

DENNING CHRONOLOGY OF FEMALE BROWN BEARS IN CENTRAL SWEDEN

ANDREA FRIEBE,¹ Zoologisches Institut, J.W. Goethe-Universität, Siesmayerstraße 70, D-60054 Frankfurt am Main, Germany
JON E. SWENSON, Department of Biology and Nature Conservation, Agricultural University of Norway, Box 5014, N-1432 Ås,
Norway and Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway, e-mail:
jon.swenson@ibn.nlh.no
FINN SANDEGREN, Research Unit, Swedish Association for Hunting and Wildlife Management, Backlösavägen 8, S-75651
Uppsala, Sweden

Abstract: During 1986–98, the denning chronology of 54 radiocollared female brown bears (*Ursus arctos*) was documented 112 times in central Sweden. An intensive study in 1998 investigated the pre-denning movement patterns of 9 females. Female brown bears spent on average 181 days in winter dens. Females that gave birth to cubs during winter spent one month longer in and at the den (196 days) than adult solitary females (168 days) or those that entered the den with cubs (161 days). Subadult females (<3 years old) spent less time in dens (163 days) than adults (183 days) and the duration of denning increased with increasing age. The mean entry date of all females was 28 October. However, significant differences in denning dates were observed depending on their reproductive status. Females that were pregnant in the fall denned earlier and emerged from the den later than females entering the den with cubs. During 1998, females moved on average 3.4 km/day. Females with cubs moved on average shorter distances than those without cubs, but from late September to date of denning, no variation in movement patterns among females in different reproductive status was found. Six weeks before female brown bears entered the den, a reduction of movements of about 5%/week was observed. In the last week before they entered the den, movements were further reduced by 40%. Female brown bears visited their den areas (1 km around the den) about once a month, which was more often than expected. Thus, we suspect that they chose a known place to den for the winter.

Ursus 12:37–46

Key words: brown bear, denning behavior, denning chronology, movements, Sweden, *Ursus arctos*

Brown bears may spend as much as half of their life in winter dens. Fascinating physiological mechanisms have evolved for bears to cope with extreme conditions during winter, but many of the behavioral strategies are still unknown. It appears advantageous for bears to take precautions prior to denning to avoid detection by humans and find favorable den areas. Disturbance of pregnant female brown bears during winter can affect fitness by lowering reproductive success (Swenson et al. 1997a). Thus, the choice of a safe place to den seems to be important. Denning behavior of brown bears in Sweden is poorly known, but if female fitness is easily influenced, knowledge of denning chronology can give us important information for bear conservation, such as how to minimize human disturbance during denning. Also, better information about brown bear denning behavior may improve the safety of humans and bears. Although the Scandinavian brown bear is not an aggressive bear as long as it is not wounded, bears at dens are associated with higher aggression (Swenson et al. 1999, Linnell et al. 2000).

Previous studies of winter behavior in bears have yielded variable results. Some researchers reported that the time of denning was related to snowstorms (Craighead and Craighead 1972, Reynolds 1976, Servheen and Klaver 1983), but others did not observe this phenomenon (Judd et al. 1986, Schoen et al. 1987, Van Daele et al. 1990). There was more agreement that denning chronology was influenced by food availability (Servheen and Klaver 1983, Schoen et al. 1987) and reproductive situation (Craighead and Craighead 1972, Servheen and Klaver 1983, Judd et al. 1986, Schoen et al. 1987, Miller 1990, Van Daele et al.

1990, Mace and Waller 1997). Generalizations of patterns observed in one study area may be difficult to apply to another area if combinations of factors influence denning behavior. In addition, variation in behavioral patterns among individuals (Judd et al. 1986, Schoen et al. 1987), and even by the same individual, has been reported (Roth and Huber 1986).

Results may be biased by the method used to study denning behavior, which complicates comparisons among studies. The frequency of telemetric locations is usually low if many individuals are followed. As a result, local movements before or after denning, which are reported to be common for bears, could easily be missed. In contrast, intensive studies are usually carried out on few bears because of personnel constraints.

Our goal was to examine denning behavior of female brown bears in central Sweden, with an emphasis on how it was influenced by reproductive status. The study had 2 parts, with differing levels of study intensity. From 1986 to 1998, we located 54 females in different reproductive categories about once a week and determined dates of denning. In 1998, we obtained daily locations of 9 females, which allowed us to study intensively daily movements and other behavior patterns prior to denning.

STUDY AREA

The study was conducted in Dalarna County and surrounding areas (61°N, 18°E), the southern study area of the Scandinavian Brown Bear Research Project in central Sweden (Fig. 1). The elevation ranges 200–730 m above

¹ Present address: Kvarnberg 2, S-79489 Orsa, Sweden.

sea level. The forest is dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and birches (*Betula pendula*, *B. pubescens*). Ground vegetation includes a variety of species of mosses, lichens, grass, heather and berries. Billberries (*Vaccinium myrtillus*) and crowberries (*Empetrum hermaphroditum*) are the main autumn food resource of brown bears in this area (Opseth 1998). The soil is mainly poor. Lakes and bogs are characteristic of this landscape.

Because of intensive forestry, unimproved roads are common and numerous. The human population density is low; only a few small villages exist. Consistent snow cover lasts from mid-November to early May. The brown bear density in the study area is about 20–25 bears per 1000 km² (Swenson et al. unpublished data).

METHODS

Bears were immobilized from a helicopter using a combination of tiletamine/zolazepam and medetomidine. All bears received a motion-sensitive radiotransmitter (Telonics Inc., Mesa, Arizona, USA) mounted in a

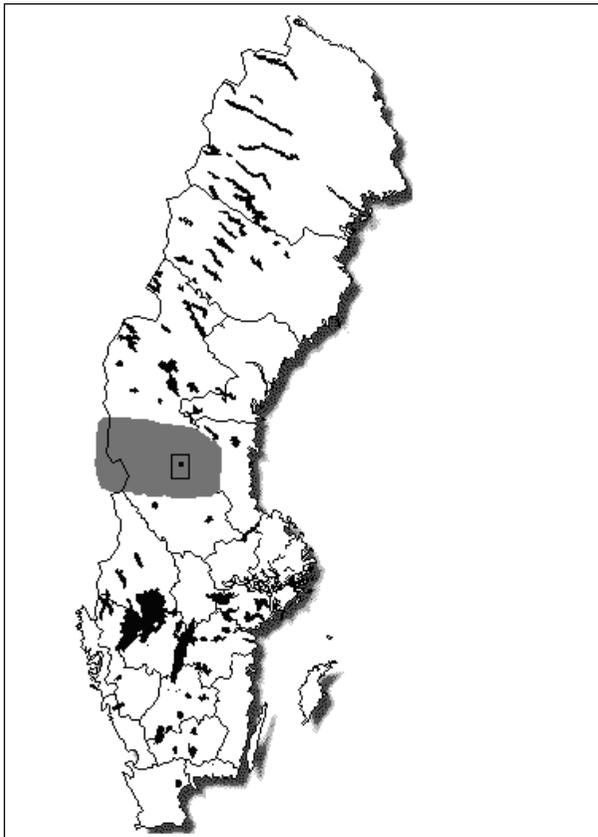


Fig. 1. Map of Sweden with the study area of denning chronology from 1986–98 marked in gray. The area where the intensive study of denning behavior was conducted in 1998 is marked with a rectangle.

neckcollar or implanted in the body cavity (yearlings). Locations were determined by triangulation from the ground or from an airplane.

Den entry and emergence dates of 54 females were documented during 1986–98 by weekly or sometimes daily location. The den entry date was defined as the midpoint between the last date we located the bear out of the den and the first date in which it stayed in the den. The date of den emergence was defined similarly as the midpoint between the last date the bear was still in the den and was first observed outside it. If the period between those dates was >7 days, the denning date was excluded from the analysis. When humans were known to have influenced denning behavior, the data were excluded from analysis as well. Duration of denning was defined as the period between the entry and emergence dates.

Females were classified into 4 categories based on their reproductive status: (1) adult females (≥ 3 years old) that gave birth to cubs during the winter, (2) adult females that entered the den with cubs (young having their first birthday during denning; very few young den with their mother during their second birthday in this area and thus are not considered here), (3) solitary, presumably non-pregnant adult females that did not emerge with cubs the following spring, and (4) subadult females (<3 years old).

Since 1986, data have been collected on several dennings from individuals in different reproductive categories. These data were analyzed using an ANOVA with reproductive status, individual, age, and year as independent variables.

In 1998, movement patterns of 9 female brown bears were recorded daily from mid-May until late November, when all bears had denned. We determined their location daily ($24 \text{ h} \pm 8 \text{ h}$) based on a minimum of 3 bearings from a car, airplane, or skis and estimated diel (24 h) movements from consecutive locations. The home ranges were measured by the convex polygon method (White and Garrott 1990). To obtain more precise information on behavior prior to denning, we located the bears twice a day ($12 \text{ h} \pm 6 \text{ h}$) during October. For this intensive study, predenning was defined as the time from first observation at the den site (radius $\leq 500 \text{ m}$) to the final entry.

If females in autumn 1998 had remained in one restricted area for more than 3 consecutive days, we investigated the location in the following spring to determine whether a den had been dug. Locations of dens were determined after the bears had left them. The surroundings were explored to detect signs of predenning behavior (e.g., nest material collection and excavations) and to investigate whether other dens had been dug there.

To determine whether females built a den in a predetermined place, we observed bears at the future den area before denning. To avoid obtaining such a small area that

preferred use could be found due to chance alone, and to account for triangulation error, we defined the den area as a radius of 1 km around the den. All telemetric positions within a den area from mid-May to the pre-denning period were considered. Because bears rested sometimes for several days at the same location, we counted sojourns of several days in the defined area as only 1 event. The number of positions within and outside the den area were compared to expected values, based on the area covered within the individual's home range, and tested using a 2 x 2 contingency table.

RESULTS

Denning Chronology

Total Data Set 1986–98.—Fifty-four radiomarked females provided information about 169 den entry dates, 165 emergence dates, and duration of denning at 112 den sites. The number of den locations found for any 1 individual varied between 1–11.

The ANOVA analysis showed that the duration of denning was influenced by individual ($F = 1.98$, 26 df, $P = 0.018$), year ($F = 2.83$, 10 df, $P = 0.007$), and reproductive status ($F = 38.13$, 2 df, $P = 0.000$), but not by age ($F = 1.11$, 15 df, $P = 0.37$). However, age interacted with the reproductive status in influencing the duration of denning ($F = 3.17$, 32 df, $P = 0.000$). On average, pregnant females spent 196 days in the den (Table 1), about 1 month longer than females that entered the den with cubs (161 days, $t = 4.57$, 14 df, $P = 0.0002$) or adult solitary bears (168 days, $t = 3.96$, 16 df, $P = 0.0006$). There was no significant difference in duration of denning between adult solitary females and those that entered the den with cubs ($t = 0.77$, 20 df, $P = 0.45$). Subadult bears spent significantly less time in the den (163 days) than adults (183 days, $t = 3.48$, 42 df, $P = 0.0006$).

Females showed an increase in duration of denning with increasing age (pregnant: $r^2 = 0.18$, 49 df, $P = 0.002$; adult solitary: $r^2 = 0.56$, 13 df, $P = 0.002$; but not significant for females that denned with cubs: $r^2 = 0.14$, 23 df, $P = 0.075$). On average, females spent 2.4 days longer in the den for each year of age ($y = 2.39x + 166$ days for all females combined, $r^2 = 0.19$, 111 df, $P = 0.0000$, Fig. 2).

The ANOVA analysis revealed that den entry date varied according to reproductive status ($F = 9.19$, 2 df, $P = 0.000$), individual ($F = 1.73$, 31 df, $P = 0.022$), and marginally with year ($F = 5.11$, 11 df, $P = 0.061$), but not with age ($F = 76.32$, 17 df, $P = 0.33$) nor age in interaction with reproductive status ($F = 1.32$, 36 df, $P = 0.15$). The mean entry date of all radiomarked females was 28 October. Pregnant females entered the dens on average on 22 October. This was 10 days earlier than for females that

denned with cubs (2 November, $t = 3.76$, 37 df, $P = 0.0003$) and 8 days earlier than for subadult females (30 October, $t = 3.42$, 43 df, $P = 0.0007$). Date of den entry did not differ between pregnant females and adult solitary females (29 October, $t = 2.30$, 32 df, $P = 0.014$). On average, 50% of the female bears had denned before 23 October (Fig. 3). The mean emergence date was 20 April. Pregnant females emerged from dens on average 24 days later than females in other reproductive categories (pregnant versus with cubs: 25 days, $t = 5.76$, 22 df, $P = 0.0000$; pregnant versus adult solitary: 24 days, $t = 6.83$, 24 df, $P = 0.0000$; pregnant versus subadults: 23 days, $t = 8.65$, 41 df, $P = 0.000$).

Intensive Study in 1998.—In 1998 the 4 pregnant females denned on 5, 14, 15, and 16 October, and females with cubs and solitary nonpregnant females denned between 20 October and 8 November (Table 2). The first snowfall was on 19 October, and there was continuous snow cover after this date until the spring melt.

Movements

Daily movements during mid-May to late November averaged 3.4 km, but varied according to weekly period (Fig. 4) and reproductive status. The maximum daily movement was 21 km. On average, females with cubs moved shorter distances (2.6 km/day) than either solitary nonpregnant females (4.3 km/day, $t = 3.30$, 38 df, $P = 0.0011$), or those that were pregnant (3.8 km/day, $t = 3.05$, 48 df, $P = 0.0018$). There was no significant difference in daily distances moved between pregnant females and those without cubs ($t = 0.68$, 48 df, $P = 0.25$). From late September to den entry, no variation in movement patterns was found among females with different reproductive status ($t = 0.12$, 20 df, $P = 0.89$, Fig. 4). Six weeks before females entered the den, a reduction of movements of about 5% per week was observed ($r^2 = 0.96$, $P = 0.003$). During the last 2 weeks before den entry, the movements were further reduced by 40% (1.24 km/day, $r^2 = 0.89$, $P = 0.001$).

Predenning Behavior

After the den site was chosen, the bears stayed close to the den, but often left and traveled up to 500 m away. Based on several observations, den excavation did not take more than an hour, but 4–10 days elapsed between entering the den site and den entry for bears that were not disturbed by humans (Table 2). On average, the females spent 7 days on pre-denning behavior.

Resting places used prior to denning often showed signs of foraging. We found many excavated tree trunks, which indicated foraging for insects. Also berries were available. In 2 instances we found moose (*Alces alces*) carcasses that the bears visited repeatedly. A female and her

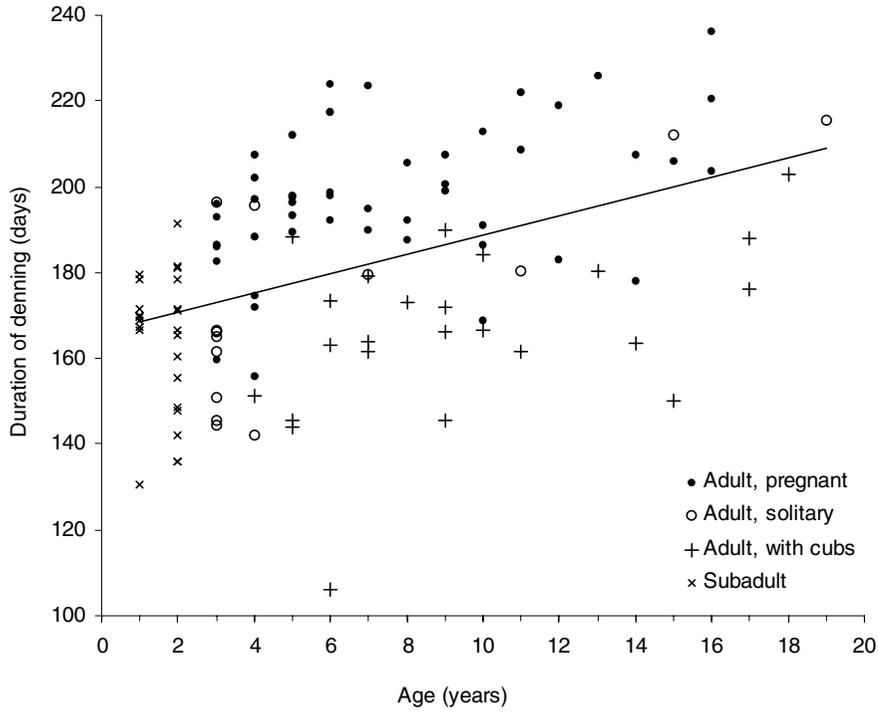


Fig. 2. Duration of denning in relation to age for female brown bears by reproductive categories in central Sweden, 1986–98.

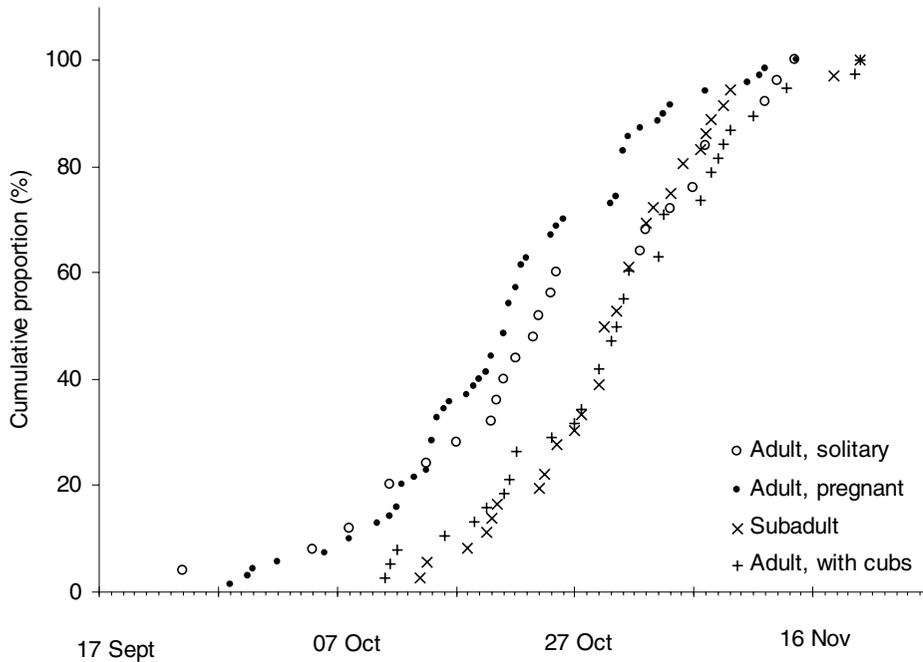


Fig. 3. Cumulative distribution of den entry dates in relation to date by female brown bears by reproductive categories in central Sweden, 1986–9. The line shows the mean cumulative proportion for all categories combined.

3 cubs spent 1 week at a carcass before starting predenning behavior. She dug a den only 600 m from the carcass. Four days after the first den entry, they went back to the carcass, and after some hours they returned to their den. A pregnant female showed similar behavior patterns with a carcass 500 m from her den. In spring 1999, after den emergence, both carcasses were revisited.

The Effect of Disturbance

Two of the 9 females, 1 pregnant and the other solitary and presumably not pregnant, were disturbed by moose hunters and their dogs, which barked at the bears. Both hunters reported that they had observed the females abandoning the den sites immediately after this disturbance. The original den of the solitary female was not found, but predenning behavior for a 4-day period had been recorded. A new den was established 4 km away, although a third bedless den was dug 100 m from the second one. There was permanent snow cover when this female redenned, but still the nest consisted of material from the ground. Predenning behavior at the final den site lasted 17 days.

In contrast, the disturbed pregnant female was active for only 3 days in the vicinity of the new den before denning. The final den was excavated 6 km from the original den site and collapsed after den emergence in spring 1999. Signs of nest material collection on the ground were numerous.

Selection of Den Areas.—The home ranges of the females overlapped and varied from 183 km² to 416 km² (Table 2). All dens were constructed inside and not in the periphery of the home range. During 1998, den areas were visited about 30% more often than expected, based on the proportion of area they comprised of the composite home ranges of the study bears (one-way $\chi^2 = 301.4$, 1df, $N = 1072$ locations, $P = 0.000$).

On average, the females were within 6 km of their fu-

ture dens, and the longest distance recorded was 22.2 km. Nearly every month the bears were within the den area where they finally dug the den. Therefore, we assume the denning places in 1998 were predetermined (Fig. 5).

DISCUSSION

Duration of Denning

Denning is an essential procedure for female brown bears and their reproductive success. Nondenning has been reported for male brown bears on Kodiak Island, Alaska, (Van Daele et al. 1990) and in Italy (Roth et al. 1996) and brown bears (sex not determined) in Croatia (Huber and Roth 1996), but as far we know this has not been observed for females.

We found that individual behavior, year, and reproductive status influenced the duration of denning. Most obvious was that pregnant females spent a longer time in their dens. Definitions of denning differ among previous studies, and also our methods from 1986–98 did not detect much pre- or postdenning behavior. This may bias the denning period upward for females in categories with long pre- or postdenning behavior. Indeed, from the airplane, we observed tracks of females with cubs around dens before the determined emergence date.

Additionally, we recorded a shorter duration of denning for subadult bears. Female bears in all categories showed an increase in duration of denning with increasing age, but for females that denned with cubs, the increase was not significant. For family groups the duration of denning may not be influenced only by the age of the mother, but also by the needs of the cubs. We found no similar results in the literature about brown bears, but Smith et al. (1994) recorded a shorter duration of denning for subadult American black bears (*Ursus americanus*).

Table 1. Denning chronology of female brown bears by reproductive categories in central Sweden, 1986–98.

Reproductive category	Den entry				Den emergence				Denning duration (days)			
	Mean	Range	(SD)	<i>n</i> ^a	Mean	Range	(SD)	<i>n</i> ^a	Mean	Range	(SD)	<i>n</i> ^a
Adult, pregnant	22 Oct	28 Sep–15 Nov	(9.58)	70 (26)	7 May	5 Apr–14 Jun	(9.71)	59 (21)	196	156–236	(14.13)	50 (21)
Adult, with cubs	2 Nov	11 Oct–20 Nov	(8.40)	38 (17)	12 Apr	6 Mar–23 May	(14.75)	35 (15)	161	106–190	(22.70)	24 (11)
Adult, solitary	29 Oct	24 Sept–15 Nov	(10.28)	25 (17)	13 Apr	1 Apr–12 May	(10.07)	16 (13)	168	131–216	(21.36)	14 (12)
Subadult	30 Oct	14 Oct–20 Nov	(6.73)	36 (20)	14 Apr	6 Mar–18 May	(9.30)	55 (30)	163	131–197	(16.41)	24 (20)
Total	28 Oct	24 Sept–20 Nov	(9.55)	169	20 Apr	6 Mar–14 Jun	(9.39)	165	181	106–236	(24.07)	112

^a Number of events (number of individual bears)

Table 2. Date of den entrance duration of predenning and home range size of 9 female brown bears in Dalarna, central Sweden, 1998.

Reproductive category	Age	Den entry	Days predenning	Size of the home range in 1998 (km ²)
Adult, pregnant	11	5 Oct	6	294
	5	14 Oct	10	416
	6	15 Oct	7	183
	8	16 Oct ^a (27 Oct) ^b	≥6 ^a (3) ^b	405
Average		13 Oct	8	
Adult, with cubs	17	25 Oct	7	213
	17	26 Oct	4	253
	7	3 Nov	7	332
Average		28 Oct	6	
Adult, solitary	4	(6 Nov) ^b	>4 ^a (17) ^b	356
Subadult	2	8 Nov	5	201
Total		24 Oct	7	

^a Before disturbance^b (After disturbance)

Movements

Movement patterns among females in all categories were similar from late September to the time of denning. Reductions in daily movements 6 weeks before bears entered their den site were not due to lethargic behavior; in fact, the opposite was found. Females were active about 60% of the time during mid-July to late August 1998 and 1999 (Myre 2000). Wenum (1997) and Roth and Huber (1986) also reported that bears were active of over 60% of the time in late autumn. Berry availability in central Sweden is high at that time, and all our recorded resting places showed signs of foraging. If food is present bears may not move much to explore for new food sources. Amstrup and Beecham (1976) observed a relationship between reduced movements and high food availability. Not until 1–2 weeks before denning did we find a drastic reduction of movements. This occurred simultaneously with predenning, when bears prepared dens and provided them with bed material.

Predenning

In our intensive study in 1998, we recorded that predenning behavior lasted 3–17 days, similar to several other studies (Craighead and Craighead 1972, Reynolds et al. 1976, Judd et al. 1986, Van Daele et al. 1990, Mace and Waller 1997), but as much as 4 weeks has been reported (Servheen and Klaver 1983). Our observations did not show that females with cubs spent the longest time in predenning behavior, as has been reported elsewhere (Mace and Waller 1997). The pregnant female that abandoned the den and redenned spent only 3 days at the final den site before denning. Thus bears may not need a long time for den construction if weather conditions, time, and reproductive status force them to start denning.

Bears appeared to select predetermined places for denning. The areas where bears finally built their dens in 1998 were visited on average more than once a month during

the entire period bears were out of the den. Krechmar and Krechmar (1989) reported that typical brown bear dens in northeast Siberia were excavated in a very short time, but that they had been constructed 1–2 months before denning. Also Craighead and Craighead (1972) observed 1 den construction 2 months before entrance. Dens in Sweden were usually constructed immediately before denning, as estimated by the age of the tracks from digging and gathering bed material that we examined at the den site.

Entry Date

Entry date seemed to be more flexible than the duration of denning and was influenced by reproductive status, year, and individual, of the variables we examined. Possibly, some bears become fat earlier (Servheen and Klaver 1983). Similar to others, we observed that females took advantage of food resources as long as possible, especially if a carcass was present (Craighead and Craighead 1972, Servheen and Klaver 1983, Schoen et al. 1987, Clevenger et al. 1990). Van Daele et al. (1990) considered that lack of food might be the major factor triggering the beginning of denning. We disagree with that hypothesis for pregnant females, because pregnant females in Sweden entered their dens mainly before snowfall, when berries were still available and abundant. Baiting with carcasses is rather common during bear hunting in Sweden (Fujita 2000). However, if carcasses remain in the forest, the time of denning may be protracted for nonpregnant bears. This was observed in our study, when females returned to a moose carcass several times.

In our intensive study in 1998, females entered their dens over 1 week earlier than the average from 1986–98. Date of snowfall was not unusually early, but this time coincided with permanent snow cover. This may be a reason for the early start of denning. Miller (1990) observed that early denning correlated with climatic conditions.

As reported by others, we found that pregnant females

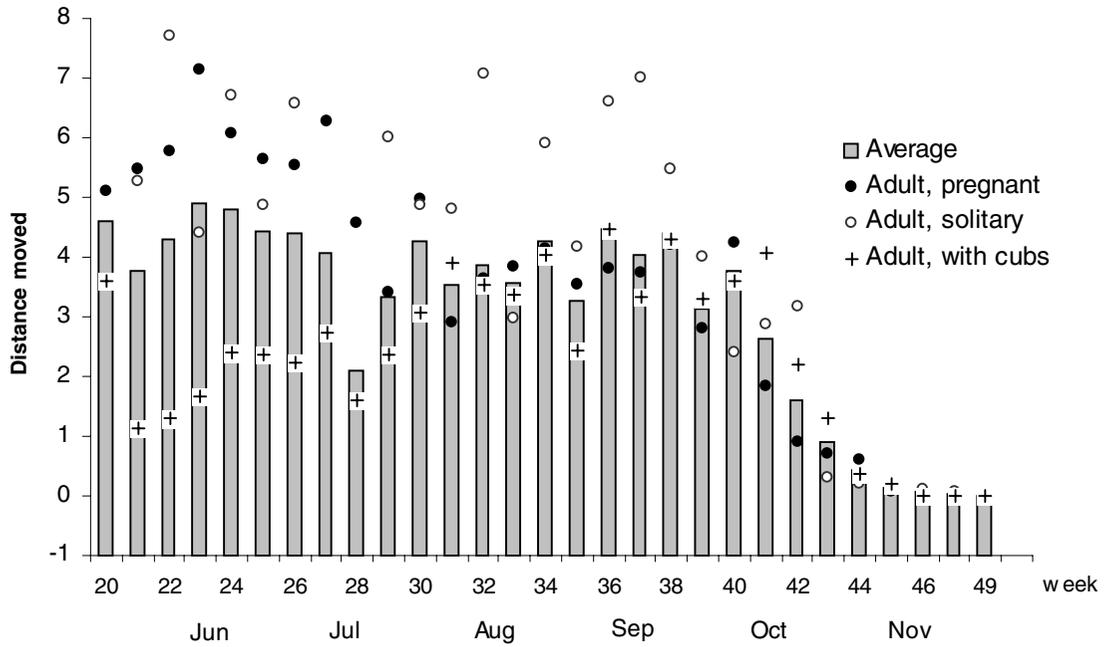


Fig. 4. Average daily movements in weekly periods for 9 female brown bears by reproductive categories in Dalarna, central Sweden, 1998.

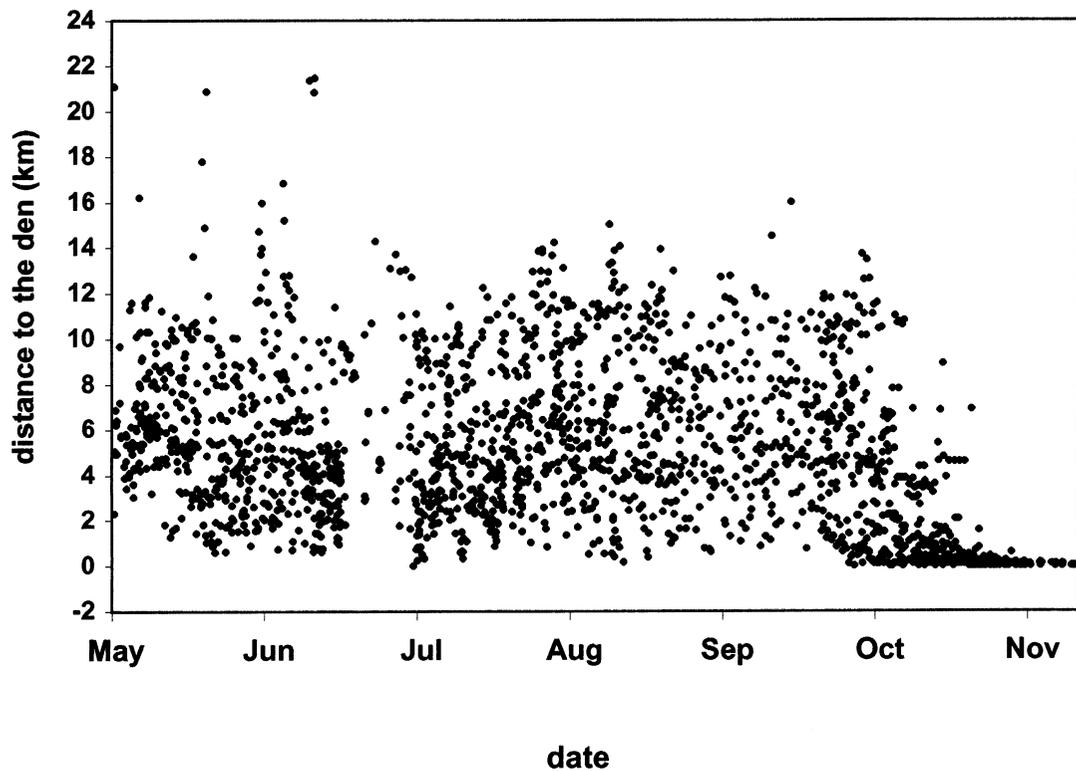


Fig. 5. Distance from radiolocations of 9 female brown bears to places where they finally dug their dens, central Sweden, 1998.

started denning first (Servheen and Klaver 1983, Judd et al. 1986, Van Daele et al. 1990), followed by females with cubs and solitary females. However, females with cubs were reported to den first by Mace and Waller (1997). Hissa et al. (1994) reported that changes in blood parameters in early fall may indicate the development of biochemical preparation for denning. This could provide a physiological explanation for early denning of pregnant females. The blastocyst is not implanted in the uterus until the female is in her winter den (Tsubota 1990, Hissa 1997).

RECOMMENDATIONS

Presently, the bear hunting season in our study area closes on 15 October, when an average of 18% of all female bears and 26% of pregnant females have denned, and an additional 16% and 24%, respectively, are engaged in pre-denning activity. Ideally, the bear hunting season should close early enough to avoid disturbing female bears that have already denned or are showing pre-denning behavior. This is because the reproductive success of pregnant females that are disturbed and change dens is reduced (Swenson et al. 1997a) and because bears may avoid areas for future denning if they have been disturbed there (Schoen et al. 1987). In addition, bears seem to show somewhat higher aggression toward people when they are disturbed at a den (Swenson et al. 1999). Although it would be ideal to remove the potential for disturbance of denned bears, this is difficult to do practically. Stopping the bear hunting season earlier may not result in less disturbance, because many other forms of activity occur during the denning period, including hunting of large and small game, skiing, ice fishing, snowmobiling, and forestry activity. For example, the moose hunting season, including hunting with dogs, closes in January in some areas, and some forms of forest grouse hunting (*Tetrao urogallus* and *T. tetrix*) occur in January. It is not practical to forbid all of these activities to reduce the rate of disturbance, which in our study area results in about 9% of denned bears changing dens each winter (Swenson et al. 1997a). However, it is useful for managers to be aware of the situation, and we have included a figure showing the cumulative proportion of pregnant females that have started pre-denning behavior and denning in relation to date (Fig. 3). This can be used if managers decide to restrict activity in an area to reduce disturbance to denning bears. The figure is applicable to our study area, but probably not for areas farther north. In our northern study in Norrbotten, the bear hunting season closes on 1 October and bears enter the den about 20 days before they do in our southern study area (Sandegren and Swenson 1997). Thus, until better data on denning are available from the north, managers should

use Fig. 3 and subtract 20 days to estimate the denning activity of pregnant females there.

ACKNOWLEDGMENTS

We thank the Swedish Environmental Protection Agency, Swedish Association for Hunting and Wildlife Management, Norwegian Institute for Nature Research, Norwegian Directorate for Nature Management, WWF (World Wide Fund for Nature) Sweden, and the Research Council of Norway for financial support to the project, Orsa Communal Forest for providing housing, and the Willkomm Stiftung in Frankfurt, Germany for financial support to A. Friebe. We thank especially S. Brunberg and E. Pettersen for help with the intensive field work, the many volunteers and students for conducting the extensive field work, and A. Söderberg for help with the databases. We also thank H. Reynolds, D. Huber, and J. Copeland for helpful comments on the manuscript.

LITERATURE CITED

- AMSTRUP, S.C., AND J. BEECHAM. 1976. Activity patterns of radio-collared black bears in Idaho. *Journal of Wildlife Management* 40:340–348.
- CLEVENGER, A.P., F. PUROY AND M.R. PELTON. 1990. Movement patterns of a European brown bear in the Cantabrian Mountains, Spain. *International Conference on Bear Research and Management* 8:205–211.
- CRAIGHEAD, F.C., JR., AND J.J. CRAIGHEAD. 1972. Grizzly bear prehibernation and denning activities as determined by radio tracking. *Wildlife Monographs* 32.
- FUJITA, R. 2000. Bait-hunting for brown bears in Sweden: Temporal and spatial occurrence and potential effects on the population. Undergraduate Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- HISSA, R. 1997. Physiology of the European brown bear (*Ursus arctos arctos*). *Annales Zoologici Fennici* 34:267–287.
- , J. SIEKKINEN, E. HOHTOLA, S. SAARELA, A. HAKALA, AND J. PUDAS. 1994. Seasonal pattern in the physiology of the European brown bear (*Ursus arctos arctos*) in Finland. *Comparative Biochemistry and Physiology* 109A:781–791.
- HUBER, D., AND H.U. ROTH. 1996. Denning of brown bears in Croatia. *International Conference on Bear Research and Management* 9(2):79–83.
- JUDD, S.L., R.R. KNIGHT, AND B.M. BLANCHARD. 1986. Denning of grizzly bears in the Yellowstone National Park Area. *International Conference on Bear Research and Management* 6:111–117.
- KRECHMAR, A.V., AND M.A. KRECHMAR. 1989. Brown bear *Ursus arctos L.* in North-East Siberia. *Soviet Journal of Ecology* 1992(3):66–74.
- LINNELL, J.D.C., B. BARNES, J.E. SWENSON, AND R. ANDERSEN. 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28:400–413.
- MACE, R.D., AND J.S. WALLER. 1997. Denning ecology of grizzly bears in the Swan Mountains, Montana. Pages 36–41 in *Final*

- report: Grizzly bear ecology in the Swan Mountains. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- MILLER, S.D. 1990. Denning ecology of brown bears in Southcentral Alaska and comparison with a sympatric black bear population. *International Conference on Bear Research and Management* 8:279–287.
- MYRE, T. 2000. Strategies for female brown bears (*Ursus arctos*) to avoid infanticide: activity patterns. *Candidatus Agriculturum Thesis*, Agricultural University of Norway, Ås, Norway.
- OPSETH, O. 1998. Brown bear (*Ursus arctos*) diet and predation on moose (*Alces alces*) calves in the southern taiga zone in Sweden. *Candidatus Scientiarum Thesis*, Norwegian University of Science and Technology, Trondheim, Norway.
- REYNOLDS, H., J.A. CURATOLO, AND R. QUIMBY. 1976. Denning ecology of grizzly bears in Northeastern Alaska. *International Conference on Bear Research and Management* 3:403–409
- ROTH, H.U., G. BOSCAGLI, AND L. GENTILE. 1996. Movements, activity and hibernation of brown bears in the Abruzzo National Park as revealed by radiotelemetry. Pages 290 in F. Bourlière, compiler. *Management and restoration of small and relictuall bears populations*. Museum d'Historie Naturelle, Grenoble, France.
- , AND D. HUBER. 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. *International Conference on Bear Research and Management* 6:177–181.
- SANDEGREN, F., AND J.E. SWENSON. 1997. Björnen—viltet, ekologin och människan. Svenska jägareförbundet, Spånga, Sweden. (In Swedish.)
- SCHOEN, J.W., L.R. BEIER, J.W. LENTFER, AND L.J. JOHNSON. 1987. Denning ecology of brown bears on Admiralty and Chichagof Islands. *International Conference on Bear Research and Management* 7:293–304.
- SERVHEEN, C.W., AND R. KLAVER. 1983. Grizzly bear dens and denning activity in the Mission and Rattlesnake Mountains, Montana. *International Conference on Bear Research and Management* 5:201–207.
- SMITH, M.E., J.L. HECHTEL AND E.H. FOLMANN. 1994. Black bear denning ecology in Interior Alaska. *International Conference on Bear Research and Managment* 9(1):513:522.
- SWENSON, J.E., F. SANDEGREN, S. BRUNBERG, AND P. WABAKKEN. 1997. Winter den abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildlife Biology* 3:35–38.
- , ———, ———, M. HEIM, O.J. SØRENSEN, A. BJÄRVALL, R. FRANZÉN, S. WIKAN, AND P. WABAKKEN. 1999. Interactions between brown bears and humans in Scandinavia. *Biosphere Conservation* 2:1–9.
- TSUBOTA, T., H. KANAGAWA, T. MANO, AND T. AOI. 1990. Corpora albicantia and placental scars in the hokkaido brown bear. *International Conference on Bear Research and Management* 8:125–128.
- VAN DAELE, L.J., V.G. BARNES, JR., AND R.B. SMITH. 1990. Denning characteristics of brown bears on Kodiak Island, Alaska. *International Conference on Bear Research and Management* 8:257–267.
- WENUM, E. 1997. Activity pattern and time budgets of grizzly bears in the Swan Mountains of Montana: A synopsis. Pages 96–100 in *Final report: Grizzly bear ecology in the Swan Mountains*. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- WHITE, G.C., AND R.A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, Incorporated, San Diego, California, USA.