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Denning behaviour of Scandinavian brown bears *Ursus arctos*

Sabrina Manchi & Jon E. Swenson

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During 1986-2001, denning behaviour of brown bears *Ursus arctos* was documented for 55 dennings of 33 radio-marked males in central Sweden, and 12 and 29 dennings of nine males and 19 females, respectively, in northern Sweden. Male brown bears spent on average 161 days (27 October - 4 April) in dens in the southern area. The duration of their denning decreased with increasing age and body mass. Comparing these data with those obtained for females in the same study area by Friebe et al. (2001), males emerged from dens earlier than females, spending significantly less time in their dens. The denning period of females was influenced by their reproductive status; pregnant females spent the longest time in their dens. Denning dates correlated clearly with timing of autumn snowfall. Males in the north denned earlier, emerged later and spent on average 45 days more in their dens than males in central Sweden. Similarly, females in the north spent on average 37 days more in their dens than females in the south. Daily movements of males tracked to their dens in 2001 showed a general trend towards lower rates of movement in the last two weeks before denning, as found in females. Mean distance between dens used in successive years varied with age and sex; it was significantly greater for subadult males than for females and adult males as a result of dispersal behaviour. Adult bears showed a high degree of fidelity to a general denning area within their annual ranges.

Key words: brown bear, den, den area fidelity, denning ecology, Sweden, Ursus arctos

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A significant feature of brown bear *Ursus arctos* ecology is winter dormancy, a complex strategy that allows them to survive the period of limited food and severe weather in winter. They can spend approximately 6-7 months a year in a den. During this period their metabolism is reduced by approximately 70% (Watts & Jonkel 1988) and they can lose 20-40% of their body weight (Kingsley et al. 1983), depending upon sex and age. Predenning accumulation of energy supplies and den site selection are therefore essential for successful winter dormancy.

The mechanisms that drive and control denning behaviour are complex and still unclear, although the lengthening of dormancy with increasing latitude suggests that environmental factors are involved (Smith et al. 1994). Some authors have hypothesised that denning

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behaviour is synchronised with the environment through an endogenous circannual rhythm that is influenced by proximate stimuli (Johnson & Pelton 1980). Decreased food availability, snowfall, low temperatures and physical conditions have been suggested as causing bears to enter dens (Schooley et al. 1994). Denning is probably controlled by an interaction of several stimuli, and the relative importance of the different factors may vary according to years and areas. The purpose of this study was to investigate the denning behaviour of male brown bears, and to compare it with data on female bears already published from the southern study area (Friebe et al. 2001). We compared denning chronology from two study areas and predicted longer dormancy periods in the more northern area. We hypothesised that the duration of denning is related to sex, reproductive status and age. We predicted that older and heavier male bears, which can probably store more fat, spend on average less time in their dens than smaller bears.

Many authors (Craighead & Craighead 1972, Reynolds et al. 1976, Hamilton & Marchinton 1980, Servheen & Klaver 1983) have reported that snowfall is a stimulus to denning, but other studies have not found this (LeCount 1983, O'Pezio et al. 1983, Judd et al. 1986, Schoen et al. 1987, Van Daele et al. 1990). We investigated whether snowfall is a proximate stimulus that could influence date of denning by male brown bears in Sweden.

Because different den types provide different degrees of protection and insulation, we also hypothesised that bears using better insulated dens would be able to remain denned for longer periods. Mean daily movements by female Scandinavian brown bears decreased prior to denning (Friebe et al. 2001). We expected the same trend in males and compared male patterns with those of females.

Many studies of bear denning behaviour have been published, but only a few of them deal with den site fidelity. The reason for this might be the necessity for long-term research, following individuals over several years. Based on 15 years of research on Scandinavian bears, we investigate whether bears tend to select the same general area for their denning each year.

Study area

Our research was carried out in an extensive manner in northern Sweden (ca 8,000 km^2) and intensively in central Sweden (ca 13,000 km^2). These areas are about 600 km apart and are near the northern and southern edges of the species' range in Sweden (Swenson et al. 2001). The northern study area was north-west of Jokkmokk, in the county of Norbotten (67°N, 18°E). The area is hilly in the east, with elevations below 300 m a.s.l., but is dominated by mountains that rise to over 2,000 m a.s.l. in the west (Swenson et al. 1998). The southern study area was in the northern part of the county of Dalarna and surrounding areas (61°N, 18°E). The terrain is generally flat to rolling; elevations range within 160-1,040 m a.s.l., but about 70% of the area is between 300 and 700 m. Lakes and bogs cover large areas. Both study areas are dominated by boreal forest, with Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* as the most common tree species. Some deciduous trees, mostly birches *Betula pendula* and *B. pubescens* are also present. Both areas are sparsely populated by humans.

Methods

Bears were captured in early spring during 1986-2001. They were immobilised from a helicopter by darting them with a mixture of tiletamine/zolazepam and medetomidine. They were then collared with radio transmitters (Telonics Inc., Mesa, Arizona USA) and weighed on a spring scale. A premolar tooth was extracted for the estimation of age by counting *cementum annuli* (Craighead et al. 1970). Male bears ≥ 4 years old were classified as adults and those 2-3 years old as subadults. Females were classified into four categories based on their reproductive status, as determined in a previous study (Friebe et al. 2001): 1) adult females (≥ 3 years old) that gave birth to cubs during the winter, 2) adult females that entered the den with offspring, 3) solitary and 4) subadult females (< 3 years old).

Locations of the marked bears were determined by triangulation from the ground and by aerial tracking. The accuracy of radio-tracking data was estimated by the quality of each position, as described by Nam & Boutin (1991).

As bears were not monitored daily every year, most den entry and emergence dates were estimated. Den entrance dates were calculated as the midpoint between the last reported movement in autumn and the first in a series of stationary locations indicating denning. Den emergence dates were similarly determined during the spring. To improve the accuracy of the estimation, we originally only examined periods that were ≤ 10 days long. However, den entry dates estimated using the 10-day criterion (N = 63) did not differ ($t = 0.01$, $df = 131$, $P = 0.99$) from the dates estimated using a 14-day criterion (N = 77). The same result was obtained for den

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emergence dates (t = 0.51, df = 120, P = 0.61; N = 59 and N = 65, respectively). Therefore we used the 14-day criterion for all comparisons. Time spent in the den was defined as the period between the midpoint dates of den entrance and emergence. Offspring ≥ 1 year old denning together with their mothers were excluded from the analysis.

Den sites were located on the ground and classified into five different den types: anthill, excavated under anthill, dug in soil, under a stone, and open nest on the ground. Systematic recordings of snow cover were available from meteorological stations in Ulvsjö and Sveg in and near the southern study area.

Differences between entrance and emergence dates and the time spent in dens were compared by study area, sex and female reproductive class using an Analysis of Variance (ANOVA) and t-tests. The data were log-transformed when not normally distributed. When ANOVA results were significant, we conducted a Tukey test for multiple comparisons of group means. Denning chronology data from the southern study area were analysed according to year, age, body mass, snow conditions and den type using a General Linear Model (GLM). Regression analysis was used to examine the relationships between: 1) duration of denning and age, 2) duration of denning and body mass, and 3) denning dates and snow condition. We specifically examined the relationship between den entry dates and the dates of the first consistent and permanent snowfall, and between den emergence with snow melting in spring from 1988 to 2001 in the southern area.

Evaluation of predenning behavioural patterns was based on measurements of straight line distances between consecutive daily locations from the beginning of September until denning. Annual home ranges (15 April - 15 November) were estimated by the 100% minimum convex polygon (MCP), the most commonly used method in other studies, using the Tracker computer program (Camponotus AB, Solna, Sweden). This method only provides an outline of the animal's home range. To determine whether a den site was 'central' or 'peripheral' within the home range, we calculated the core areas using the Kernel 50% model. This provided a more objective method of determining the areas of concentrated and peripheral use (Powell et al. 1997) within each annual home range.

In order to document den area fidelity, the distances between dens used in successive years were measured for each bear monitored for ≥ 3 years. Den distances were analysed according to age and sex using 2-sample t-tests.

We used a chi-squared test with the Bonferroni correction in order to test whether males and females used different types of dens at the same frequency. The RMS (Root Mean Squared Deviation), the square root of the sum of the X- and Y-coordinate variances, was used as a 'dispersion' index for the dens. A significance level of 0.05 was used for all tests.

Results

Denning chronology

Southern study area

During 1985-2001, more than 100 male brown bears were monitored once or twice a week, and in 2001 the movement patterns of three adult males were recorded daily from September to late November in the southern study area. We documented 77 den entry dates and 56 emergence dates for 33 individual males over periods of 1-5 years; their ages ranged within 2-30 years. During 1986-1998, 54 radio-marked females provided information about 169 den entry dates and 165 emergence dates (Friebe et al. 2001). All radio-marked bears denned in all years.

Date of den entrance for males varied from 5 October to 18 November; the mean was 27 October (SD = 8.7, N = 77). Exit dates were between 6 March and 25 April; the mean was 4 April (SD = 10.6, N = 65). The average male denning period was 161 days (SD = 13.7, N = 56).

Comparing these results with those obtained for females in the same study area (Friebe et al. 2001), we found that pregnant females denned earlier than subadult females, females with cubs or yearlings, and males (F = 6.75, df = 4, P = 0.00 and Tukey test: P < 0.05). Males emerged from dens 17 days earlier than females

Table 1. Mean denning duration (in days) of male and female brown bears by reproductive categories in central and north Sweden during 1985-2001. Data for females in the southern study area are from Friebe et al. (2001).

	South			North		
Category	Mean duration	SD	N	Mean duration	SD	N
Pregnant females	194.7	20.1	47	226.3	14.6	15
Females with cubs or yearlings	165.7	23.6	24	200.6	15.8	7
Solitary adult females	175.5	20.0	11	208.7	7.6	3
Subadult females	163.5	15.4	29	200.7	8.5	4
Males	160.6	13.7	56	206.1	9.5	12

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(t = 8.52, df = 174, P = 0.00) and spent significantly less time in the den (mean female denning period = 178 days, N = 111; t = 6.06, df = 163, P = 0.00). However the denning period of females was influenced by their reproductive status (Friebe et al. 2001) and pregnant females spent the longest time in their dens, 34 days longer than males (Table 1).

Duration of denning by males in the south varied by age (F = 8.64, P = 0.00). Females in this area showed an increase in the duration of denning with increasing age (Friebe et al. 2001), but the denning period of males decreased with increasing age (r = 0.31, df = 46, P = 0.03; Fig.1). Subadult males spent on average seven days more than adults in the den (t = 2, df = 36, P = 0.05). We obtained the same results when comparing the duration of denning and male body mass; denning period decreased with increasing body mass (r = 0.36, df = 37, P = 0.02).

Duration of denning by males in the south varied among years (GLM: F = 2.84, df = 12, P = 0.00). This was due to significant differences among years for den entry dates (F = 3.08, df = 14, P = 0.00) but not for dates of emergence (F = 1.25, df = 12, P = 0.28). Because the first snowfall dates recorded in Sveg and Ulvsjö were not statistically different (t = 0.15, df = 19, P = 0.88), we used the mean dates of the two meteorological stations. Regression analysis revealed a clear positive relationship between male den entry dates and date of first snowfall in the southern study area (r = 0.86, df = 10, P = 0.00; Fig. 2). However, males usually emerged from den before the snow had melted (Fig. 3), and there was no apparent relationship between den emergence dates and presence of snow in the spring (0 cm: r = 0.09, df = 10, P = 0.79; ≤ 20 cm: r = 0.33, df = 10, P = 0.29).

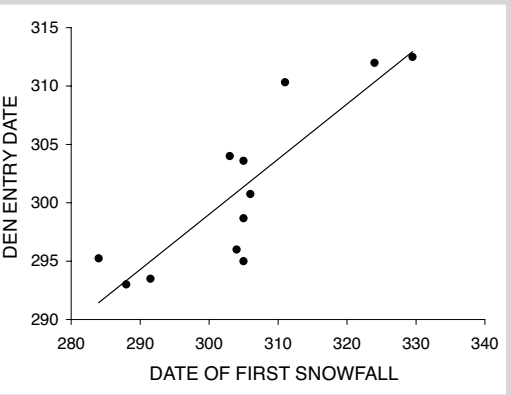


Figure 2. Relationship between date of first snowfall and den entry dates (both in Julian dates) for male brown bears in the southern study area in central Sweden.

Northern study area

The mean entrance date was 8 October (SD = 7.6, N = 15) for nine males tracked to their dens over a 16-year period (see Table 1); the earliest entrance date recorded was 24 September, the latest was 18 October. Exit date varied from 27 April to 8 May. The mean was 1 May (SD = 3.7, N = 12). Duration of the denning period was on average 203 days (SD = 9.5, N = 12).

We obtained information from 19 radio-marked females on 29 denning periods. On average they denned on 9 October (SD = 8.3, range: 14 September-27

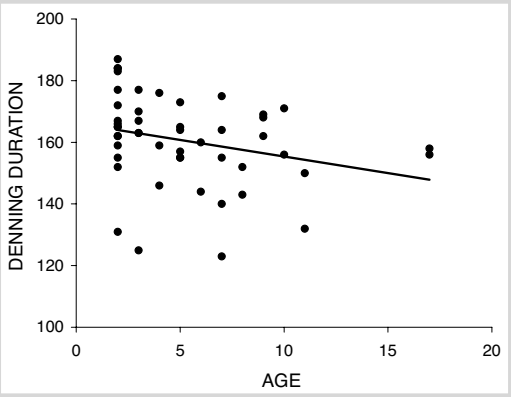


Figure 1. Relationship between the duration of denning (in days) and age (in years) of male brown bears in the southern study area in Sweden.

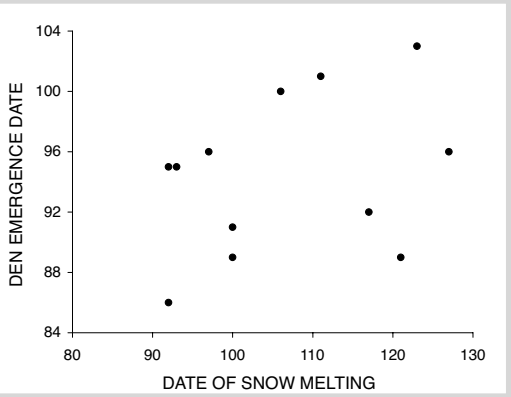


Figure 3. Relationship between den emergence dates (Julian dates) and snow-melting (< 20 cm of snow on the ground) for male brown bears in the southern study area in Sweden.

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October; N = 50) and emerged on 10 May (SD = 12.2, range: 7 April-1 June; N = 30) and spent 215 days (SD = 18, N = 29) in the den, about 10 days more than males (t = 2.00, df = 36, P = 0.05; see Table 1). Comparing the males and females yielded results similar to those from the southern area; pregnant females had the longest mean denning period (226 days; SD = 14.5, P = 0.00). No significant differences in denning period were observed for males and females that were alone, accompanied by offspring, or subadult females (Tukey test: P > 0.05; see Table 1).

As expected, denning duration for both sexes differed among study areas (GLM: F = 114.14, df = 1, P = 0.00; Fig. 4). Males in the south denned later (t = 8.59, df = 21, P = 0.00), emerged earlier (t = 14.32, df = 67, P = 0.00) and spent on average 45 days less in their dens than males in the north (t = 13.82, df = 21, P = 0.00). Similarly females in the south denned later (t = 11.37, df = 107, P = 0.00), emerged earlier (t = 7.07, df = 55, P = 0.00) and spent on average 37 days less in their dens than females in the north (t = 8.94, df = 57, P = 0.00).

Predenning movements

Daily movements of three adult males averaged 4 km (SD = 2.3) during the pre-denning season (15 September - denning), ranging from 0 to 22.4 km. During the last six weeks before denning, all the males showed the same movement pattern (distance travelled per day, F_{Id} = 1.15, df = 2, P = 0.39), but it varied according to week

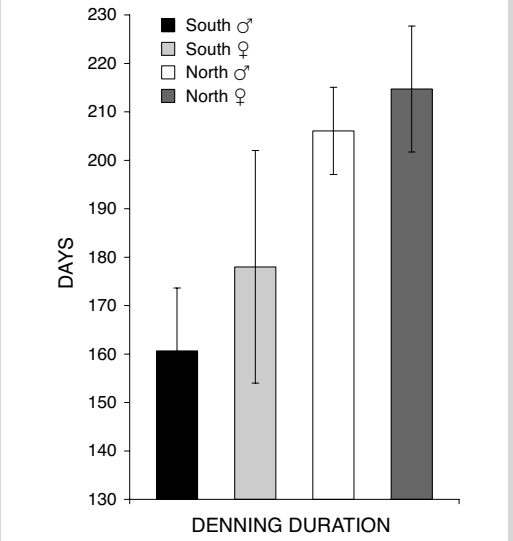


Figure 4. Comparison of denning duration (in days ± SD) for brown bears in Sweden between study areas and sexes.

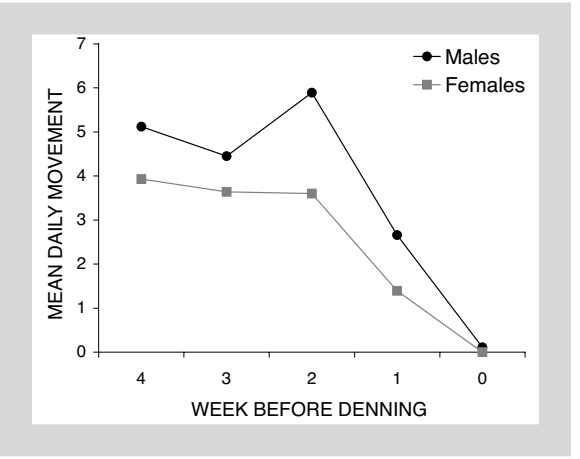


Figure 5. Mean daily movements (in km) of male and female brown bears in the southern study area in central Sweden during the last four weeks before denning. Data for females are from Friebe et al. (2001).

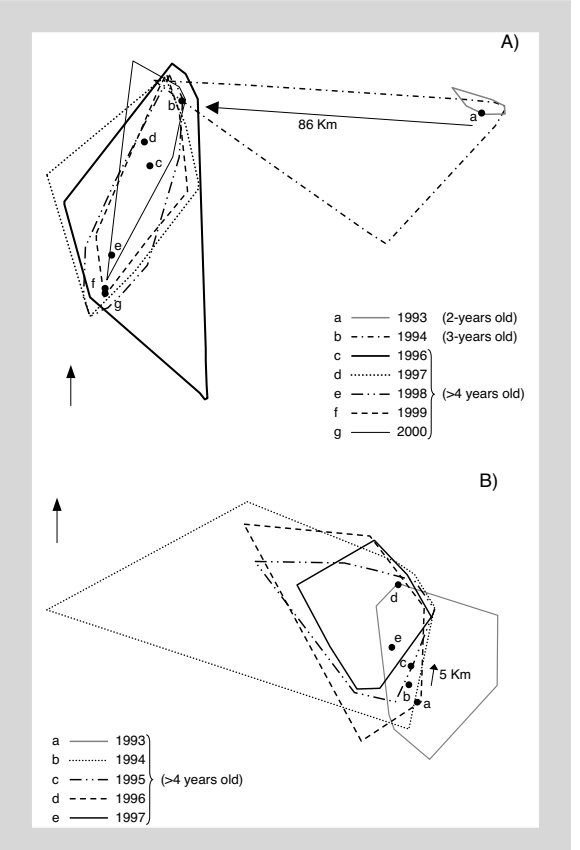


Figure 6. Examples of den positions in successive years and relative annual home ranges (MCP100%) of two male brown bears (A: W9311; B: W9006) in the southern study area, Sweden.

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Table 2. Mean distances and ranges (in km) between dens of successive years for male and female brown bears in central Sweden.

	Males				Females			
Age (years)	Distance	SD	Range (km)	N	Distance	SD	Range (km)	N
1-2	7.1	4.2	1- 14	13	8.1	5.1	0-19	15
2-4	59.1	76.9	0-357	23	8.6	8.8	0-39	37
>4	11.6	24.5	0-151	42	7.1	4.9	0-25	124

(F_w = 33.93, df = 4, P = 0.00). Rates of movement declined as the time of denning approached, especially during the last two weeks before denning (Fig. 5). A similar trend was found in the females (Friebe et al. 2001), although the daily distance that the males travelled was on average longer than that of the females (GLM: F_w = 15.50, df = 4, P = 0.00; F_{sex} = 4.95, df = 1, P = 0.03; see Fig. 5).

Home ranges and den use fidelity

In the southern study area we estimated 76 annual home ranges (MCP 100%) for 16 individual male bears during 1986-2001. The number of radio locations from which the ranges were calculated varied from 24 to 146. The average size of annual ranges was 179.7 km^2 (SD = 103.2, range: 53-488; N = 21) for males 1-2 years old denning alone for the first year, 1,147.8 km^2 (SD = 1,390.9, range: 60-4,028; N = 13) for subadults (2-4 years old) and 1,603.8 km^2 for adult males (SD = 1,480.8, range: 326-8,851; N = 42).

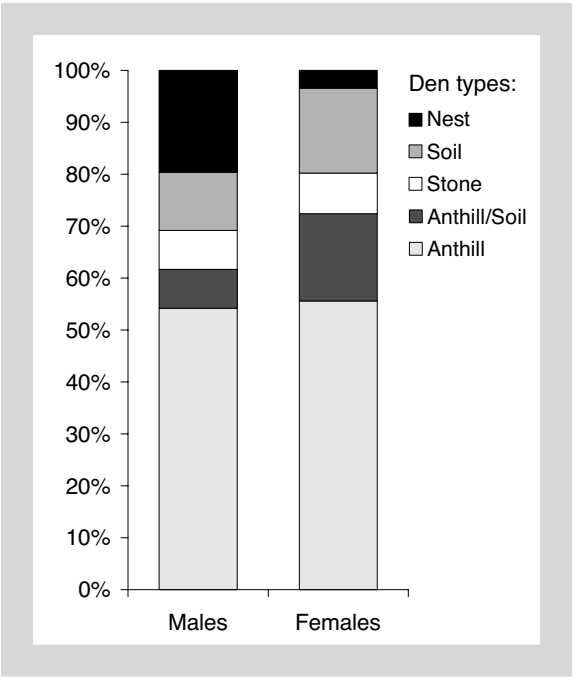


Figure 7. Use of different den types by male and female brown bears in central Sweden.

We defined 43% of dens (N = 32) as central and 57% (N = 42) as peripheral. Dens of individual adult males were always localised in the overlapping area of most annual ranges (Fig. 6B). However, all analysed subadult males spent their first winter alone close to the mother's den area, and then moved long distances for the next denning (Fig. 6A).

Mean distance between dens used in successive years varied with age in males (F = 13.97, df = 1, P = 0.000; Table 2). Subadult males (2-4 years old) had longer distances between dens used in successive years than any other sex/age group, and only this group showed a significant difference between sexes ($t_{MF,\ 1\text{-}2\ years\ old}$ = 0.56, df = 25, P = 0.58; $t_{MF,\ 2\text{-}4\ years\ old}$ = 2.95, df = 22, P = 0.007; $t_{MF,\ >4\ years\ old}$ = 1.90, df = 41, P = 0.06; see Table 2). The average distance between pairs of random points within male home ranges (306 km, N = 47) was significantly greater than mean distances between dens of adult males (W = 918, P = 0.00).

The RMS index revealed a more dispersed distribution of male dens than of female dens in the southern study area; this result was observed both in subadult (RMS_M = 58.9, N = 25; RMS_F = 36.6, N = 35) and in adult (RMS_M = 98.83, N = 86; RMS_F = 41.57, N = 179) bears.

Den type

We inspected 317 dens used by 46 males and 44 females in the southern study area. Anthills were used by 54% of the males and 56% of the females (Fig. 7). The use of den types differed between sexes (χ^2 = 28.36, df = 4, P = 0.00). Males used above-ground sites significantly more than females (k = 10; χ^2_M = 15.33; χ^2_F = 7.07, P < 0.05).

Male bears using above-ground over wintering sites spent on average 26 days less at these sites than males

Table 3. Duration (in days) of denning for male brown bears using four different den types in central Sweden.

Den type	Denning duration	SD	N
Anthill	161	15	17
Soil*	165	11	8
Open nest	148	16	5
Stone	174	9	4

*Soil dens also include anthill/soil dens.

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using dens in rocks or stones ($F = 2.84$, $df = 3$, $P = 0.05$). No significant differences were found for the other types (Tukey test: $P > 0.05$; Table 3). No differences in age or body mass were found among males that selected different types of dens ($F = 1.46$, $df = 3$, $P = 0.25$ and $F = 1.85$, $df = 3$, $P = 0.16$, respectively).

Discussion

Denning chronology

Winter dormancy is a complex behavioural and physiological adaptation to decreased food availability and winter weather. Although many authors have studied the denning ecology of different bear species and populations, knowledge about the factors that control when and where a bear will den is still incomplete.

The results we obtained from the comparison between the northern and southern study areas supported the hypothesis of increasing denning periods along a south-north latitudinal gradient, in agreement with what Weaver & Pelton (1994) and Smith et al. (1994) reported for North American black bears *Ursus americanus*. The duration of dormancy for brown bears in northern Sweden exceeded that of the bears in central Sweden by more than one month. The longer denning periods in more northerly latitudes are most likely the result of harsher climates, longer permanence of snow cover and consequently of more limited food availability.

Although some authors have not recognised the importance of snow, the high correlation we found between den entry dates and autumn snowfall strongly suggested that this factor is involved in stimulating denning in male Scandinavian brown bears. A lack of significant differences in the mean denning dates of different sex and age groups, other than pregnant females, suggests that the first snowfalls triggered most bears to move simultaneously into their dens. Similarly Craighead & Craighead (1972) reported that most grizzly bears in Yellowstone National Park also denned simultaneously in response to a snowstorm. However, when snow arrived later than usual on our study area, as occurred in 1989 and 2000, most of the bears had entered their dens before snowfall, indicating that other factors obviously are involved.

In contrast to den entry dates, the dates of den emergence for male Scandinavian brown bears were similar every year, even though the snow melting dates varied. Spring emergence may be regulated by factors such as increasing duration of daylight and warmer temperatures.

The pattern of den entry and emergence dates among the female reproductive classes and the males were the same in the northern and southern study areas. Although the results were not always significant, the pattern was consistent; pregnant females are the first to den and the last to emerge, and adult males are the last to den and the first to leave their dens. A similar pattern of denning times has been found elsewhere for brown and North American black bears (Reynolds et al. 1976, Hamilton & Marchinton 1980, Tietje & Ruff 1980, LeCount 1983, O'Pezio et al. 1983, Servheen & Klaver 1983, Judd et al. 1986, Smith 1986, Schoen et al. 1987, Miller 1990, Van Daele et al. 1990, Huber & Roth 1996, Mace & Waller 1997, Haroldson et al. 2002).

The length of time a bear can spend in its den is related to the stored fat supplies and to the rate of catabolism of the fat (Schwartz et al. 1987). Sex-specific differences in time of denning may be explained by the generally smaller surface area:volume ratio of male bears that allows them to remain active for longer without excessive energy loss. During winter, large bears lose proportionally less weight per day than small bears, and larger bears can probably store more fat. This may explain why older and heavier male bears spent on average less time each year in their dens compared to smaller males. Pregnant females, however, have higher and more complex nutritional demands than other female classes. Mass loss during hibernation by non-lactating bears is proportional to their metabolic body mass, whereas the rate of mass loss by denning, lactating females is higher relative to non-lactating bears (45% and 95% for black bears and grizzly bears, respectively; Farley & Robbins 1995). Schooley et al. (1994) hypothesised that pregnant females may act conservatively and den after they have stored sufficient fat reserves for winter survival and reproduction, even when food is still abundant. In a study on black bears in Florida, Wooding & Hardisky (1992) reported that bears had adapted to winter food availability by decreasing the length of denning in comparison to the northern latitudes. Pregnant bears, however, denned for a longer period; they may be forced to den by intrinsic factors.

Predenning movements

Large home ranges and the long distances that male bears can cover made it extremely difficult to obtain daily information for a consistent number of individuals. In autumn, when the availability of berries in central Sweden is high and bears may not move much to explore new food resources (Friebe et al. 2001), it was possible to locate three radio-marked males daily. Data from three males were not sufficient to reach conclu-

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sions on the behaviour of males, but it was enough to show a trend in the movement pattern. Similarly to what was reported for the female brown bears (Friebe et al. 2001), males showed a drastic reduction in movement during the last two weeks before denning. Servheen & Klaver (1983) have shown that reduced movements prior to den entry coincided with a condition of prehibernation lethargy.

Den use and fidelity

The function of a bear's den is to reduce energy loss and to provide protection from disturbance during winter. Energy conservation is enhanced by the excavation and insulation of dens; radiant heat from the earth increases the temperature inside the den (Tietje & Ruff 1980). Different den types insulate bears differently, and may affect the heat loss and the amount of fat catabolised to maintain body temperature.

The most common den type used by Scandinavian brown bears is the anthill type (dug under and into large and inactive *Formica* anthills, usually with *Vaccinium* spp. shrubs growing on it, which stabilise the excavated anthill). This preference may be due to the combined effects of high insulation efficiency and high availability.

In comparing the use of different den types between sexes, we found that above-ground open nests were used mainly by male bears. The open dens are probably less efficient than anthills, excavated ground or stone dens in insulating and consequently in reducing energy loss. Males might be able to use these open nests because of greater fat storage and less weight loss during hibernation compared to females. Males that denned in an open nest spent the shortest time in den, on average 26 days less than males that selected stone dens.

Previous studies on North American black bears have yielded variable results concerning den positions within the home ranges. Tietje & Ruff (1980) reported peripheral denning for black bears in Alberta; they hypothesised that smaller bears may den at or beyond summer range peripheries to reduce potential intra and inter-specific predation. Conversely, Kolenosky & Strathearn (1987) found that most bears in Ontario denned near the centre of their ranges, suggesting that den location may be related to the social status of the individual. In male Scandinavian brown bears we did not find any evident trend to den at the centre or at the periphery of their annual ranges. The studies are difficult to compare, however, because they are affected by the home range estimation procedure, by the temporal scale on which the home range is defined, and by the criterion selected to define the 'centre' and the 'periphery' of the home range. Some authors considered annual ranges, others considered seasonal ranges, and most authors did not specify the criterion used to define when a den site is central and when it is peripheral.

Similar to most studies, we found that no bear reused the same den. However, our results showed that adult male bears in central Sweden denned in the same general area in subsequent years. The mean distances between dens used by adult males were short compared to the distance between random locations within their annual home ranges and were not statistically different from those of the females. These results suggested a high degree of fidelity to a general denning area for both sexes. As the area chosen for denning is the area of overlap of the animal's different annual ranges, we can hypothesise, in agreement with what Miller (1990) reported for brown bears in Alaska, that it should be advantageous for adult bears to return to good and well-known denning areas, rather than risk denning in an area with the same characteristics but where an individual has had no previous experience.

The mean distance subadult males denned from a previous year's den site was significantly greater than that of females and adult males, as a result of the dispersal behaviour that is typical of males at this age (Swenson et al. 1998). Our results showed that 2-3 year-old males, in their first year alone, had small home ranges and denned close to their mothers. Males 3-4 years old usually dispersed further, whereas females of the same age remained within or near their mothers' ranges. Adult males, having established their home ranges after dispersal, continued to den in the same general area in subsequent years. Because few females dispersed from their natal area, but denned close to their mothers' areas, we predicted that in central Sweden the distribution of male dens would be more dispersed in the landscape than female dens. The RMS index confirmed our hypothesis.

Conclusions

Although denning behaviour is probably regulated by a complex interaction of several stimuli, the first autumn snowfall was an important factor triggering male brown bears to den in central Sweden. The significantly longer denning periods of bears in northern Sweden compared to those in central Sweden confirmed the hypothesis of a decreasing denning period along a north-south latitudinal gradient, the consequence of harsher climates and less food availability in northern areas. Larger bears can store more fat, and the smaller surface

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area:volume ratio of males allow them to remain active for longer; as a result male bears spent a shorter time in their dens than females, and their denning period decreased with increasing age and body mass. Consistent with these results, open nests, probably less efficient in insulating than other types of den, were mainly used by male bears. Whereas subadult males dispersed far from areas of their mothers, adult bears denned in the same area in subsequent years, suggesting a high degree of fidelity to a denning area.

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