and sedges (Table 1).

Analysis of excavation piles for 54 dens revealed substantial use of sandy areas for denning. Mean proportions ($\pm SE$) of soil components (Soil Classification Working Group 1998) at these den sites were 0.04 ± 0.01 boulders, 0.08 ± 0.01 cobble, 0.07 ± 0.02 gravel, 0.59 ± 0.05 sand, and 0.24 ± 0.05 silt-clay. Excavation piles contained lesser amounts of silt-clay and gravel than

TABLE 2.—Observed and expected number of dens in each habitat type for grizzly bears in the central Arctic, Northwest Territories, and Nunavut, Canada, 1995–1999.

Habitat of den	Proportion of habitat in study area	Number of dens in habitat	
		Observed	Expected
Lichen veneer	0.02	0	1.34
Esker habitat	<0.01	7	0.42
Wetland	0.08	0	4.35
Tussock–hummock	0.09	0	5.20
Heath tundra	0.32	23	17.60
Spruce forest	<0.01	5	0.14
Bedrock	0.04	0	1.94
Riparian tall shrub	<0.01	3	0.17
Birch seep	0.01	5	0.59
Heath–boulder	0.16	11	8.66
Heath–bedrock	0.11	1	6.13
Boulder field	0.15	0	8.47

sand. Cobble and boulders in excavation piles were common, of which some boulders were very large (>50 cm diameter).

Thirty-seven dens contained substantial amounts of nest or bedding material, which we observed bears gathering together immediately prior to entering dens. Bedding material was often, but not always, removed from den cavities onto excavation piles, presumably upon exit by bears. This leads us to believe that bedding material may have been used to plug den entrances once bears entered dens, in addition to providing a sleeping nest for bears within dens, or a bed on which to rest following den emergence when snow still persists. Bedding material was composed primarily of mats of crowberry, dwarf birch, and moss.

Denning habitat.—Bears entirely avoided denning in 5 of the 12 major habitat types available to them (wetlands, tussock–hummock, lichen veneer, boulder fields, and bedrock). Esker habitat, which previously had been regarded as a major denning habitat for barren-ground grizzly bears (Banci and Moore 1997; Mueller 1995), accounted for 7 of 56 den sites (Table 2). The remaining dens were located in typical heath tundra habitat, tall shrub riparian habitat, birch seep, spruce forest, heath tundra habitat with >30% boulder content, and heath tun-

dra habitat with >30% bedrock content. One den was located in a nonvegetated sand embankment adjacent to the Hood River. Compared with the proportional availability of habitat types in 3 Landsat TM images covering study area (Table 2), selection of denning habitat by bears was significantly different from random ($G = 127.7$, $d.f. = 6$, $P < 0.0001$). Comparison of Bonferroni confidence intervals indicated that esker habitat was selected more than expected by chance ($0.10 > P > 0.05$). In addition to those habitats in which no dens were found, heath tundra with >30% bedrock content was avoided for denning ($P < 0.05$).

DISCUSSION

Duration of denning may have adaptive significance for grizzly bears; however, mechanisms that drive and control when and for how long grizzly bears den are unclear. Environmental factors are likely involved as evidenced by lengthening of den periods along latitudinal and elevation gradients (Smith et al. 1994). For example, mid-October dates of den entrance and late-April dates of den emergence in the central Arctic are similar to those of barren-ground grizzly bears inhabiting the Tuktoyaktuk Peninsula and Richards Island, Northwest Territories (Nagy et al. 1983), and the

Brooks Range (Reynolds 1980; Reynolds et al. 1976) and Arctic National Wildlife Refuge (G. W. Garner et al., in litt.) in Alaska. These denning periods are considerably longer than for southern and Pacific-coastal grizzly bear populations. Grizzly bears inhabiting the East Front of the Rocky Mountains, Montana, enter dens in early November (median = 7 November, $n = 45$) and emerge from dens near 7 April ($n = 43$ —Aune 1994), a full 2 and 3 weeks after and before den entrance and emergence, respectively, of bears in the central Arctic. Males and females on Chichagof and Admiralty Islands, Alaska, enter dens an average of 1–2 weeks later than bears in the central Arctic, although dates of den emergence are similar to those of this study (Schoen et al. 1987). The latest dates of den entrance are found for grizzly bears on southwest Kodiak Island, Alaska, where mean dates of den entrance for males and females are in mid-November and early December, respectively (Van Daele et al. 1990).

Environmental factors influencing onset and duration of dormancy in bears may include specific weather conditions such as snowfall (Craighead and Craighead 1972), temperature (Rogers 1987), and scarcity of food. Milder winters, for example, may result in later dates of den entry or earlier than usual dates of den emergence, or even in no dormancy at all as on Kodiak Island (Van Daele et al. 1990). In this study, mean temperature for May in 1997 at Contwoyto Lake weather station in central study area was 0.6°C warmer than in May 1996. Both male and female grizzly bears emerged from dens significantly earlier in 1997 than 1996, possibly as a result of above-average temperatures in spring 1997. Physiological factors linked to physical condition may also indicate readiness for denning or emergence. In addition, age, which is related to body size, may influence duration of denning. For example, older and larger males likely den for shorter periods of time than

subadults. In this study, however, subadult sample sizes were too small to measure an effect. Further, some endogenous control related to photoperiod may initiate a metabolic shift toward or from dormancy (Folk et al. 1976). Most likely, a combination of abiotic and biotic stimuli influence when it is appropriate for grizzly bears to enter and emerge from dens.

Concurring with most studies on grizzly bear denning habits, males in this study entered dens later and emerged earlier than females (Craighead and Craighead 1972; Craighead et al. 1995; LeFranc et al. 1987; Reynolds et al. 1976; Schoen et al. 1987; Van Daele et al. 1990). Studies with larger sample sizes than those presented here were able to show clear differences between dates of den emergence for females with and without cubs, especially when single females were compared with females with cubs-of-the-year (Schoen et al. 1987; Van Daele et al. 1990). For grizzly bears, males generally emerge 1st from dens, followed by single females and females that entered dens with young, followed by females with cubs-of-the-year (Craighead and Craighead 1972; Craighead et al. 1995; LeFranc et al. 1987; Pearson 1975; Schoen et al. 1987). Differences in duration of denning among males and females may result from differences in metabolic rates. Male bears, being relatively larger and with lower metabolic rates than females, likely have less need than females to spend time in protective dens to maintain lean body mass during winter. Upon emergence, females with cubs-of-the-year may require more time to lead young away from safety of den than do females with yearlings or older cubs. There is also likely some advantage for females with cubs-of-the-year to suckle their young and allow them to grow within the den for as long as possible before emerging. Adult grizzly bears do not appear to require food immediately after leaving dens, and may be anorectic for up to 3 weeks post-

emergence (Nelson et al. 1983). We suspect that a female with cubs-of-the-year will remain in or close to her den until she is forced to leave the den in search of food herself, which may not be necessary until weeks after bears of different reproductive status have left their dens.

In addition to timing and duration of denning, choice of den site may have adaptive significance for grizzly bears. Grizzly bears use stored fat to survive during winter, and ability to minimize loss of body fat during dormancy in part determines a bear's ability to survive during winter (Folk et al. 1972). Apart from decreasing metabolic rate, grizzly bears can minimize energy loss to environment during dormancy by choosing the most appropriate sites for denning. The best sites for denning may depend on several factors, including den aspect, slope, and habitat characteristics such as vegetation cover and soil substrate.

Generally, the southern aspect of den entrances observed in this study agree with results of previous accounts of grizzly bear dens in the Arctic (Banci and Moore 1997; Mueller 1995; Reynolds et al. 1976). A southern aspect may take advantage of radiant heat from sunlight in spring and fall and northerly prevailing winds during winter, the latter of which can produce large snow banks on lee slopes to the south. Large snow banks covering den entrances likely help protect and insulate dens from the very cold temperatures experienced in the study area during winter.

The average slope into which dens of study animals were excavated was steep (>25%). Dens may be easier to dig on steep slopes, where soil may be exposed early in spring to sunlight and warm ambient air resulting in a deeper layer of thawed soil above permafrost than in more level areas. Reynolds et al. (1976) observed that 75% of 52 grizzly bear dens in the eastern Brooks Range, Alaska, were excavated in well-drained areas above the permafrost

layer. Natural caves accounted for the remainder of dens (Reynolds et al. 1976). In addition, den excavation on steep slopes may allow for dens to be constructed on near-horizontal or even upward-sloping planes, creating a warm-air trap in nest cavities (Harding 1976).

Steep, southerly-facing slopes also often produce well-developed patches of dwarf birch and berry-producing shrubs. In this study, dwarf birch and crowberry had the highest percentage coverage of any plant species around den entrances. The roots of these shrubs may add to the structural integrity of den cavity ceilings. Mats of crowberry were also the main component of insulating bedding material found in the majority of grizzly bear dens. The high presence of grasses around dens in this study may be attributed to the colonizing abilities of these plants after disturbance.

Grizzly bears in this study appeared to den in mainly sandy soil, sometimes with silt-clay and cobble content. Sandy soils may provide better insulation than very fine silty or clayey soils because of lower bulk density resulting in higher levels of trapped air. Gravel may be too loose for construction of structurally sound dens.

Although few dens were constructed in eskers (Table 2), esker habitat was selected more than predicted. Typical heath tundra, heath tundra with >30% boulder content, spruce forest, tall shrub riparian areas, and birch seep areas were used as expected. Because the pooled sample size of dens was small ($n = 55$), power for Bonferroni confidence intervals in our habitat analysis was low ($1 - \beta < 0.80$). Large contributions of these habitat types to the G -statistic, however, are suggestive that bears might prefer to den in spruce forest, tall shrub riparian, and birch seep habitats, but the statistical power needed to demonstrate this pattern is lacking. Not surprisingly, no dens were observed in tussock-hummock meadows, wetlands, or boulder and bedrock fields,

likely because of poor digging substrate, poorly drained soils, or both. Heath tundra with >30% bedrock may have been avoided as denning habitat because of shallow digging substrate.

Previous studies (Banci and Moore 1997; Mueller 1995) suggested that large glacio-fluvial deposits such as eskers were extremely important for grizzly bear denning habitat. For example, Mueller (1995) reported that 29 of 32 bear dens encountered during surveys (91%) were located in eskers, when esker habitat was expected to make up 1.5% of the surrounding landscape. Banci and Moore (1997) reported finding 34 of 52 bear dens (65%) in eskers, mainly from unknown and uncollared bears. Such exclusive use of esker habitat for denning is not supported by data obtained from radio-collared grizzly bears in this study. Although bears are denning in eskers or other glacial-fluvial habitats such as kames and drumlins, and they are doing so to an extent greater than expected by chance, use of eskers reported here is considerably less than what has previously been reported in the central Arctic.

One reason for disparity between results obtained in this study and those of Mueller (1995) and Banci and Moore (1997) may lie in differences in methods of data collection. Mueller (1995) and Banci and Moore (1997) relied heavily on ground and aerial searches of older (>1 year) den sites of uncollared, unknown grizzly bears. Based on differences in visibility of den sites among different habitats, however, probability of identifying den sites from aerial and ground searches likely differs among habitats searched. Dens in eskers, for example, are easier to identify from ground or air than dens in heavily vegetated habitats such as tall shrub riparian areas. Bias in ability to correctly identify den sites equally among all habitats available to bears questions the validity of results of den surveys based on searching for dens of unknown bears. Fur-

ther, habitat types were not equally searched, according to availability, during den surveys by both Mueller (1995) and Banci and Moore (1997). Mueller (1995), for example, spent 53% of the time searching relatively rare esker habitat for dens. Not surprisingly, Mueller's (1995) data was biased toward finding dens in eskers. By using radio-telemetry to collect data on denning habits of grizzly bears, we eliminated such biases in our study.

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