Effects of sex and age on den site use by Scandinavian brown bears

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Abstract: We asked whether den site characteristics of Scandinavian brown bears (*Ursus arctos*) were related to bear sex or age by analyzing the nearest distances to human structures within 10 km, the forest composition within 50 m, and topography within 5 m of 391 winter dens used by 114 individuals during 1986–2003 in south-central Sweden. Subadult males and subadult females used more pine (*Pinus sylvestris*) than spruce (*Picea abies*) denning habitats than did adult males. Adult males selected nest dens over rock dens more strongly than did subadult males, and they selected nest dens over anthill, soil, and rock dens more strongly than did subadult females, pregnant females, or females with cubs. Topography differed among den types but showed a poor relationship with different age–sex classes of bears. Abandoned dens were located closer to plowed roads than dens used successfully all winter. Adult males denned farther from permanently occupied houses and plowed roads than did other categories of bears, perhaps because they were least tolerant of human disturbance. In general, den sites of adult males differed the most from other age–sex classes of bears.

Key words: abandonment, brown bear, den site characteristics, denning habitat, Scandinavia, Sweden, *Ursus arctos*

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Brown bears (*Ursus arctos*) spend up to half their life hibernating in winter dens, and females give birth there. Because winter dormancy typically results in a 20–40% weight loss (Kingsley et al. 1983), bears benefit by choosing den sites that conserve energy and reduce disturbance by people or detection by predators.

Friebe et al. (2001) reported that among brown bears in Scandinavia, females with cubs have the longest and males the shortest denning periods, similar to reports for North American black bears (*U. americanus*) and brown bears (LeCount 1983, O'Pezio 1983, Schoen et al. 1987, Schwartz et al. 1987, Miller 1990, Van Daele et al. 1990, Ciarniello et al. 2005). Studies from Scandinavia suggest that human disturbance influences abandonment of winter dens and choice of den location (Swenson et al. 1996, Swenson et al. 1997, Elfström et al. 2008), and that abandonment of winter dens by pregnant females reduces reproductive success (Swenson et al. 1997). After females give birth, the cost of den relocation rises dramatically, because young cubs are exposed to thermal stress and perhaps predation before they are fully mobile. Therefore, females with cubs should tolerate greater levels of disturbance without abandoning dens (Linnell et al. 2000).

Linnell et al. (2000) concluded that brown bears tolerate industrial activity as long as the source of the noise is some kilometers from the den. Nevertheless, dens visited directly by people were often abandoned. Because males may show infanticidal behavior (Swenson 2003, Bellemain et al. 2006), females that avoid adult males in the spring breeding season may have a greater probability of successfully raising their young. Hence, for both energetic reasons and perhaps to avoid human disturbance or potentially predaceous male brown bears, different age–sex classes of bears may select different denning habitat.

Manchi and Swenson (2005) reported that mean distances between dens used in successive years by Scandinavian brown bears varied with age and sex due to dispersal behavior, and that duration of denning decreased with increasing age and body

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mass. Elfström et al. (2008) found that bears in this same area showed distinct preferences in selection of denning habitats at a landscape scale, but found no major differences related to age and sex at this large scale. However, habitat use may be scale dependent (Aebischer et al. 1993), and therefore it is still unclear whether there are differences in use of denning habitat among age–sex classes of Scandinavian brown bears at other scales. In American black bears, Klenzendorf et al. (2002) reported that different age and sex classes used different den types, and Pelton et al. (1980) and Manville (1987) reported that females were more selective than males.

Here, we describe denning habitat of Scandinavian brown bears and evaluate differences related to age and sex. We analyzed the nearest distances to human structures within 10 km, the forest composition within 50 m, and topography within 5 m of 391 dens. We also compared the habitats at dens used during the entire winter with habitats where dens were abandoned during the winter.

Study area

The study area encompassed about 21,000 km^2 in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (67°N, 13°E), covering the southern part of brown bear distribution in Scandinavia (Fig. 1). The area was dominated by coniferous forest (60%) of mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Deciduous forest, composed mainly of birches (*Betula pubescens*, *B. pendula*), alder (*Alnus incana*), and mountain ash (*Sorbus aucuparia*) covered 8% of the area. The ground vegetation was mainly ericaceous shrubs (*Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum*) and mosses. Bogs covered 15% of the landscape. Other features were open habitat (mainly grassland, 7%), open water (7%), and mountain forest (alpine birch, *B. pubescens* ssp. *czerepanovii*, and open canopy coniferous; 4%) (Elfström et al. 2008). Precipitation was 350–450 mm during the vegetation period (mean temperature ≥5°C) with 800–1100 degree-days (Swenson et al. 1996). Snow cover normally lasted from about November to April or early May (Swenson et al. 1996). Elevations ranged from 140 m in the east to 1,045 m in the west toward the Norwegian border. About 11% of the study area was below 160 m, 31% between 160 and 320 m, 50% between 320 and 650 m, and 8% above 650 m. The terrain in the southeastern part was relatively flat, with more topographically diverse and elevated terrain in the west. The slopes were less than 8° in over 90% of the study area (Elfström et al. 2008).

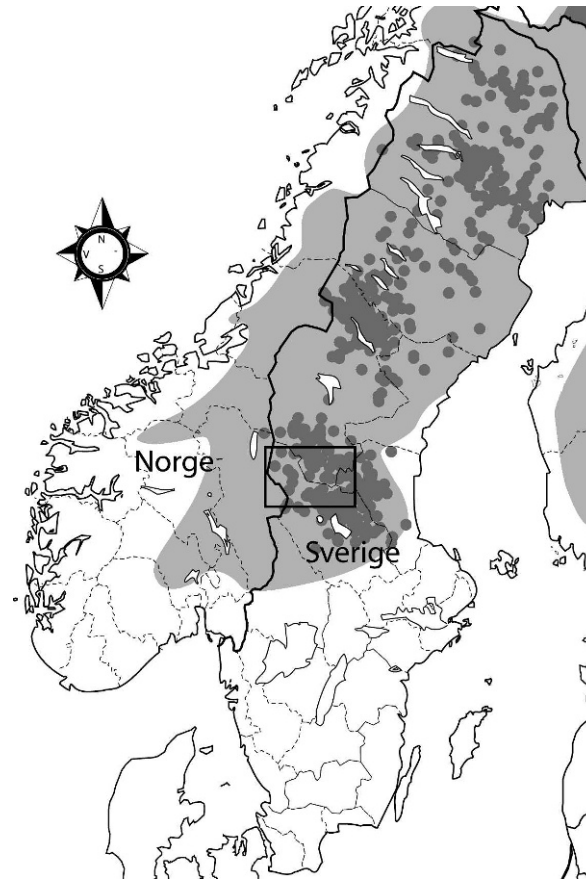

Fig. 1. Rectangle represents study area in south-central Sweden. The shaded area is the distribution of brown bears, with dark plots indicating areas of higher bear densities where female bears were shot in Sweden.

Methods

Bears were immobilized and fitted with radio-transmitters (Arnemo et al. 2006, Arnemo and Fahlman 2007) after being darted from a helicopter with DAN-INJECT® equipment (DAN-INJECT AdS, Børkop, Denmark). We determined the locations of denned bears during 1985–2003 by triangulation from the ground and by aerial telemetry. Coordinates of the dens were obtained with global positioning system (GPS) units when the dens were

visited on the ground. Some bears were tracked with radiotransmitters from their year of birth. For bears that were not marked during their first year, age was estimated using cementum annuli of an upper premolar (Matson et al. 1993).

We separated radiocollared brown bears into 5 age–sex classes: adult males ≥5 years old, subadult males <5 years old (Dahle and Swenson 2003), subadult females in prereproductive status, pregnant adult females that gave birth during denning, and adult females with cubs (i.e., females that denned with cubs, which became yearlings in the den). Very few females in this area entered the den with yearlings (we detected only 1). Eight adult females entered the den alone and did not have young when they left the den; they were excluded from the analysis due to small sample size. We considered age as a continuous factor explaining variation in den site characteristics.

We placed dens into 4 categories: anthill den, soil den, rock den (under a large rock or glacial boulder), and nest den (a nest of sticks on the ground; Sandegren and Swenson 1997). We described the habitat within 50 m around the den, referred to as the den site. The forest composition within the den site was placed into 1 of 3 habitat categories: dominated by birch, Norway spruce, or Scots pine. We obtained distances to human structures within 10 km of dens from a 1:50,000 Geographical Sweden Data (GSD) map, but these data were corrected during field work when necessary. We obtained elevation to the nearest 5 m from the GSD map. Degree of slope was estimated visually within 5 m of the den by comparing the vertical length from the uppermost point to the lowermost point with the length of its horizontal axis. Not all parameters were measured for every den.

We analyzed dens that were abandoned during the winter separately from successful dens. Bears in our study area apparently select their den site during the nondenning season, so factors affecting selection of the first and subsequent den sites during a winter may differ (Kolenosky and Strathearn 1987, Friebe et al. 2001). These subsequent dens (20 second dens and 3 third dens used the same winter) were excluded from all analyses. We found only 1 case of a bear reusing a den in successive years, and only 1 case of a den being reused by another bear. Therefore, we took a conservative approach and analyzed these dens only the first time they were used. Because a bear must select a den each year, each den was considered to be independent, as in similar studies (Schwartz et al. 1987, Hayes and Pelton 1994, Clark et al. 1998, Hightower et al. 2002). However, to test whether pooling data across individuals was justified, we extracted the residuals for each parameter for each bear. We then plotted the residuals for individual bears and evaluated potential effects of repeated measures of individuals.

All statistical analyses were performed using SPSS for Windows® version 12.0 (SPSS Inc. 2003). We used Pearson χ^2 statistics to evaluate differences among age–sex classes, den type, and denning habitat, and to test differences between dens that were abandoned and not abandoned during the winter. We used 2 x 2 Pearson χ^2 comparisons with continuity correction if our global test was significant. A significance level of $\alpha = 0.05$ was assumed in our global tests. We considered repeated measures in our 2 x 2 comparisons by restricting the significance level according to Bonferroni [$\alpha = 0.05/(k - 1)$, where k represents number of tests].

To evaluate elevation and slope at den sites according to age–sex classes of bears and den types, in addition to covariate interactions, we used a general linear model one-way analysis of variance. We used Levene's test of homogeneity of variance for each dependent variable across all level combinations of the between-subject factors. We replaced missing values with the corresponding mean value for all parameters in the analysis. If statistical significance was found in the global test, we used η^2 (eta-squared) statistics to describe the proportion of total variability attributable to a factor. The estimates of effect size gave a partial η^2 value for each effect and each parameter estimate. We used post hoc multiple comparisons tests to determine which means differed within age–sex classes, den types, or both. We used the conservative Scheffé test if equal variance could be assumed for the dependent variable, and Tamhane's T2 conservative pairwise comparisons test if we could not assume equal variance.

We investigated whether elevation, slope, or distance to the nearest permanently occupied house, vacation house, plowed road, or unplowed road influenced whether a bear abandoned its den during the winter, using a backward Wald stepwise logistic regression and $\alpha = 0.10$ as the cutoff value for removal. The distances were log-transformed to obtain normal distributions. We replaced missing values with the corresponding mean value for all parameters in the analysis.

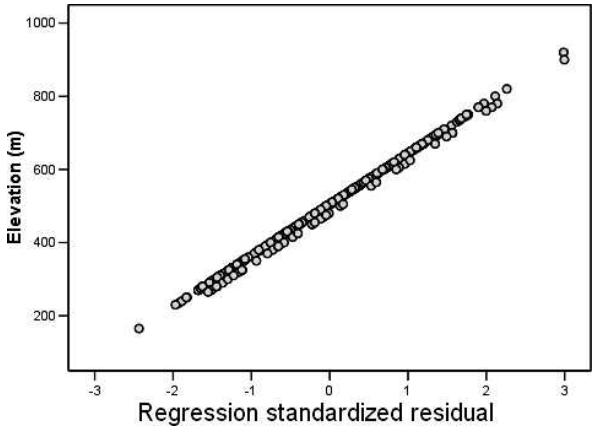

Fig. 2. Scatterplot of residuals for elevation at den sites of each Scandinavian brown bear in the 1986–2003 study.

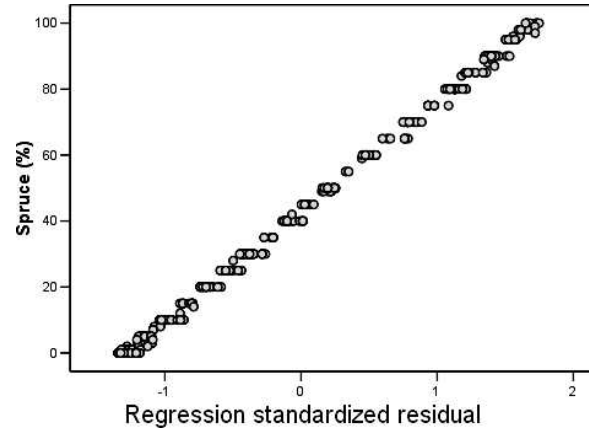

Fig. 3. Scatterplot of residuals for proportion of spruce at den sites of each Scandinavian brown bear in the 1986–2003 study.

We examined the distance of dens from human structures to determine whether this affected den site selection by age–sex classes of bears. Distances were log-transformed to obtain normal distributions. We tested 2 types of structures: houses and roads. For each type, we considered 2 levels of activity: plowed and unplowed roads, and permanently occupied and vacation houses. We expected that if these structures affected den site selection among age–sex classes, the effect would be greater at the higher level of activity. We used one-way analysis of variance for the global test, and the post hoc Tukey honest significant difference test with $\alpha = 0.05$ to identify differences among categories if the global test was significant.

Results

We documented 417 winter dens used by 114 individuals during 1986–2003. When additional dens (from the same winter) and reused dens were excluded, 391 dens were left for analysis (but type of den was missing for 3 dens). The mean age of bears when entering dens was 7.7 years (SD = 5.4, range 2–30).

The plotted scatter of residuals across individual bears showed no pattern that suggested an effect of individual for any den site parameter (Fig. 2 and 3). This suggests that pooling data across individuals did not affect our analyses.

Types of den used by categories of bears

The type of den used by bears was not independent of age–sex class ($\chi^2 = 59.41$, 12 df, $P < 0.001$, Table 1). Adult males selected nest dens over rock dens more strongly than did subadult males ($\chi^2 = 10.26$, 1 df, $P = 0.001$, Table 1,2). Adult males selected nest dens over anthill ($\chi^2 = 13.08$, 1 df, $P < 0.001$), soil ($\chi^2 = 19.96$, 1 df, $P < 0.001$), and rock dens ($\chi^2 = 14.56$, 1 df, $P < 0.001$) more strongly than did subadult females. Adult males selected nest dens over anthill ($\chi^2 = 16.63$, 1 df, $P < 0.001$), soil ($\chi^2 = 12.75$, 1 df, $P < 0.001$), and rock dens ($\chi^2 = 11.72$, 1 df, $P = 0.001$) more strongly than did pregnant females. Adult males selected nest dens over anthill ($\chi^2 = 14.38$, 1 df, $P < 0.001$), soil ($\chi^2 = 10.70$, 1 df, $P = 0.001$), and rock dens ($\chi^2 = 15.62$, 1 df, $P < 0.001$) more strongly than did females with cubs (Table 1, 2). No significant differences in type of dens used were found among subadult males, subadult females, pregnant females, or females with cubs.

Topography at den site used by different categories of bears

Variation in den elevation was most closely related to type of den (ANOVA: $F = 11.59$; 3, 296 df; $P < 0.001$). Our test of homogeneity of variance was significant, indicating that we could not assume equal variance (Levene's test of equality of error variances: $F = 1.43$; 49, 261 df; $P = 0.041$). Anthill dens were higher in elevation than rock and nest dens (anthill–rock: mean difference = 146.80 m, SE = 27.13, $P < 0.001$ and anthill–nest: mean difference = 112.54 m, SE = 23.64, $P < 0.001$, Table 3), and soil dens were higher than rock dens (soil–rock: mean difference = 89.27 m, SE = 27.16, $P = 0.016$, Table 3). Elevation showed no significant relation-

Table 1. Sex and age distribution of brown bear among types of dens in south-central Sweden, 1986–2003. Pearson $\chi^2 = 59.41$, 12 df, $P < 0.001$ for dens successfully used and dens abandoned during the winter combined.

	Age–sex class[a]										
	MS		MA		FS		FP		FC		Total
Den type	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
Anthill	22	9.4	40	17.0	54	23.0	73	31.1	46	19.6	235
Soil	5	8.5	6	10.2	23	39.0	17	28.8	8	13.6	59
Rock	6	25.0	0	0.0	7	29.2	6	25.0	5	20.8	24
Nest[b]	5	15.6	18	56.3	3	9.4	5	15.6	1	3.1	32
Non-abandoned dens	38		64		87		101		60		350
Abandoned dens	4		4		3		12		3		26
Individual bears	27		27		41		39		26		160

[a]MS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.
[b]A nest of sticks on the ground.

ship with age–sex class (ANOVA: $F = 0.57$; 4, 296 df; $P = 0.68$).

Slope at den sites also was related to type of den (ANOVA: $F = 3.42$; 3, 296 df; $P = 0.018$). Our test of homogeneity of variance was not significant, indicating that we could assume equal variance (Levene's test of equality of error variances: $F = 0.97$; 49, 261 df; $P = 0.54$). Nest dens were on flatter slopes than soil dens (soil–nest: mean difference = 8.21°, SE = 2.57, $P = 0.038$, Table 3). Slope was not significantly related to age–sex class (ANOVA: $F = 1.60$; 4, 296 df; $P = 0.17$).

Denning habitat by category of bears

We found a significant relationship between denning habitat and age–sex class ($\chi^2 = 20.67$, 8 df, $P = 0.008$, Table 4). Subadult males and subadult females selected pine-dominated over spruce-dominated denning habitats more than did adult males ($\chi^2 = 11.26$, 1 df, $P = 0.001$ and $\chi^2 = 14.56$, 1 df, $P < 0.001$, respectively, Table 4). No significant differences in denning habitat were found among subadult males, subadult females, pregnant females, or females with cubs.

Factors associated with den abandonment

A stepwise logistic regression model showed that only distance to the nearest plowed road was associated with whether a bear used the den the entire winter; abandoned dens were closer to plowed roads ($\beta = -0.517$, 1 df, $P = 0.005$). Altitude, slope, and distance to the nearest permanently occupied house, vacation house, and unplowed road showed no significant effect. We found no relationships between types of den or denning habitat and whether dens were used successfully or were abandoned during the winter ($\chi^2 = 1.14$, 3 df, $P = 0.77$ and $\chi^2 = 3.54$, 2 df, $P = 0.17$, respectively).

Influence of human structures on denning sites by bears category

Differences in den placement among bear categories relative to human structures were greater for structures with higher human activity. There was no significant difference among bear categories in distance from nearest vacation houses (ANOVA: $F = 1.12$; 4, 233 df; $P = 0.35$) or from nearest unplowed roads (ANOVA: $F = 0.96$; 4, 213 df; $P = 0.43$). However, there were significant differences for distance to nearest permanently occupied houses (ANOVA: $F = 3.00$; 4, 205 df; $P = 0.020$) and

Table 2. Comparison of types of dens used by different age–sex class of brown bears in south-central Sweden (dens used the entire winter combined with dens abandoned during the winter), 1986–2003. All other 2 x 2 χ^2 comparisons among age–sex class and type of dens showed $P > 0.002$, non-significant when using the Bonferroni correction.

Age–sex class[a]	Type of den	df	χ^2	*P*
MA–MS	rock nest	1	10.26	0.001
MA–FS	anthill nest	1	13.08	0.000
	soil nest	1	19.96	0.000
	rock nest	1	14.56	0.000
MA–FP	anthill nest	1	16.63	0.000
	soil nest	1	12.75	0.000
	rock nest	1	11.72	0.001
MA–FC	anthill nest	1	14.38	0.000
	soil nest	1	10.70	0.001
	rock nest	1	15.62	0.000

[a]MA = adult males, MS = subadult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

Table 3. Topography of den sites among age–sex classes and den types used successfully the entire winter for brown bears in south-central Sweden, including topography of dens that were abandoned during the winter, 1986–2003.

	Elevation (m)			Slope (°)		
	Mean	SD	*n*	Mean	SD	*n*
Age–sex class[a]						
MS	481.1	158.3	40	13.3	15.6	35
MA	530.2	160.3	63	6.3	10.3	55
FS	496.4	140.3	90	12.2	12.9	83
FP	500.9	128.3	100	9.5	12.1	99
FC	505.8	119.0	63	13.7	15.7	54
Total	503.6	139.4	356	10.7	13.3	326
Den type						
Anthill	532.2	126.4	231	9.6	12.5	205
Soil	472.6	152.9	56	14.0	13.3	55
Rock	385.8	99.1	24	14.3	10.6	23
Nest[b]	418.2	136.8	31	4.9	8.6	29
Total	503.7	139.3	354	10.7	13.3	324
Abandoned dens	478.7	140.9	26	8.0	10.1	23

[a]MS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.
[b]A nest made of sticks on the ground.

nearest plowed roads (ANOVA: $F = 7.06$; 4, 290 df; $P = 0.000$). The post hoc Tukey test indicated that adult males denned on average 1.7 km (SE = 1.2) farther from permanently occupied houses than subadult males ($P = 0.017$) and 1.5 km (SE = 1.2) farther than subadult females ($P = 0.044$, Table 5). The post hoc Tukey test also indicated that adult males denned farther from plowed roads than all other categories of bears, but that there were no other differences among bear categories (Fig. 4, Table 5). Adult males denned on average 2.4 km (SE = 1.3) farther from plowed roads than subadult males ($P = 0.001$), 2.0 km (SE = 1.2) farther than subadult females ($P = 0.002$), 2.5 km (SE = 1.2) farther than pregnant females ($P < 0.001$), and 2.4 km (SE = 1.2) farther than females with cubs ($P < 0.001$; Fig. 4, Table 5).

Discussion

We found differences among Scandinavian brown bear age–sex classes in den types, denning habitat, and topography at den sites, with adult males differing the most from other categories. As expected, human structures with higher human activity affected den placement more than those with lower levels of activity. Adult males used denning habitats with less potential human influence than other categories of bears. Abandoned den sites were located significantly closer to plowed roads than dens used all winter.

The topography at den sites differed by den type. Anthill dens occurred at higher elevations than soil, rock, and nest dens; nest dens were on flatter slopes than soil dens (Table 3). Topography (elevation and slope) at den sites did not differ by age–sex classes, except for adult males that used nest dens. Bears in

Table 4. Distribution of den sites in habitat types by age–sex classes of brown bears in south-central Sweden, 1986–2003. Pearson $\chi^2 = 20.67$, 8 df, $P = 0.008$ for dens used and dens abandoned during the winter combined. Includes denning habitats for dens abandoned during winter.

	Age–sex class[a]										
	MS		MA		FS		FP		FC		Total
Denning habitat	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
Pine	16	13.8	8	6.9	37	31.9	33	28.4	22	19.0	116
Spruce	11	7.5	34	23.3	28	19.2	46	31.5	27	18.5	146
Birch	4	10.3	8	20.5	10	25.6	13	33.3	4	10.3	39
Non-abandoned dens	31		50		75		92		53		301
Abandoned dens	3		4		3		9		3		22
Individual bears	25		27		40		39		26		157

[a]MS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

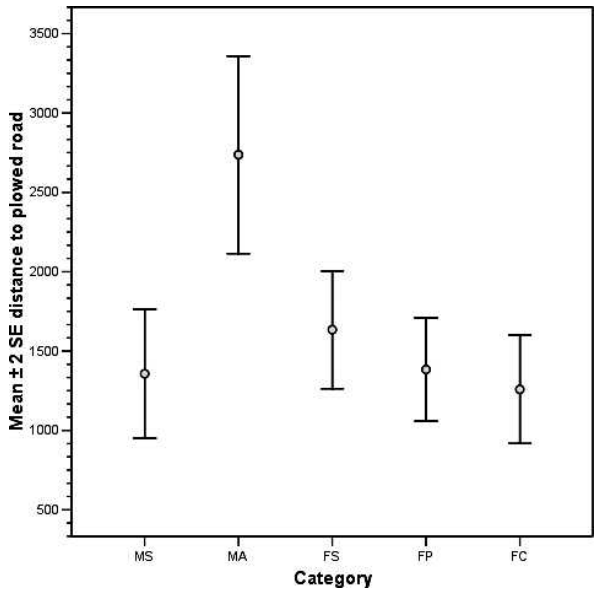

Fig. 4. Mean distance (m) from brown bear dens to the nearest plowed road by age–sex class of bears in south-central Sweden, 1986–2003. Adult males (MA) were significantly different from all other age–sex classes: subadult males (MS), subadult females (FS), pregnant females (FP), and females with cubs (FC), post hoc Tukey test: $P = 0.001$, $P = 0.002$, $P < 0.001$, and $P < 0.001$, respectively.

nest dens are most dependent on snow cover for insulation, due to lack of other elements that could provide insulation (Martorello and Pelton 2003). Although we found no difference in selection of topography at den sites among age–sex classes, adult males, subadult females, and lone females selected flatter slopes at the landscape scale in the same area (Elfström et al. 2008). Schoen et al. (1987) reported that female North American brown bears on Admiralty and Chichagof Islands, Alaska, denned on higher and steeper slopes than males.

Subadult males and subadult females used pine-dominated more than spruce-dominated denning habitats than did adult males. Different vegetation composition between adult males and all other age–sex classes at den sites has been reported in American brown bears (Darling 1987) and black bears (LeCount 1983); in the latter study, adult males denned in more open areas.

Dens of adult males differed the most from other age–sex classes of bears. This may be because of the different physiological demands of adult males (Schwartz et al. 1987, Hellgren 1995). Swenson et al. (2007) reported that adult male brown bears in Scandinavia have larger body mass than adult females and that relative loss of body mass during denning is greater among females than males. Because adult males have greater fat stores than smaller bears and do not have to allocate resources for lactation, they may have different requirements for den sites.

Adult males denned farther from plowed roads than other categories of bears (Fig. 4, Table 5) and farther from permanently occupied houses than subadult males and subadult females (Table 5). Abandoned dens were closer to plowed roads than successfully used dens, suggesting that plowed roads are a source of disturbance, probably from increased human access to the forest for forestry, hunting, skiing, or snowmobiling. In the same study area, but at the landscape scale of analysis, Elfström et al. (2008) showed that brown bears selecting den locations avoided roads that had high traffic and easy access (such as plowed roads).

Linnell et al. (2000) suggested that females with cubs should tolerate greater levels of disturbance without abandoning dens than other categories, because Swenson et al. (1997) reported that abandoning a den was associated with lower reproductive success by female brown bears. The shorter distances to human structures shown by denned females and subadult males (Fig. 4, Table 5) may result from their greater tolerance of disturbance than that of adult males. Alternatively, because adult males occupy den sites farther from human activity and structures, females and subadult males may choose den sites closer to permanently occupied houses and plowed roads to avoid adult males. Manville (1987) reported that American black bear males also denned farther from human activity than females. During the nondenning period in our study area, Nellemann et al. (2007) found that bears avoid recreational resorts and settlements, and there is a higher proportion of subadults in areas within 10 km of recreational resorts and settlements, and a relatively higher proportion of old males (>7 years) ≥10 km from these areas. Rode et al. (2006) concluded that Alaskan female brown bears with young appear to prioritize avoidance of male bears over avoidance of humans when choosing habitats during the nondenning period.

Management implications

We found that female and subadult male brown bears denned closer to human activity and settlements than adult males. Other studies in this area

Table 5. Distance (m) to nearest human-related features of successfully used brown bear dens in south-central Sweden in relation to age–sex class, and den type, 1986–2003. Data includes distances to dens that were abandoned during winter.

Age–sex class[a]		Permanently occupied house	Vacation house	Plowed road	Unplowed road
MS	mean	3146.2	1618.3	1406.1	678.7
	SD	2051.0	1062.3	1286.4	840.1
	n	26	30	33	27
MA	mean	5187.8	2026.8	2778.1	919.1
	SD	2325.6	1213.4	2237.2	907.3
	n	37	41	48	47
FS	mean	3793.8	1865.6	1655.7	882.1
	SD	2170.4	1399.3	1685.7	1101.8
	n	55	52	77	56
FP	mean	3986.2	1821.4	1500.8	759.8
	SD	2065.5	1355.9	1517.0	569.3
	n	47	56	66	46
FC	mean	3754.8	1500.0	1260.3	626.7
	SD	1672.1	905.8	1232.2	391.4
	n	31	40	46	30
Total	mean	4011.0	1783.8	1719.5	799.4
	SD	2159.9	1233.1	1716.2	839.4
	n	196	219	270	206
Den type					
Anthill	mean	4161.5	1795.1	1819.3	823.7
	SD	2160.0	1227.4	1781.7	716.9
	n	123	150	180	139
Soil	mean	3474.3	1660.0	1612.4	935.0
	SD	2264.8	1346.2	1888.9	1358.8
	n	35	35	42	30
Rock	mean	4585.7	1471.4	992.7	334.1
	SD	2721.8	696.9	970.5	244.5
	n	7	7	15	11
Nest[b]	mean	3952.1	1919.0	1599.6	607.1
	SD	1803.6	985.1	1161.6	479.9
	n	24	21.0	24.0	21
Total	mean	4011.0	1783.8	1719.5	799.4
	SD	2159.9	1233.1	1716.2	839.4
	n	196	219	270	206
Abandoned dens	mean	4339.3	2328.9	991.4	725.0
	SD	2246.6	1698.1	782.0	693.0
	n	14	19	25	12

[a]MS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.
[b]A nest made of sticks on the ground.

have shown that females with cubs have the longest and males the shortest denning periods. Taken together, this could suggest a higher probability of humans encountering and potentially disturbing females with cubs in dens close to settlements and plowed roads.

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