WINTER DENNING OF BLACK BEARS IN EAST-CENTRAL ONTARIO

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Abstract: One hundred ten dens of 57 black bears (*Ursus americanus*) were examined in east-central Ontario from 1976 to 1980. Most bears denned within summer range boundaries. Entry dates ranged from 20 September to 29 November. Denning sequence was yearlings, pregnant females, solitary females, females with cubs, adult males, and subadults of both sexes. Bears that fed on acorns denned later than non-acorn feeders. Eighty-nine percent of dens (N = 110) were excavations below ground level, and 84% occurred on well-drained upland sites. Dens of individual bears in consecutive years were similar. There was no indication of den reuse. Cubs orphaned during the spring hunt constructed and lined dens similar to those of older bears. In 1 instance, a 2-year-old male was denned with an adult female and 2 newborn cubs. Thirty-three percent of yearlings and 11% of subadults abandoned dens due to investigator disturbance; young males abandoned dens more frequently than females. Emergence extended from 23 March to 1 May with a peak around 5–20 April. Males were the 1st group to emerge and females with cubs, the last. Adjustment of hunting seasons to harvest specific sex and age groups selectively during the fall would be only marginally successful due to the lengthy den entrance period and overlap of entrance times among groups. During the spring hunt, females with cubs could be afforded greater protection by closing the hunting season earlier.

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The black bear occurs throughout much of the forested regions of North America (Hall and Kelson 1959). The evolution of denning to circumvent unfavorable weather conditions and lack of food during winter (Johnson and Pelton 1980) is an adaptation contributing to the successful occupancy of diverse habitats throughout the continent (Hamilton and Marchinton 1980). Duration of winter denning is a function of latitude and varies from a few days or weeks in Mexico (Leopold 1959) to 6 or more months in Alaska (Rausch 1961). The importance of winter dormancy to the species' survival has prompted researchers to investigate denning ecology (Erickson 1964, Jonkel and Cowan 1971, Amstrup and Beecham 1976, Lindzey and Meslow 1976, Pelton et al. 1980, Tietje and Ruff 1980, Beecham et al. 1983, LeCount 1983) and the physiology of denning bears (Nelson et al. 1973; Folk et al. 1972, 1976, 1980; Craighead et al. 1976).

Specifics of site selection have been determined for various geographic areas, but details of denning in eastern Canada have never been examined. A knowledge of denning enhances understanding of local habitat requirements and allows predictions about the impact of future resource development and changing land use patterns on specific black bear populations. Temporal and behavioral differences in denning by various cohorts may permit selective harvests by adjustment of seasons (Lindzey 1981).

This report describes pre-denning and post-denning activities, characteristics of den sites, and denning chronology of black bears in the boreal-deciduous forest of east-central Ontario.

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STUDY AREA

The 233-km^2 primary study area is 40 km north of the eastern edge of Lake Nipissing at approximately 46°45′ North latitude and 79°20′ West longitude (Fig. 1). Typically morainic sand and gravel deposits overlie Archean granite and granitized sedimentary gneisses that occasionally protrude to a height of 30 m (Boissonneau 1968). Lying within the Great Lakes-St. Lawrence Forest Region (Rowe 1972), the area contains elements of deciduous and boreal forests. The original forest, dominated by red and white pines (*Pinus resinosa, P. strobus*), was altered by intensive logging shortly after the turn of the century. Recently, selective logging and fire have produced a diverse habitat containing a mixture of deciduous and coniferous trees ranging from 0 to 70 years in age.

The climate of the area is broadly classified as humid continental (Atlas of Canada 1957) with cool summers and no dry season. Based on the period 1941–78, mean temperatures during January and July for North Bay were −12.8 C and 18.3 C, respectively. Extremes ranged from −40.0 to 33.3 C. Average total precipitation was 98.8 cm and mean snowfall 284.0 cm. Approximately 188 days were frost-free each year (Annual Meteorological Summary, North Bay Airport, 1978).

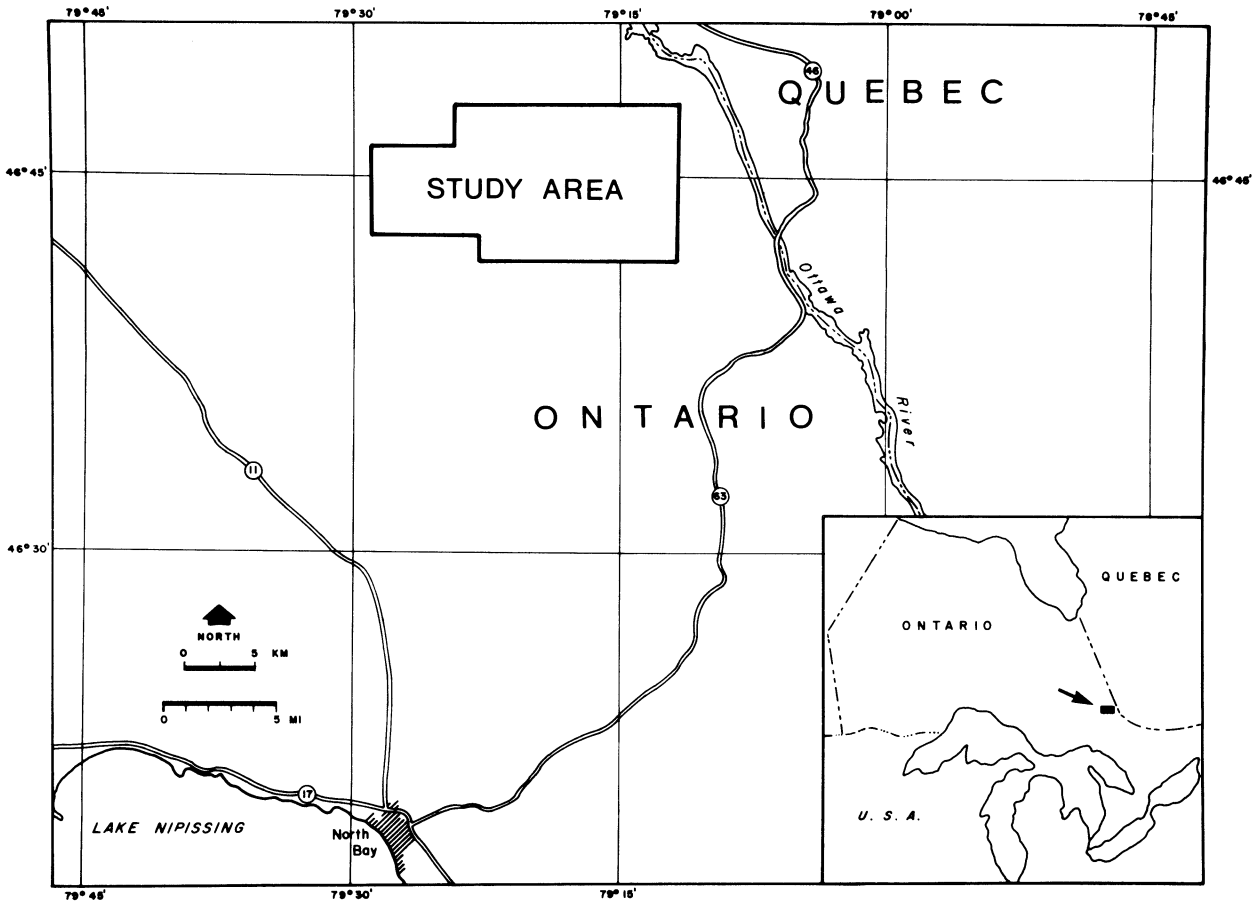

Fig. 1. Location of the North Bay study area.

METHODS

We captured bears in Aldrich leg snares or barrel traps and immobilized them with a mixture of ketamine hydrochloride and xylazine hydrochloride (Addison and Kolenosky 1979). We weighed and measured immobilized bears and extracted a premolar to determine age (Stoneberg and Jonkel 1966). We fitted the bears with radiocollars (Voigt and Lotimer 1981), released them at capture sites, and subsequently obtained radiolocations with aircraft, truck-mounted, and hand-held units using standard triangulation techniques (Mech and Frenzel 1971, Voigt and Lotimer 1981). Location frequency varied from several per day to once weekly. During the immediate predenning period, we increased flights to at least 1 every 3 days.

Repeated inactive fixes at a specific site indicated bears had denned. Motion sensors determined inactivity (Lotimer 1980) in 1979 and 1980, although we relied on signal pattern during earlier years. Accuracy of denning dates was 1–2 days for bears accessible by ground-tracking and 1–5 days for individuals accessible only from aircraft. Investigator disturbance of dens occasionally prompted den abandonment and construction of a 2nd den. Consequently, we analyzed 1st and 2nd dens separately to avoid potential differences resulting from hasty site selection and construction (Tietje and Ruff 1980). We obtained internal den measurements later in winter when we examined bears. Sample sizes of den characteristics sometimes varied because not all parameters were obtained for every den. Dates of emergence from dens were obtained for only a few individuals because spring breakup restricted ground travel.

We delineated summer range perimeters by the minimum area method (Mohr 1947); summer range

designation (20 May–31 Aug) followed Tietje and Ruff (1980). We determined the relationship between den locations and summer range boundaries by calculating the number of dens that occurred within the outer 25% and 50% concentric area polygons drawn around centers of activity (Hayne 1949). To determine if bears denned in portions of their range used exclusively by them or denned in sections shared with other bears (Deary and Kolenosky, unpubl. data), we divided the study area into grid cells of 500 meters square (Voigt and Tinline 1979) and counted the number of dens that occurred in exclusive and shared cells.

We established feeding patterns of individual bears during the fall by examining scats and feeding sites of radio-collared bears. We classified ages as follows: adults ≥ 4 years; subadults, 2–3 years; yearlings, 1 year; and cubs < 1 year.

We used 3-way analysis of variance to test differences of mean denning dates among age groups, sex, and years. Multiple regression analysis was used to determine the relationship between den entry and weather factors. Average wind speed; total precipitation; minimum, maximum, and mean temperatures on day of den entry and 3 days before were analyzed through a stepwise multiple regression procedure. Chi-square and *t*-tests were used to test differences among other parameters. Statistical tests followed Sokal and Rohlf (1969). The 0.95 confidence level was accepted as significant.

RESULTS

We located 98 1st dens (86 females, 12 males) and 12 2nd dens (8 females, 4 males) of 57 bears from 1976 to 1980. Four 1st dens (3 females: 1 male) located from 1970 to 1975 and a den constructed by a female cub that abandoned the family den during handling procedures in November 1977 were incorporated into the data base. Ages of denned bears ranged from 0.9 to 18.9 years.

Den Location

Forty of 47 (85%) females, ages 1–18 years, and 2 of 3 (67%) yearling males denned within the boundaries of their summer range. Of that group, more bears (72%) denned within the inner 50% area polygon than expected ($P < 0.01$) if den sites were randomly distributed. The outer 25% area was used less than expected ($P < 0.025$) as only 3 bears denned within that section. We felt that using concentric range areas that circumscribed geometric activity centers, a technique sensitive to changes in range shape and range use, was more valid that the simple distance measurements use by Tietje and Ruff (1980) to show den location-range relationships. Use of the latter is probably valid only if all ranges are approximately the same size and all sections of ranges are used equally, conditions that rarely occur. Analyses of our data using the method of Tietje and Ruff (1980) supported our findings that most bears denned centrally (67%) rather than peripherally (33%).

For 8 individuals that denned outside summer range boundaries, straight-line distances from dens to range perimeters varied from 0.2 to 2.0 km and averaged 0.9. One adult female denned outside her range in 1976 and again in 1979. She was the only individual that denned beyond summer range boundaries more than once.

Bears, especially adult females, desire seclusion and security when denning (LeCount 1983). In our area, dens of 13 of 14 females with shared ranges occurred in range cells that were not shared with other bears. All but 1 were adults.

Commencement of Denning

Before entering winter dens, bears reduced their activity and spent most of their time in the den vicinity. They often appeared lethargic (Beecham et al. 1983) when approached closely. Only 2 of 10 adult and 1 of 2 subadult females that went on lengthy (17–48 km, $\bar{x} = 29$) fall foraging movements (Rogers 1977) denned immediately upon their return. For the other 9, elapsed time between their return and denning varied 3–37 days and averaged 15. There was no relationship between the reproductive status of females and the length of time they spent in the den vicinity before entering dens.

During the immediate predenning period some bears used surface nests or beds as resting sites before final winter denning. At least 3 bears used 1 type best described as a predenning nest. These occurred under the trunks of relatively large (> 40 cm dbh) fallen trees. They consisted of circular nests 20–50 cm deep and 100 cm in diameter constructed of dead leaves, grass, and ferns. Unlike winter dens, there was no excavation into the soil, and at least 30% of the nest was exposed. An 11-year-old female used a nest for at least 3 consecutive days (4–7 Oct 1976) before our approach caused her to abandon it. The female subsequently denned 2.1 km southwest of the nest in

an excavated den under a fallen log. A 4-year-old female abandoned a nest used 26–29 October 1977 when we approached, but the bear remained in the immediate vicinity until finally denning 250 m northwest of the nest on 15 November. A 7-year-old female used a surface nest sometime between 21 and 30 October 1977, but loss of her radiocollar prevented us from determining the actual date of use.

The 2nd type of surface nest was similar to grizzly bear (*U. arctos*) daybeds described by Craighead and Craighead (1972). Construction of the bed was similar to the predenning nests, except that all were on the surface with no covering from trunks or roots. All 4 nests found were less than 10 m from the winter den. Well-used trails between den and beds indicated extensive use and suggested bears alternated between the 2 sites before final denning. These beds and nests apparently serve as temporary resting sites during the immediate predenning period, when bears experience a metabolic shift from an active to an inactive state (Lundberg et al. 1976, Beecham et al. 1983).

Bears entered dens from 20 September to 29 November with a mean of 27 October (Table 1). Differences among groups were significant only for yearlings vs. adults ($P < 0.002$), with yearlings denning earlier. Bears denned later in 1979 ($P < 0.009$) than in other years. There was no difference in mean denning dates between males and females ($P > 0.4$). Bears that fed on acorns, the last major fall food available, denned an average of 8 days later ($P < 0.05$) than non-acorn feeding individuals regardless of sex or age. Among years, the period in which bears entered dens ranged 27–66 days and averaged 48.

Almost 95% of the bears denned when the average minimum temperature 3 days before den entry ranged from −6 to 6 C ($r = 0.554$); 59% denned when minimum temperatures were between −2 and 2 C. Total precipitation and average wind speed were only weakly correlated ($r = -0.1938$ and -0.1608, respectively) with den entry dates.

Site Selection and Den Characteristics

Den site locations were classified into 2 site types, lowland and upland. Lowland consisted of stands dominated by black spruce (*Picea mariana*), cedar (*Thuja occidentalis*), and larch (*Larix laricina*); drainage ranged from moderate to poor. Upland consisted of mixed hardwood, mixed softwood, or a combination of the 2, to monotypic stands of white birch (*Betula papyrifera*) and poplar (*Populus* spp.) on mod-

Table 1. Dates when black bears entered dens, North Bay study area, 1976–80.

Group	1976		1977		1978		1979		1980		All years	
	N	Range	N	Range	N	Range	N	Range	N	Range	N	Mean
Yearlings	0	—	0	—	8	20 Sep–3 Nov	5	14 Oct–2 Nov	2	29 Sep–17 Oct	15	18 Oct
Pregnant females	6	14 Oct–2 Nov	6	1 Oct–12 Nov	5	27 Sep–9 Nov	8	26 Oct–29 Nov	4	29 Sep–4 Nov	29	27 Oct
Solitary females	3	20 Oct–31 Oct	0	—	5	28 Sep–22 Nov	3	29 Oct–9 Nov	1	22 Sep	12	27 Oct
Females and cubs	3	15 Oct–7 Nov	6	3 Oct–29 Oct	8	4 Oct–6 Nov	5	26 Oct–7 Nov	4	24 Oct–19 Nov	26	28 Oct
Adult males	1	6 Nov	0	—	1	18 Oct	1	12 Nov	1	8 Nov	4	3 Nov
Subadults	1	10 Nov	2	9 Nov–15 Nov	1	6 Nov	4	26 Oct–19 Nov	1	13 Oct	9	5 Nov
Yearly mean	14	27 Oct	14	25 Oct	28	23 Oct	26	4 Nov	13	23 Oct	95	27 Oct

erate to well-drained sites. One hundred of 113 dens occurred on upland sites (Table 2). The proportion of females and males that denned on upland was similar. Even in lowland sites, most bears denned on elevated spots with fair-to-moderate drainage. Only 3 bears (2 adult females, 1 adult male) denned in black spruce and/or cedar swamps with poor drainage. When examined on 20 March 1980, the bed of 1 female was wet, and water dripped directly onto the bear; temperature at the time was about 10 C. Her glossy coat and excellent physical condition indicated she had not been unduly affected by her questionable den site selection.

Of the 1st dens examined, 89% ($N = 98$) were excavations. Of the remainder, 3 were in hollow logs, 2 in hollow trees, 3 in rock caves, and 3 under piles of human-made debris. Forty-one percent of the excavated types were under standing trees or stumps, 23% under fallen logs or trees, and 36% were dug directly into the soil. Eleven 2nd dens were excavations; the other was in the base of a hollow tree. Five of the excavated types were under a standing tree or stump, 4 under a fallen log or tree, and 2 were dug directly into the soil.

Forty-two percent of 1st dens ($P < 0.001$, $N = 94$) faced east (45°-135°). Percentages of 1st dens opening north, south, and west were 21, 19, and 18, respectively; 4 opened vertically. More 2nd than 1st dens opened west ($P < 0.025$), but among 2nd dens there was no difference ($P < 0.06$) in direction of opening.

Eighty-seven percent of bears raked leaves, grass, moss, ferns, and rotted wood into their dens to line chambers and close den entrances (Table 2). Within groups, there was no significant difference for entrance closure, lining, and habitat type between 1st and 2nd dens, so data for both types were combined when comparing different sex and age groups. Degree of den entrance closure was classified as open (<20%), partially closed (20%–90%), and completely closed (>90%) (Table 2). More females than males ($P < 0.05$) had closed den entrances. For females, entrance closures of adults, subadults, and yearlings were similar. The 2nd den of a female cub had a closed entrance. The degree of entrance closure for adult and yearling males was similar.

More females than males (Table 2) lined dens. More adult females than subadult females ($P < 0.025$) lined dens. No other significant differences in proportion of dens lined were detected among different sex or age groups.

Den Dimensions

Chamber size of excavated dens was smallest for yearlings and increased progressively for subadults, solitary adults, females with cubs, and pregnant females (Table 3). Den chambers of family groups were larger ($P < 0.001$) than chambers of single individuals. Similarly, den entrance size (height + width) for yearlings, subadults, and solitary adults ($\bar{x} = 72$ cm) was smaller ($P < 0.001$) than entrances for females with cubs and pregnant females ($\bar{x} = 97$ cm). Tunnel dimensions were greater for pregnant females than solitary adults ($P < 0.02$) or subadults ($P < 0.05$). The single yearling den with an exceptionally large tunnel was probably an appropriated red fox (*Vulpes vulpes*) or timber wolf (*Canis lupus*) den. Both the entrance and chamber of the single adult male

Table 2. Den characteristics of black bears, North Bay study area, 1976–80.[a]

	Entrance			Lined		Habitat	
	Open	Partial	Closed	+	−	Upland	Lowland
Females							
Adults	39	13	28	73	7	72	9
Subadults	4	0	3	4	3	7	0
Yearlings	3	2	3	6	1	7	1
Cubs	0	0	1	1	0	1	0
Totals	46	15	35	84	11	86	10
Males							
Adults	4	2	0	4	2	4	2
Yearlings	7	1	1	3	6	10	1
Totals	11	3	1	7	8	14	3

[a] Includes 1st dens of 3 adult females and 1 adult male located in 1970, 1974, 1975.

Table 3. Dimensions ($\bar{x} \pm$ SD in cm) of excavated black bear dens, North Bay study area, 1977–80.

Group	Entrance			Tunnel				Chamber			
	N	Ht.	Wd.	*N*	Ht.	Wd.	Ln.	*N*	Ht.	Wd.	Ln.
Yearlings	6	32 ± 8	39 ± 7	1	66	96	125	11	53 ± 13	64 ± 23	87 ± 33
Subadults	5	31 ± 7	41 ± 8	4	31 ± 8	43 ± 7	45 ± 15	5	56 ± 7	77 ± 13	109 ± 14
Solitary adults	4	36 ± 4	40 ± 2	3	38 ± 0	42 ± 4	38 ± 8	6	61 ± 14	87 ± 8.7	105 ± 19
Females & cubs	4	50 ± 16	46 ± 17	1	38	71	91	6	64 ± 6	97 ± 27	101 ± 18
Pregnant females	7	47 ± 9	54 ± 16	5	49 ± 10	54 ± 4	47 ± 9	14	63 ± 18	108 ± 18	119 ± 35
Adult females	1	61	64	0	—	—	—	1	81	102	170

den were larger than entrances or chambers of any female dens.

Den Characteristics of Individual Bears

We found 5 different 1st dens for 3 bears; 4 1st dens for 2 bears; 3 1st dens for 4 bears; and 2 1st dens for 14 bears. All individuals examined with 3 or more dens were adult females; the remainder included both sexes of varying ages. Site selection and construction characteristics of most dens of individual adult females were similar each year. All 5 dens of 1 female were excavated into sloping hillsides of 20° in upland forest. All were lined, and entrances of all, except 1, were closed or partially closed. Entrance direction was more variable, but 3 of 5 faced east and the other 2, west. All 5 1st dens and 1 2nd den of another female were excavations less than 1.2 m deep into almost level ground. All entrances were closed, except in 1980, when the den was examined early (20 Sep), so the closure process may not have been completed. Only 1 of 6 was not lined; 5 of 6 were in upland forest. Entrance direction, however, was more variable, as 3 faced west, 2 east, and 1 north.

Two females, with 3 dens each, had contrasting den types. All dens of 1 were deep excavations greater than 2 m, whereas the other had extremely shallow excavations (< 0.5 m). The 1st bear could not be seen unless the observer crawled partially into the den; the 2nd was readily visible from ground level. Two of 3 entrances of the 1st bear's dens faced directly into prevailing northwest winds. However, because the dens were on elevated ground deposits surrounded by relatively open swamps, the depth of excavation probably prevented the wind from blowing into the den. The entrance of the 3rd den located was plugged with lichen, labrador tea (*Ledum groenlandicum*), and moss. Den entrances of the shallow denning bear were open 2 years and only partially closed the other year. Only small amounts of lining were used each year.

Dens of subadults showed more year-to-year variation. They often used a hollow log, or occasionally a standing tree, during the 1st year of independence and constructed an excavated or earth den the following year. Cubs orphaned during the spring hunt constructed and lined dens similar to those of older bears. Three cub dens were in standing trees, 4 in hollow logs, and 7 were excavated ground dens.

Other than family groups, co-occupancy of dens is apparently rare in Ursidae. Lentfer et al. (1972) re-

ported the use of a den by 2 brown bears (*U. arctos*) in Alaska. The pair, judged to be 2-year-olds, probably were littermates that were denning for the 1st time without their mother. Rogers (1977) recorded the reuniting of a black bear family group after the mating season. He indicated the group remained together until 9 June of the following year, which implies they all denned together. On 2 April 1978, we examined a den that contained an adult female, 2 3-month-old cubs, and a 2-year-old male. We suggest that the male was a member of her previous litter that had not separated at the usual age of 16–17 months (Rogers 1977). The 2 had probably continued to associate during the male's 2nd summer and simply extended that association into the denning period. The possibility that the 2 were unrelated and were simply occupying the same den appears less likely.

Effects of Investigator Disturbance

Responses of denned bears to investigator presence varied from indifference to extreme agitation and subsequent den abandonment. With the exception of 2 family groups handled in November 1977, disturbance at dens was kept to a minimum. However, all dens, except for those of a few males, were approached closely enough to confirm occupancy and determine entrance direction and closure. During the fall most denned adults appeared lethargic and often displayed no more reaction to our approach than a brief stare. Others reacted with indifference and yawning.

From 1976 to 1980, 19% of all dens ($N = 97$) were permanently abandoned. Abandonment rates did not differ among years. Age did not significantly influence abandonment rates, but rates were higher for yearlings (5 of 15) than for adults (12 of 73), or subadults (1 of 9). Abandonment rates for the 2 sexes were similar, although rates were slightly greater for yearling males (3 of 7), than yearling females (2 of 8). The single subadult male abandoned his den but none of 8 subadult females did so. Barren adult females abandoned dens more readily (4 of 13) than pregnant females (5 of 30) or family groups (3 of 26). None of 4 adult males permanently abandoned a den.

In addition to permanent abandonment, 6 of 97 (6%) bears temporarily left their dens during, or shortly after, the approach of investigators. Three of these incidents occurred in 1978 and 3 in 1980. In 1980, 7 of 14 different 1st dens located were temporarily or permanently abandoned, even though examinations were later in the season. During all years, there was no correlation between yearly mean denning dates and rates of abandonment.

For all groups, rates of abandonment were inversely related to duration of denning. Of 14 dens examined in which the bears had denned 1 day or less, 6 were permanently abandoned and 1 was temporarily vacated. For 44 dens that had been occupied for 2–15 days, 8 were permanently and 2 temporarily abandoned. For 36 dens occupied for more than 15 days, only 4 were permanently and 3 temporarily abandoned.

After permanently abandoning a den, individual bears traveled 0.3–3.4 km to a 2nd den. Mean distance traveled by adult females (2.2 km, $N = 5$) was almost double that of yearlings (1.2 km, $N = 4$), but the differences were not significant ($P > 0.2$).

In the spring, reaction to intrusion varied with age, month, temperature, and den type. Bears checked before mid-March, when daily maximum temperatures rarely exceeded 5 C, were still in a heavy state of torpor and exhibited little reaction even when pricked by a needle. As the season progressed, all bears, especially those on southern exposures, became more alert and reactive. In contrast to older bears, which reacted slowly, most yearlings were capable of immediate activity and flight after disturbance. After removal of the female, they attempted to escape through the entrance or retreated to the back of the den, where they often attempted to dig an exit hole.

Shedding of Foot Pads

Black bears shed and replace foot pads annually during winter dormancy (Rogers 1974). During spring den studies from late February to early April, we examined degree of pad shedding and replacement for 24 yearlings and 51 older bears. The percentage of the total pad (plantar + digitals) shed and replaced for each foot was summed to produce a single value for each bear.

Rates of shedding and replacement were related to age and reproductive status. By mid-March, replacement was $\geq 90\%$ complete for 71% of the yearlings, but only for 14% of the older bears ($P < 0.001$). The percentage of adult females ($N = 33$) in which replacement was greater than 60% during mid-March was 60, 40, and 22 for barren females, females with yearlings, and lactating females, respectively. The delay in replacement of the latter may have been hormonal or may have been due to the increased

energy demands of lactation. Mean ages of the 3 groups varied less than 1 year, so differences were not a function of age. Degree of replacement for 2 adult males examined in early March was 0 and 25%, suggesting a prolonged rate of replacement for that group.

Rate of replacement for younger bears was related to physical condition. Five of 6 yearlings in which replacement was $\leq 60\%$ complete were below average weight for their sex class. Mean replacement for 6 2-year-olds above average weight was 35% vs. 10% for 4 below average weight.

For individual bears in which shedding and replacement were still in progress, pads of the front feet were replaced earlier than those of the hind feet ($P < 0.005$, $N = 53$).

Shedding and replacement of foot pads appears to be a prolonged physiological process that requires most of the denning period for completion. The pads of 2 adult females examined 16 November 1977 had already begun to loosen, but replacement (for most adults) was still incomplete 4 months later. Unfortunately, neither of these 2 individuals was examined the following spring, so we did not determine replacement progress.

Emergence and Post Denning Behavior

We established exact dates of emergence for 4 bears and approximate dates for the remainder. Emergence extended from 23 March to 1 May with a peak around 5–20 April. In our area, emergence became general when maximum daily temperatures were at least 10 C for 2–4 consecutive days, which occurred on 5–15 April during most years.

On 17 April 1976, a 14-year-old female and 1 of 4 yearlings had just emerged when we observed them at 1200 hours. Upon our approach, both retreated up a large white pine (60 cm dbh). The 3 remaining yearlings were still in the den and appeared unaware of our presence. When we checked for survivors, we forced them out of the den, but all exited slowly. Their hesitant movements suggested they had not been out earlier. The only fresh sign in the area was the fecal plug and 1 other scat of the female. Approximately 30% of the ground was still snow covered. Daily maximum temperatures during the 3 preceding days exceeded 16 C and approached 25 C that day.

The earliest bear known to emerge was a yearling male observed lying on the snow near its den at 1530, 23 March 1979. Water dripping into the den as a result of the warm temperature (19 C) and steep (60°) south-facing slope may have triggered its exit. In 1978, when spring was delayed, all instrumented bears were still denned on 7 April. Maximum daily temperatures 1st exceeded 10 C on 18 April, dropped to 2 C on 20 April, and were more than 10 C from 23 to 28 April. In 1981, when temperatures exceeded 10 C on 4 of 7 days between 30 March and 5 April, 6 of 10 bears had emerged by 6 April. Two were still at their dens; the other 4 had moved distances of 500–2,600 m. Of the 4 still denned, 2 had emerged by 10 April, 1 by 16 April, and the other by 21 April. The last to emerge was a 19-year-old female with 2 cubs.

In 1980, maximum temperatures exceeded 12 C for 3 consecutive days, 6–9 April, and for 4 consecutive days, 19–22 April. They remained above 10 C on 23 and 24 April. When checked 22 April, only 2 of 10 bears were still denned. A 3-year-old female emerged the next day and the other, a 2-year-old male, remained denned until 1 May. Eight others were 375–1,925 m from their dens.

Shortly after emergence most groups vacated dens sites and did not return. Females with cubs, however, usually remained in the den vicinity for 2–30 days. The female constructed a bed or nest at the base of a large tree 20–200 m from the den. Sizes of 24 nests varied, but most were 20–25 cm high and 50–70 cm in diameter. Composed of needles, leaves, and grass, these nests were invariably constructed at the bases of the largest trees available.

Apparently the main function of these nests and associated trees is to provide a comfortable spot for resting and nursing. The large tree provides a safe haven for the cubs while the female is actively foraging. At that time of the year the recently emerged cubs would be especially vulnerable to inclement weather and predators. Potential predators include large male bears (Jonkel and Cowan 1971; Kemp 1972, 1976) and timber wolves (Rogers and Mech 1981). On 15 May 1980, we observed 2 cubs in a hemlock (*Tsuga canadensis*) and the female standing upright at the base with her forepaws outstretched above her head threatening a large male about 20 m away. The male moved slowly in an arc around the tree, maintaining his distance. We noticed no overt acts of aggression, and after about 5 minutes he disappeared. He may have left voluntarily, or possibly the circling aircraft disturbed him.

Reaction of family groups to approach by humans

was similar, although degree of defense by the female varied from individual to individual. Typically, the cubs climbed to the top of the tree while the female paced within 10–20 m of the base. Some females would ascend as high as 4–10 m and attempt to frighten the investigators away by huffing, jaw chopping, and growling. Jonkel and Cowan (1971) reported similar defense behavior by bears when confronted by humans.

DISCUSSION

It is generally considered that denning by bears evolved as a mechanism to circumvent the dual problems of inclement weather and food shortages during winter (Lindzey and Meslow 1976, Johnson and Pelton 1980, Rogers 1981). Although such a strategy would have highest survival value in more northerly regions, black bears in the more southerly latitudes of their North American ranges also den (Hamilton and Marchinton 1980, Novick et al. 1981, LeCount 1983). A circannual rhythm modified by weather and food supply has been postulated as the primary factor determining the onset of denning in black bears (Johnson and Pelton 1980). Accumulating evidence indicates that food may be a more important proximate stimulus than weather. A relationship between food scarcity and earlier denning has been documented for Alberta (Tietje and Ruff 1980), Pennsylvania (Alt 1980), and Tennessee (Johnson and Pelton 1980). In New York (O'Pezio et al. 1983) and Idaho (Beecham et al. 1983) bears denned later when fall foods were more available. Physical condition (Jonkel and Cowan 1971) and the cumulative effects of weather (Lindzey and Meslow 1976, Novick et al. 1981) are undoubtedly important in establishing general denning times for specific areas but appear to have less influence on yearly variations. In our study, mean denning dates differed by only 4 days during 4 of 5 years in spite of yearly differences in weather. However, for all years, bears that fed on acorns denned significantly later than non-acorn feeders, attesting to the importance of food in maintaining late fall activity. We observed several bears feeding on acorns after 5–15 cm of snow had accumulated on the ground and minimum daily temperatures were well below freezing. Failure of more bears to feed on acorns was probably related to the unpredictability of the crop. The widely scattered red oaks (*Quercus rubra*) usually produced moderate-to-abundant acorn crops only about every 3 years. Quite simply, in most years the potential energy returns would not warrant the search effort.

Sequence of denning was similar to that reported in the literature with yearlings, pregnant females, and females with offspring denning earlier than adult males and subadults of both sexes. The final decision to den also varied among individuals. Certain adult females were early denners, whereas others were late, regardless of presence of offspring. Cubs orphaned during the spring hunt, and consequently never exposed to the den selection or construction process, instinctively constructed dens and did so over a broad range of weather conditions.

Spring emergence is probably a function of warmer temperatures and increased day length (Lindzey and Meslow 1976). Temperature thresholds that initiate emergence apparently vary among regions. In Ontario that threshold is around 10 C, as most bears emerged when maximum daily temperatures were at least 10 C for 2–4 consecutive days. That threshold is similar to Minnesota, where most bears emerged when ambient temperatures greater than 10 C caused rapid snow melt (Rogers 1974). O'Pezio et al. (1983) suggested that if a temperature threshold does exist, it is less than 10 C for the Catskill region of New York. In Arizona, bears emerged but did not leave den sites in spite of 12–15 C midday temperatures in February and early March (LeCount 1980). In southern California, general emergence occurred during 1 spring when daily maximum temperatures fluctuated between 12–22 C (Novick et al. 1981).

The duration of denning by black bears varies latitudinally and altitudinally. Bears den for approximately 3 months in the more southerly ranges such as North Carolina (Hamilton and Marchinton 1980), Tennessee (Johnson and Pelton 1980), and southern California (Novick et al. 1981). Bears den for over 6 months in Alaska (Rausch 1961) and in the mountains of Montana (Jonkel and Cowan 1971). Denning lasts for approximately 4.5 months in New York (O'Pezio et al. 1983) and central Arizona (LeCount 1983). Regional differences appear related more to entry dates than emergence times (Johnson and Pelton 1980). In east-central Ontario, entry and exit dates approximated those in Minnesota (Rogers 1977) and east-central Alberta (Tietje and Ruff 1980), 2 areas with similar climate and habitat. Average yearly denning duration of 5.5 months was almost identical for all 3 areas.

Denning provides protection from inclement weather (Lindzey and Meslow 1976), eliminates food

dependency (Nelson et al. 1973), and affords security from potential predators (Pelton et al. 1980). Requirements of a suitable den site include adequate drainage, seclusion, ease of construction, and ample insulation. Site selection is probably related to availability; the design is modified during construction to satisfy individual needs. Dens have varied from simple nestlike depressions (Smith 1946, Erickson 1964) to more elaborate excavations under fallen logs or tree roots (Jonkel and Cowan 1971, Fuller and Keith 1980). Bears have also used rocks (LeCount 1983), elevated tree cavities (Switzenberg 1955, Beeman 1975, Pelton et al. 1980) and human-made structures (Bray and Barnes 1967, Jonkel and Cowan 1971) as den sites.

In southern latitudes, where protection from cold winter rains is especially important, tree cavities were preferred den sites (Johnson and Pelton 1981). In addition to reducing heat loss, elevated tree cavities provide more effective protection from humans and free-ranging dogs. In some sections of southern bear ranges, trees suitable for den sites are scarce because of development and logging (Hamilton and Marchinton 1980). In northern latitudes, where protection from extreme cold temperatures is more critical, excavated ground dens would be most efficient in reducing energy loss (Tietje and Ruff 1980). Adequate snow cover and closure of the entrance further enhances their insulative value. In our area, most dens were excavated below roots or trunks of fallen trees, were lined, and had closed or partially closed entrances. In addition, over 60% of the entrances faced east or south, 2 directions that would be least directly affected by the prevailing northwest winds. Most dens were surrounded by thick undergrowth that obscured entrances and enhanced seclusion. Dens of adult males were more frequently in more inaccessible and secluded spots than those of other groups. The types and construction of dens in our area were similar to those reported by Tietje and Ruff (1980) in the boreal forest of northern Alberta, where winters are equally severe.

Only 1 bear, a yearling female, denned in a hollow tree about 10 m above ground. Failure of more bears to use elevated tree dens was at least partially due to the scarcity of suitable trees in the area. It is also likely that bears using exposed tree dens would lose energy at a faster rate than those in ground dens insulated with a good cover of snow.

Heat loss would also be affected by body position and size of den chambers. Denned bears invariably adopted the fetal position with paws and nose tucked against the stomach as described by Folk et al. (1976). The ventral region generally faced toward the den opening. With family groups, the female was near the entrance and the young near the back. Those positions would maximize security and heat conservation for the young. The female, with a better ratio of body mass to surface area, would be less affected by the cooler temperatures near the entrance than her smaller offspring. Most denned bears older than yearlings shivered continuously to generate heat and help maintain body temperature. Jonkel and Cowan (1971) reported similar behavior for denned bears in Montana. Most dens appeared small, and all were only large enough to accommodate the occupants; dens of family groups appeared crowded. Beecham et al. (1983) in Idaho, Tietje and Ruff (1980) in Alberta, and O'Pezio (1984) in New York noted a correlation between bear size and den chamber size. Smaller dens were considered more energetically efficient than larger dens.

In our area, there was no evidence that bears reused dens from previous years, although many dens persisted for a number of years and appeared quite habitable. The construction of new dens suggested the availability of den sites was not a limiting factor in our area.

In east-central Ontario, most bears denned near the centers of their ranges. Although sample sizes, except for adult females, were small, our results were in contrast to earlier findings of peripheral denning reported in northern Alberta (Tietje and Ruff 1980) and northeastern Minnesota (Rogers 1977). Tietje and Ruff (1980) hypothesized that smaller bears may den at or beyond summer range peripheries to reduce potential predation by large males and possibly wolves. Presumably, detection of dens near range boundaries would be more difficult because clues such as scent and signs of activity would be less abundant along the periphery. Although the relative amount of scent marking that occurs along the periphery of a bear's range is not well understood, the profusion of sign such as trails, beds, and raked leaves in the vicinity of many dens suggested such sites would be readily recognizable by potential predators. If so, the presence of that sign would appear to negate any advantage that might be gained by denning along range peripheries.

We suggest that den location may be related to the social status of the individual, with mature, resident females being sufficiently confident to den in the cen-

tral portion of their range, whereas less confident subadults and subordinate adults may feel safer along range peripheries. Adults may enhance their feeling of security by denning in sections of their range where they have exclusive use. Of 14 females with shared ranges (Deary and Kolenosky, unpubl. data), 13 denned in areas not shared with other bears. Among the various age classes, there was no difference in the proportion of central and peripheral denners. If social status is a determining factor, our data would be weighted toward central denners, because most delineated ranges were those of resident, adult females.

Young bears, when denned, appeared less secure than established resident adults. When approached, they exhibited greater alertness and abandoned dens more frequently. Presumably those behavioral patterns enhance survival by enabling younger bears to avoid direct conflict with larger bears.

MANAGEMENT IMPLICATIONS

Knowledge of denning dates may be useful in setting seasons to selectively harvest specific sex and age groups of black bears (Lindzey 1981). Generally, a later opening of the fall season and an earlier closing of the spring season will reduce the proportion of adult females in the kill. Depending upon management objectives, establishment of seasons will depend upon local climatic conditions and the denning patterns of the local bear population.

In Ontario, the fall hunting season for black bears extends 1 September-15 October in regions north of the French and Mattawa rivers (46 North latitude) and 15 September-30 November farther south. Attempts to adjust seasons to selectively harvest specific sex and age groups during the fall would be only marginally successful because of the lengthy den entrance period. Although adult females denned earlier than adult males and subadults of both sexes, differences were insufficient to allow meaningful adjustments. Also, weather conditions and availability of food contributed to annual variations. Thus, to be effective, it would be necessary to know the size of the fall food crop and fall weather conditions before establishing seasons. Yearlings could be protected by delaying the fall season opening, but because that group is not a favored target, special protection is not warranted.

Adjustment of the spring season to protect specific groups, especially females with cubs, appears more feasible. Although reduced activity (Lindzey and Meslow 1976) and postdenning lethargy typified behavior of recently emerged bears, those characteristics were especially pronounced for females with cubs. The latter typically confined their activities around a large tree with a nest at the base in the vicinity of the den for up to 1 month. Lack of mobility of the young cubs (Lindzey and Meslow 1976) and incomplete keratinization of the pads of the female (Rogers 1974) were considered responsible for the restricted movement during that period. Among the bears that we examined, pad replacement was most delayed for lactating females. Perhaps the demand of lactation slows other less critical physiological processes. Because females with cubs emerge last (Johnson and Pelton 1980, Tietje and Ruff 1980, O'Pezio et al. 1983) and remain relatively sedentary for 4–6 weeks (Deary and Kolenosky, unpubl. data), they are 1 of the least vulnerable groups during the spring hunt. If desired, they could be afforded additional protection by earlier closure of the spring season.

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