BLACK BEAR DENNING ECOLOGY IN INTERIOR ALASKA

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Abstract: From 1988 to 1991 we observed the denning activity of 27 radio-collared black bears (*Ursus americanus*) at 57 dens on the Tanana River Flats, near Fairbanks, Alaska. This is the northernmost population of black bears studied using radio telemetry, and nears the northern extreme of their range. We compared differences in den chronology, morphology, and habitat use, among sex, age, and reproductive classes. All bears pooled across all years gave a mean den entry date of 1 October, a mean emergence date of 21 April, and a mean den period of 205 days. Females denned earlier (30 Sep vs. 4 Oct), emerged later (23 Apr vs. 15 Apr), and had longer den periods (208 days vs. 195 days) than males. No significant differences were observed in denning chronology between adults and subadults, or among female reproductive classes. Differences in den characteristics between sex, age, and female reproductive classes were generally insignificant, except that males had larger dens than females, and females denning with young had the largest dens among the female reproductive classes. Most dens were excavated (83%, n = 41), and all contained nesting material. Reuse was low (18%, n = 34) and 10 dens (29%) were flooded to varying levels. Bears significantly favored willow/alder and black spruce habitat types for den sites, avoiding marshland and heath meadow habitat types.

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Mechanisms that drive and control denning behavior in black bears are still unclear, largely due to the extreme variability exhibited by bears across a wide range of climates. Environmental factors clearly are involved as evidenced by the lengthening den periods along latitudinal and elevational gradients (Table 1). Specific weather conditions have been implicated, such as snowfall (Jonkel and Cowan 1971), temperature (Rogers 1987), precipitation (Hellgren and Vaughan 1989), or some combination of these (Lindzey and Meslow 1976, Johnson and Pelton 1980, Novick et al. 1981, Rogers 1987). There also appear to be some physiological factors that are keyed to physical condition and the readiness for denning (Lindzey and Meslow 1976, Schwartz et al. 1987). Ultimately, some endogenous control related to photoperiod may initiate a metabolic shift towards dormancy, irrespective of actual denning behavior (Folk et al. 1976, Johnson and Pelton 1980, Nelson et al. 1983, Nelson and Beck 1984). The simplest explanation is that a reduced food supply, correlated with increasingly long winters, results in increasingly long denning periods, but this concept becomes muddled when data from milder climates are included. Researchers in those areas find that den periods do shorten, but not necessarily concomitant with reduced food availability, and in a few areas some bears den while others remain active all winter (Lindzey and Meslow 1976, Alt 1977, Hamilton and Marchington 1980, Novick et al. 1981, LeCount 1983, Hellgren and Vaughan 1987, Graber 1990). This seemingly contradictory evidence indicates that denning is probably controlled by an interaction of several of these factors, and perhaps other, as yet unidentified ones. One step in understanding the controlling mechanisms behind denning black bears is to determine the limits of variability from the extremes of the black bear's range.

We investigated the denning ecology of black bears located near the northern extreme of their range in interior Alaska (Manville and Young 1965). Several studies conducted on black bear in southcentral Alaska (Modafferi 1982; Smith 1984; Schwartz et al. 1983, 1987; Miller 1987, 1990) and Hatler's (1967) work in interior Alaska provide a broad perspective of black bear ecology under similar environmental conditions. Specifically, we tested the following null hypotheses: (1) denning chronology will not vary significantly among sex, age, and reproductive classes; (2) den characteristics will not vary significantly among sex, age, and reproductive classes; and (3) den-site habitat selection will be in proportion to habitat availability.

This study comprises part of a cooperative research project between the U.S. Army and the Alaska Department of Fish and Game (ADF&G) to establish baseline information on population dynamics of black bears on military land in interior Alaska (Hechtel 1991). Special thanks to J. Kerns (U.S. Army, Fort Wainwright Natural Resources Office) who initiated and funded this project, N. Mosso (ACWRU) who administered the paperwork, provided equipment, and much needed moral support, and to H. Staaland (Department of Biology and Nature Conservation, Agricultural University of Norway) for providing office space and logistic support during analysis and manuscript preparation. The Institute of Arctic Biology provided needed equipment and logistical support. P.

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Table 1. Variation in black bear denning chronology and den types, listed in descending order of the approximate total denning period. Dates not specified in the publications were calculated from available data and represent approximate overall means.

	Approximate mean dates				Den type (%)[a]					
Location	Entrance	*n*	Emergence	*n*	Exc	Nat	Tre	Gnd	Oth	Reference
Susitna, Alas.	9 Oct	116	6 May	116	56	41	3	--	--	Schwartz et al. (1987)
Interior Alas.	1 Oct	41	21 Apr	26	83	5	--	12	--	This study
Kenai, Alas.	18 Oct	164	19 Apr	164	96	3	1	--	--	Schwartz et al. (1987)
Mont.	Late Oct	127	Early May	127	14	72	--	10	3	Jonkel and Cowen (1971)
Colo.	25 Oct	128	5 May	55	35	62	--	3	--	Beck (1986)
Id.	20 Oct	43	20 Apr	23	72	28	--	--	--	Beecham et al. (1983)
Alta.	18 Oct	33	7 Apr	31	95	5	--	--	--	Tietje and Ruff (1980)
Ont.	27 Oct	95	12 Apr	95	87	7	1	3	--	Kolenosky & Strathearn (1987)
Minn.	Late Oct	85	Mid Apr	78	--	--	--	--	--	Rogers (1987)
Me.	7 Nov	53	23 Apr	47	33	15	--	52	--	Hugie (1982)
Yellowstone	Early Nov	6	Mid Apr	6	17	33	--	--	50	Barnes and Bray (1967)
Mitkof Isl.	11 Nov	11	13 Apr	11	--	69	31	--	--	Erickson et al. (1982)
Ariz.	16 Nov	51	6 Apr	51	76	24	--	--	--	LeCount (1983)
Wash.	10 Nov	11	21 Mar	10	--	--	--	--	--	Lindzey and Meslow (1976)
N.Y.	28 Nov	62	2 Apr	38	--	--	--	--	--	O'Pezio et al. (1983)
Mich.	Mid Dec	31	Mid Mar	31	23	16	--	61	--	Manville (1987)
Tenn.	Mid Dec	12	Late Mar	12	--	14	64	21	--	Pelton et al. (1980)
Calif.	17 Dec	39	30 Mar	39	--	--	--	--	--	Graber (1990)
Pa.	Late Dec	17	Mar	17	--	--	--	--	--	Alt (1977)
Pa.	--	43	--	43	30	39	--	31	--	Carr (1980)
Ark.	Late Dec	38	Late Mar	38	--	--	74	21	--	Smith (1986)
N.C.	Late Dec	5	Late Mar	5	--	--	20	80	--	Hamilton & Marchington (1980)
N.C.-Tenn.	--	95	--	95	12	24	56	7	--	Wathen et al. (1986)
Va.-N.C.	29 Dec	23	30 Mar	23	41	10	3	48	--	Hellgren and Vaughan (1989)
Tenn.	5 Jan	17	7 Apr	14	--	26	54	20	--	Johnson & Pelton (1980, 1981)

[a] Exc = excavated dens; Nat = natural cavities; Tre = Tree dens with elevated entrances; Gnd = ground dens; Oth = any other den types.

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STUDY AREA

The study was conducted on the Tanana River Flats, a 2,000-km^2 area located immediately south of Fairbanks, Alaska (64° 50'N × 148° 00'W) extending from the Tanana River south. Due to limited access, most activity was concentrated in the U.S. Army's Tanana Flats Training Area (TFTA), located in the northcentral portion of the Flats. The study area was bordered on the north, east, and west by the Tanana River which provides a substantial barrier to casual movements by bears.

The topography was flat with elevations ranging from

120 to 185 m over most areas. Three widely scattered hills offer the only relief with elevations of 282, 287, and 429 m.

Average annual temperature for the Fairbanks area was -3°C, with 29 cm of precipitation and an average of 154 cm of snowfall. Monthly average temperatures during the denning period (Oct to Apr) ranged from −24° C (Jan) to −1°C (Apr), with extremes of −54°C and 23°C (NOAA Monthly climatological summaries, Fairbanks International Airport).

Vegetation is broadly characterized as interior muskeg with black spruce (*Picea mariana*) occurring throughout. Specific habitat classifications for the Tanana Flats basically follow a vegetation map prepared by Coady (1973) and described by LeResche et al. (1974). Additionally we subdivided 1 spruce habitat into separate white spruce (*P. glauca*) and black spruce habitats. The 6 habitat types are identified by their dominant vegetation: (1) marshland—marshes, shallow ponds and their aquatic margins, and shallow streams where movement of water is slow enough to allow emergent vegetation; (2) heath meadow—("muskeg" or "tussock tundra") low shrubs and widely scattered trees in which scattered patches of shrub birch (*Betula glandulosa*) are common; (3) willow/alder—willow (*Salix* spp.) and alder (*Alnus* spp.) thickets; (4) birch/aspen—paper birch (*B. papyrifera*), quaking aspen (*Populus tremuloides*), and cottonwood (*P. balsamifera*) forests; (5) black spruce/tamarack—black spruce, and tamarack (*Larix laricina*) forests; and (6) white spruce—white spruce forests (Coady 1973).

METHODS

Bear Capture

Bears were captured using Aldrich leg-hold snares (Flowers 1977), barrel traps (Schwartz et al. 1983), or darted from helicopters. Bears were anesthetized with either a Ketamine HCL/Xylazine (Ketaset/Rompun) combination or with Tiletamine HCL/Zolazepam HCL (Telazol) combination. Adult bears were fitted with standard radio collars and subadults with special "break-away" collars (Telonics, Mesa, Ariz). Captured bears had standard morphological measurements taken, a premolar tooth extracted for aging (Willey 1974), numbered ear-tags installed, and a lip tattooed. These procedures complied with the American Society of Mammalogists' guidelines (1987) and were approved by an independent University of Alaska Fairbanks animal welfare committee.

Radiotracking

Radiotracking began as soon as possible after the collars were attached. Locations were obtained from the air at 1 to 2 week intervals and for each location we recorded habitat type and the activity of the bear.

Den Chronology

Denning activity was determined from aerial reconnaissance, but because logistics and weather precluded daily flights, most den entry and emergence dates were estimates. Entrance dates were estimated by taking the median between the last nondenned observation and the first denned observation. Emergence dates were estimated from the median of the last denned and the first emerged observations. Bears were considered emerged when first observed, even though they may have remained in the den area. Den periods refer to the total number of days spent in the den. Bears with more than 24 days between locations were excluded from analysis.

Statistical tests compare years, sexes, ages (adult versus subadult), and female reproductive classes at den entry (pregnant, with cubs or yearlings, barren adults, and subadults). Bears ≥4 years old (the earliest age of conception) at the time of den entrance were considered adults. Reproductive condition was assessed post-hoc by visually identifying females that emerged in the company of offspring. As a result, any adult females losing cubs prior to den emergence would have been classified as barren. Because assumptions of normality were not met, the Kruskal-Wallace and Mann-Whitney *U* tests were used to examine differences among the various groups (Wilkinson 1988).

Den Characteristics

Den sites were visited during March or April, and the den characteristics were described following Schwartz et al. (1983). Bears were sedated with Telazol injected using a jab stick, removed from the den, and handled as previously described. After measuring the den, the bear was returned to the den and the entrance was resealed with snow. A radio transmitter was left at the den site enabling us to relocate the den the following summer.

During summer, den sites were revisited to describe the vegetation, collect soil samples, and ascertain whether the den had been used prior to the preceding winter. Soil samples were collected from either the floor or wall of the den or from the tailings pile. Samples were placed in plastic bags and frozen upon return to the laboratory.

Soil samples were thawed at room temperature and well mixed. A subsample ranging from 10 to 30 g was removed and initially air dried, followed by drying in an oven at 65°C until weight was constant. Dried samples were placed in a muffle furnace at 400°C for 22.5 hours to remove the organic component. Percent organic content was then calculated. A second subsample was removed and similarly dried prior to mechanical analysis. The Bouyoucos hydrometer method (Bouyoucos 1962) was used for particle size determination of den soils. A 50-g sample of dried and sieved soil was used for this standard analysis, and for those samples having a high organic content, the dry weight of the sample was corrected by the amount of organic matter lost from the peroxide treatment. Following calculation of the percentage of sand, silt, and clay in each sample, a textural triangle was used to classify the soil. Soil moisture content was not calculated because of variability in the condition of dens at the time of collection. Some dens had flooded or contained standing water, therefore some samples were saturated and actually obtained under water, while others were very dry. This variability precluded meaningful analysis, although soil moisture content could be a factor in den selection by bears in a study area that is characterized by relatively flat and low-lying habitats.

Statistical tests for den characteristics compare differences in den characteristics among years, sex, age classes, and female reproductive classes. Most variables were normally distributed except for entrance width, chamber volume, and nest length, which were log-normally distributed. Multivariate Analysis of Variance was used to test for differences ($P \leq 0.05$), followed by post-hoc tests of specific effects using SYSTAT's MGLH procedure (Wilkinson 1988).

Den entrance aspects were divided into 5 categories, four-90° divisions, each centered on a compass direction (N, S, E, and W), plus a fifth category of flat (no aspect). Chi-square was used to test for differences between observed frequencies and expected, assuming equal distribution within the 5 categories ($P \leq 0.05$).

Den-Site Habitat

Habitat types delineated on the vegetation map were visually compared to 1986 infrared aerial photos and extensively verified on the ground to ensure accuracy. Percent of available habitat was determined by measuring the areal coverage of each habitat type within bear home ranges, using a digital planimeter on a 1:15,840 scale map (McDonald et al. 1991). The den-site habitat types were summed for all bears and then compared with the percentage available within these same bears' home-range polygons. A Chi Square test was used to test the null hypothesis of no difference between use and available habitats considering all habitats simultaneously ($P \leq 0.05$), then a 95% Bonferroni joint confidence interval was used to test for differences considering each habitat individually (Neu et al. 1974, Byers et al. 1984).

RESULTS

From 1988 to 1990, we aerially located 57 dens of 27 individual bears (16 F and 11 M) and we visited 41 dens on the ground to obtain measurements.

Den Chronology

Mean time intervals between radio locations used to establish den entry and emergence dates for all years were 10.9 $\pm$ 7.5 days (range 0-24 days). If den entrance dates for 1990-91 (a year with difficulties obtaining flights) are not included, the mean interval drops to 7.9 $\pm$ 4.8 days (range 0-16 days) and the statistical differences observed remain valid.

Den entry was significantly earlier and the total den period was significantly longer in 1988-89 than other years (Table 2). Sample sizes for the various categories vary, because we failed to observe the entrance and/or emergence of some bears. Our sample may be biased towards females and bears with an earlier entry date, a later emergence date, and a longer total den period. For example, we know that 11 male and 3 female bears had shorter denning periods then those we reported but they were excluded from analysis because they entered dens after our final flight in the fall and/or emerged prior to our first flight in the spring.

Differences in denning chronology between the sexes show a consistent pattern of males denning later than females (4 Oct vs. 30 Sep), emerging earlier (15 Apr vs. 23 Apr), and having a shorter total den period than females (195 days vs. 208 days) (Table 2). Inclusion of the 11 males, and 3 females with shorter, though unrecorded, den periods would increase the observed difference between the sexes.

Differences in denning chronology between adult and subadult black bears were generally insignificant (Table 2). Adults denned significantly earlier than subadults in 1989; however, our sample includes few adult males which would probably reduce this difference.

Among the female reproductive classes, pregnant females denned first and had the longest den period, followed by females with young, subadults, and then

Table 2. Comparisons of Tanana Flats black bear denning chronology among years, sex, age, and female reproductive classes. Asterisks designate a significant difference between groups.

	Den entry dates[a]				Den emergence dates[b]				Den period (days)			
Group	Mean	SD	*n*	Range	Mean	SD	*n*	Range	Mean	SD	*n*	Range
1988-89	22 Sep*	5	7	19 Sep-30 Sep	23 Apr	2	9	19-24 Apr	216*	3	6	209-217
Males	29 Sep*	2	2	27 Sep-30 Sep	22 Apr	4	2	19-24 Apr	209*	0	1	209
Females	19 Sep*	0	5	19 Sep	24 Apr	0	7	24 Apr	217*	0	5	217
Adult	19 Sep	0	3	19 Sep	24 Apr	0	4	24 Apr	217	0	3	217
Subadult	24 Sep	6	4	19 Sep-30 Sep	23 Apr	2	5	19-24 Apr	214	5	3	209-217
1989-90	3 Oct	5	18	26 Sep-09 Oct	19 Apr	7	17	10-26 Apr	201	9	14	187-212
Males	6 Oct	5	4	05 Oct-09 Oct	13 Apr*	3	5	10-17 Apr	190*	2	3	181-191
Females	2 Oct	6	14	26 Sep-09 Oct	23 Apr*	5	12	10-26 Apr	204*	8	11	187-212
Adult	1 Oct*	5	12	26 Sep-05 Oct	19 Apr	7	12	10-26 Apr	203	10	9	187-212
Subadult	8 Oct*	4	6	05 Oct-09 Oct	21 Apr	6	5	14-26 Apr	196	5	5	190-203
1990-91	3 Oct	11	16	25 Sep-19 Oct		No data				No data		
Males	5 Oct	12	6	25 Sep-19 Oct		No data				No data		
Females	2 Oct	12	10	25 Sep-19 Oct		No data				No data		
Adult	3 Oct	11	16	25 Sep-19 Oct		No data				No data		
Subadult		No data				No data				No data		
Pooled yrs	1 Oct	9	41	19 Sep-19 Oct	21 Apr	6	26	10-26 Apr	205	10	20	187-217
Males	4 Oct	8	12	25 Sep-19 Oct	15 Apr*	5	7	10-24 Apr	195*	10	4	188-209
Females	30 Sep	9	29	19 Sep-19 Oct	23 Apr*	4	19	10-26 Apr	208*	9	16	187-217
Adult	1 Oct	9	31	19 Sep-19 Oct	21 Apr	7	16	10-26 Apr	207	10	12	187-217
Subadult	2 Oct	8	10	19 Sep-09 Oct	22 Apr	4	10	14-26 Apr	203	11	8	190-217
Pooled yrs	-female reproductive classes											
Pregnant	23 Sep	4	5	19 Sep-26 Sep	24 Apr	1	6	24-26 Apr	213	4	5	210-217
W/cub, yrl	25 Sep	1	5	24 Sep-26 Sep	26 Apr	0	2	26 Apr	212	0	2	212
Barren	3 Oct	10	13	19 Sep-19 Oct	20 Apr	7	5	10-26 Apr	202	12	4	187-217
Immature	2 Oct	10	6	19 Sep-09 Oct	25 Apr	1	6	24-26 Apr	207	10	5	197-217

[a] Median of last active observation and first denned observation.
[b] Median of last denned observation and first active observation.

barren adult females (Table 2). Emergence started with barren females, followed by pregnant (at den entry) females, subadults, and females with yearlings.

Den Characteristics

Den Construction.—Thirty-four of the 41 dens we visited (83%) were excavated, 5 (12%) were on the surface, and 2 (5%) were located in natural cavities. Nine excavations had tunnels (90 cm ± 10) leading into the den, the others opened more or less directly into the sleeping chamber. Three of the surface dens were massive piles of grasses and sedges that the bears collected and then tunneled into. Two surface dens were open nests with an ice chamber created by snow as it melted away from the bears. One of the natural cavities was created when the roots of a partially toppled white spruce created a large (4 × 6 m) subterranean chamber. The other had been created by water eroding a tunnel along the bottom of a ravine. Six of 34 (18%) dens revisited the following summer showed evidence of reuse (vegetation growing on the den walls or tailings, indicating the existence of the den for greater than 1 year). Most dens were relatively stable (only 3 had collapsed), but 10 dens (29%) had flooded by the following June. All dens had nests, averaging 80% (± 24, n = 34) chamber coverage, and composed mainly of grasses and sedges.

Soil.—Analysis of soil samples from 27 dens revealed the following particle size profile (mean ± SD): clay (13.1% ± 7.8), silt (55.6% ± 18.8), and sand (30.6% ± 19.8). This is classified within the textural triangle as silt-loam (Bouyoucos 1962). Organic content was 10.5% ± 9.9, and the mean depth to frozen ground was 55.6 cm ± 14.6 (n = 25). The particle-size profile did not significantly differ from the values reported for Tanana Series Soils in a general survey of the Fairbanks area (Rieger et al. 1963).

Den Measurements.—Comparisons of the measured variables (Table 3) among years showed that only nest thickness varied, with 1988-89 nests being significantly thicker (18 cm ± 8, n = 9) than those in 1989-90 (12 cm ± 5, n = 21) and 1990-91 (8 cm ± 3, n = 9). Comparisons between sexes showed males to have higher den entrances (48 cm ± 12, n = 13 vs. 38 cm ± 8, n = 25), and longer dens (188 cm ± 57, n = 12 vs. 147 cm ± 44, n = 25) than females. There were no significant differences between adults and subadults. Comparisons among female reproductive classes showed den length for females with offspring to be significantly longer (188 cm ± 28, n = 5) than barren adults (138 cm ± 25, n = 8) or subadults (117 cm ± 24, n = 7). They were also longer than dens of pregnant females (163 cm ± 70, n = 5) but this difference was not significant.

Aspect.—Even though the study area is flat, many dens were located in areas with small elevated humps allowing the aspect of entrance holes to be determined. Thirty-eight percent (n = 13) opened towards the north, 32% (n = 11) were flat with no aspect, 18% (n = 6) faced west, 9% (n = 3) faced east, and 3% (n = 1) faced south. Assuming equal availability, north-facing den entrances were used significantly more than expected. The other directions and flat aspect were not significantly different from expected.

Den-Site Habitat.—All but 3 dens were located on the Tanana Flats. One bear moved across the Tanana River to hills northwest of the study area, and 2 bears denned on Tanana River islands.

Analysis of habitat availability measured within each bear's home range, showed no significant differences among years or groups. Samples of den-site habitat were insufficient for individual group comparisons. Analysis of all dens versus habitat availability was significant for all habitat types considered simultaneously. Subsequent 95% joint confidence intervals revealed a preference for the willow/alder and black spruce habitats, and an avoidance of marshland and heath meadow habitats (Fig. 1). There was no difference between use and availability in the birch/aspen or white spruce habitat types.

Table 3. Tanana Flats black bear den characteristics. Asterisks indicate significant differences for the indicated variable within that particular subgroup of bears.

					Significance			
Den characteristic	Mean (cm)	SD	n	Range (cm)	Yrs	Sex	Age	Repro
Entrance height	42	10	38	28-76	-	*	-	-
Entrance width	43	10	38	19-62	-	-	-	-
Entrance area (m^2)	0.2	0.1	38	0.1-0.4	-	*	-	-
Chamber height	63	17	39	32-105	-	-	-	-
Chamber width	106	28	39	41-169	-	-	-	-
Chamber length	139	50	37	71-295	-	-	-	-
Chamber volume (m^3)	1.0	0.7	37	0.2-3.5	-	-	-	-
Den length	160	52	37	81-295	-	*	-	*
Nest thickness	12	6	39	3-30	*	-	-	-
Nest length	98	38	39	41-232	-	-	-	-
Roof thickness	23	8	15	5-36	-	-	-	-

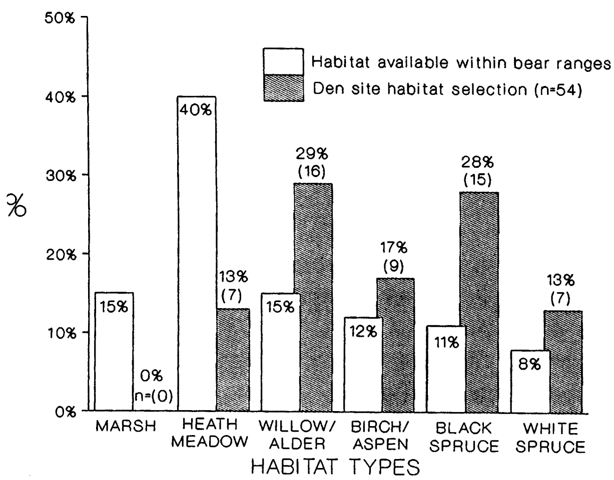

Fig. 1. Den-site habitat selection for Tanana Flats black bears. Marsh and heath meadow habitat types were used significantly less than available. Willow/alder and black spruce habitats were used significantly more than available.

DISCUSSION

Den Chronology

The observed denning periods for black bears in interior Alaska are generally consistent with other bear populations in Alaska and are among the longest reported. In the Susitna River Basin, in southcentral Alaska, the reported denning periods of 218 days for black bears (Schwartz et al. 1987) and 201 days for brown bears (Miller 1990) are the longest known den periods for each species. Our den periods of 205 days reflect both the earlier entrance and earlier emergence of the Tanana Flats population compared to these southcentral Alaskan bears. Earlier emergence is probably due to an earlier snowmelt in the low-lying Flats as compared to the mountainous terrain of the Susitna River Basin, and may be in response to den flooding (Alt 1984).

Annual comparisons reveal an earlier mean entry date for 1988 which, when coupled with later emergence, cause the total den period to be longer in 1988 also. Variation in date of den entry has been attributed to abnormal temperatures (LeCount 1983, Miller 1990), abnormal precipitation (Lindzey and Meslow 1976), variable food availability (Tietje and Ruff 1980, Beecham et al. 1983, Schwartz et al. 1987), or some combination of these factors (Lindzey and Meslow 1976, Johnson and Pelton 1980). Early den entrance on Tanana Flats did not correspond with any obviously significant differences in weather data among years (NOAA, monthly climatological data summaries). Temperature, precipitation, and snowfall were similar among years and there was no clear connection between den-entry dates and specific weather data. We have no data on food availability, but there was no obvious difference among years, and lowbush cranberries (*Vaccinium vitis-idaea*), a preferred food, (Hatler 1967, Smith 1984) were still available after bears had denned. Therefore the difference among years is probably a result of some combination of these factors or an artifact of the smaller sample size in 1988.

Comparisons of the separate bear classes generally agree with the trends observed in other populations. Our comparisons between sexes show a consistent trend of males denning last and emerging first, similar to most other studies (Jonkel and Cowan 1971, Lindzey and Meslow 1976, LeCount 1983, Schwartz et al. 1987). Comparisons of age classes showed generally insignificant differences though 1 group (entrance dates, 1989-90) showed adults to den significantly earlier than subadults. This is probably the result of our biased sample against adult males. Comparisons of female reproductive classes revealed no significant differences but they followed the same pattern as in most other studies (Tietje and Ruff 1980, Beecham et al. 1983, O'Pezio et al. 1983, Schwartz et al. 1987). Specifically, pregnant females denned first, followed by females with young, subadult females, and then barren adult females. Pregnant females also had the longest denning period followed by females denning with young, subadult females, and then barren adult females.

An extended denning period by pregnant females in harsh climates may be a conservation measure to mitigate the upcoming increased energy expenditure of parturition and lactation (Tietje and Ruff 1980). Once some minimum physical condition is attained, which enables successful reproduction (Rogers 1976, Alt 1989), then the energetic costs of denning may be less than the costs of continuing to forage under potentially adverse environmental conditions. Bears in the Tanana Flats may have difficulty extending their denning period because of the already shortened growing season, characteristic of this harsh climate. Females may therefore select their den sites with greater care or preparation such that their total energy loss over the denning season is reduced (Johnson et al. 1978, Pelton et al. 1980, Tietje and Ruff 1980). Limited evidence for this was found when 5 of our 9 "best" dens, (i.e., those that had been excavated with long tunnel entrances and with substantial amounts of additional nesting material) were dug by pregnant females or females with young.

Den Characteristics

Folk et al. (1972) found that radiant heat from the earth raised the temperature of an unoccupied, excavated den near Fairbanks, Alaska by 37°C over ambient air temperature. This would result in substantial energy conservation according to the model by Johnson et al. (1978), which found a 15% energy savings in a simulated closed-tree den over a surface-ground den in Tennessee. The insulative value of additional nesting material would allow even greater energy conservation by reducing conductive heat loss from the bear to the ground (Reynolds et al. 1976, Tietje and Ruff 1980). It is not surprising that in the Tanana Flats, where temperatures can reach −50°C for extended periods, most den sites were excavated and that all dens included nest material. Nests were actually thicker in 1988-89, but we hesitate to suggest that the bears in some way predicted the exceptionally cold winter that occurred. Many of the excavated dens had additional nesting material covering the dens and entrances. Three surface dens were composed entirely of accumulated nesting material and subsequent tunneling into the grass. One female, while denning with 3 yearlings, had constructed a huge pile of grass (approximately 2.5 m diam. × 1.5 m high) and then tunneled into the middle of the pile to construct the den chamber. It appears that black bears are able to adjust their den requirements to meet the environment they occupy by utilizing whatever materials are available.

While excavated dens appear to be favored, we point out that some bears denned quite successfully without the advantages of an excavated den. Because black bears on the Tanana Flats, with limited habitat options, can still create dens sufficient to withstand the most extreme environmental conditions, it seems unlikely that they would fail to do so in any other areas. Therefore, den sites, based on micro-site habitat suitability alone, are probably rarely, if ever, limiting. This is especially true for black bears occurring in areas where snowfall can provide additional insulative protection. Other factors, such as human disturbance (Johnson and Pelton 1981) and risk of predation (Alt and Gruttadauria 1984, Rogers and Mech 1981, Smith and Follmann 1993) may interact with denning requirements to create a limitation on available den sites.

Because of the flat nature of the study area, the reason for significant selection of north-facing den entrances is unclear. It is possible that even small changes in slope, if angled towards the north, may effectively delay snowmelt and thus extend occupation of the den.

Den-Site Habitat

Bears avoided the heath meadow habitat types probably because they are often wet bogs, with few trees for structural support, and dens may become flooded earlier in the spring. We did have some dens located in drier sections of heath meadows, usually under an isolated stand of tall shrubs or on a built up pile of nesting material. The selection for willow/alder and black spruce habitats can perhaps be explained by the use of their root systems for structural support of the den. Schwartz et al. (1987) reported a similar preference for black bears denning in the relatively flat Kenai Peninsula, Alaska.

CONCLUSIONS

We reject the null hypothesis that denning chronology will not vary between sexes and conclude that female black bears on the Tanana Flats den earlier and remain denned longer than males. We fail to reject the null hypotheses of no difference in denning chronology among age or female reproductive classes. We reject the null hypothesis that den characteristics will not vary significantly among sex, age, and reproductive classes and conclude that males have larger dens than females and females with cubs have the largest dens among females. We also reject the null hypothesis that den-site habitat selection will be in proportion to habitat availability because Tanana Flats black bears significantly favored black spruce and willow/alder habitats while avoiding marshland and heath meadow habitat types.

These results illustrate the denning ecology of the northernmost population of bears studied to date and are similar to the results of other Alaskan black bear studies. Managers can consider these results as suggesting the limits of possible responses from black bears when evaluating programs that may affect denning ecology of their local populations. Also it appears that evaluation of denning habitat on a micro-site scale is not justified unless other nonenvironmental factors are judged to be important. Large-scale habitat evaluation and, if necessary, seasonal protection from disturbances in the appropriate habitat types, is probably a more efficient means of ensuring adequate denning habitat availability.

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