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We analyse the selection of denning habitats by Scandinavian brown bears *Ursus arctos* and test if there are differences related to sex and age. At the landscape level, the vegetation types within a 500-m radius around 250 dens used during 1990-2000 in south-central Sweden were analysed using a Geographical Information System (GIS). Compositional analysis (CA) was used to test if bears selected or avoided certain habitat types for denning. There were relatively few differences in habitat selection among bears of different age or sex. Overall, as a group the bears showed distinct preferences in selection of denning habitats; selecting for open canopy (Scots pine *Pinus sylvestris*) forests and habitats with moist soil with rich vegetation, before closed canopy (older Norway spruce *Picea abies* and Scots pine) forests, young forest and clear cuts, mountain coniferous forests and bogs. Denning bears avoided water, alpine mountain-birch forest, deciduous forest, peat, exposed bedrock and gravel pits. Bears denned more on lower altitudes, easterly aspects and steeper slopes than was available. Furthermore, bears avoided intermediate-size roads, perhaps because they are the source of human disturbance, providing a combination of easy winter access (because they are ploughed) and relatively high traffic intensity.

Key words: brown bear, denning site selection, GIS, habitat selection, human disturbance, Sweden, Ursus arctos

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Bears *Ursus* spp. select winter dens based on preferences for sites and habitats, given the availability of sites and habitats. Variation in den utilisation occurs because different habitats present different environmental conditions and provide different denning options for bears. Evolutionary forces may also influence den selection, by increasing the reproductive fitness of genotypes selecting dens in which energetic losses are minimised (Hayes & Pelton 1994). Conditions that promote long-term reproductive fitness may also differ among levels of habitat selection, which suggests that patterns of habitat selection may be scale-dependent (Aebischer et al. 1993, McLoughlin et al. 2002). Selection patterns that allow animals to avoid situations that limit individual fitness have been suggested to be strongest at largest scales, e.g. the population range. Here, we analyse den selection by brown bears *Urus arctos* at the landscape scale, comparing each den site to random sites surrounding it.

Denning ecology studies of bears in North America have documented a wide range of physical and environmental conditions throughout the bears' ranges and have demonstrated the adaptability that bears display in selecting denning sites (Beecham et al. 1983). Habitat selection is of fundamental importance to understanding the natural history of animals (Conner et al. 2003). Several studies worldwide have described different denning habitats, denning sites or dens used by brown bears, such as in Scandinavia (Swenson et al. 1996, Swenson et al. 1997, Friebe et al. 2001, Manchi & Swenson 2005), Croatia (Huber & Roth 1997), Poland (Jakubiec 2001), Russia (Vaisfeld & Chestin 1993), China (Li et al. 1994) and Alaska (Miller 1990, Van Daele et al. 1990). However, only a few studies have compared the choice of denning sites with those available: Schoen et al. (1987) in Alaska, Naves & Palomero (1993) in Spain, Groff et al. (1998) in Italy, and Petram et al. (2004) in Slovenia. Here, we evaluate den site selection of Scandinavian brown bears, because effective management and conservation demands accurate information on specific habitat requirements (Clark et al. 1993, Lyons et al. 2003).

Manville (1987) reported differences in denning habitat selection between the sexes in North American black bears *Ursus americanus*, with females being more selective than males. Abandonment of winter dens by pregnant females has been shown to cause an elevated mortality among bear cubs (Swenson et al. 1997). After females give birth, the cost of den relocation rises dramatically, as young cubs will be exposed to thermal stress and 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 show a tolerance for industrial activity as long as the source of the noise was some kilometres away from the den. Nevertheless dens visited directly by people were often abandoned.

We tested whether the denning habitats used by brown bears mirrored the proportion of habitats available on a landscape scale, and if not, which habitats were selected or avoided. We also tested if the sexes differed in their selection of denning habitats, and if dens used the entire winter differed from dens that had been abandoned. Lastly, we tested the hypothesis that denning brown bears avoid roads in order to reduce the potential for disturbance.

Methods

Study area

The study was conducted in the counties of Dalarna and Gävleborg in south-central Sweden and in the county of Hedmark in southeastern Norway (67°N, 13°E) and covers the southern part of the brown bear distribution in Scandinavia. The study area encompasses about 20,700 km^2 (Fig. 1) and is dominated by coniferous forest (60.3%), mainly Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Deciduous tree species make up a minor fraction of the area (8.2%) and are mainly birches *Betula pubescens*, *B. pendula*, alder *Alnus incana* and mountain ash *Sorbus aucuparia*. The ground vegetation is mainly ericaceous shrubs *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum hemaphroditum* and mosses. Bogs are a relatively frequent element (15.0%) in the landscape; other features present are open fields, mainly grass (7.3%), open water (7.1%) and mountain forest (3.9%; Table 1). Precipitation ranges within 350-450 mm during the vegetation period (mean temperature $\geq$5°C) with 800-1,100 degree-days (Swenson et al. 1996). Snow cover lasts from about November to April/early May (Swenson et al. 1996). Elevations range from 140 m a.s.l. in the east, to 1,045 m a.s.l. in the west towards the Norwegian border. About 11% of the study area is below 160 m, 31% is within 160-320 m, 50% is within 320-650 m, and 8% is above 650 m a.s.l. The terrain in the southeastern part of the study area is relatively flat, whereas the western part is topographically

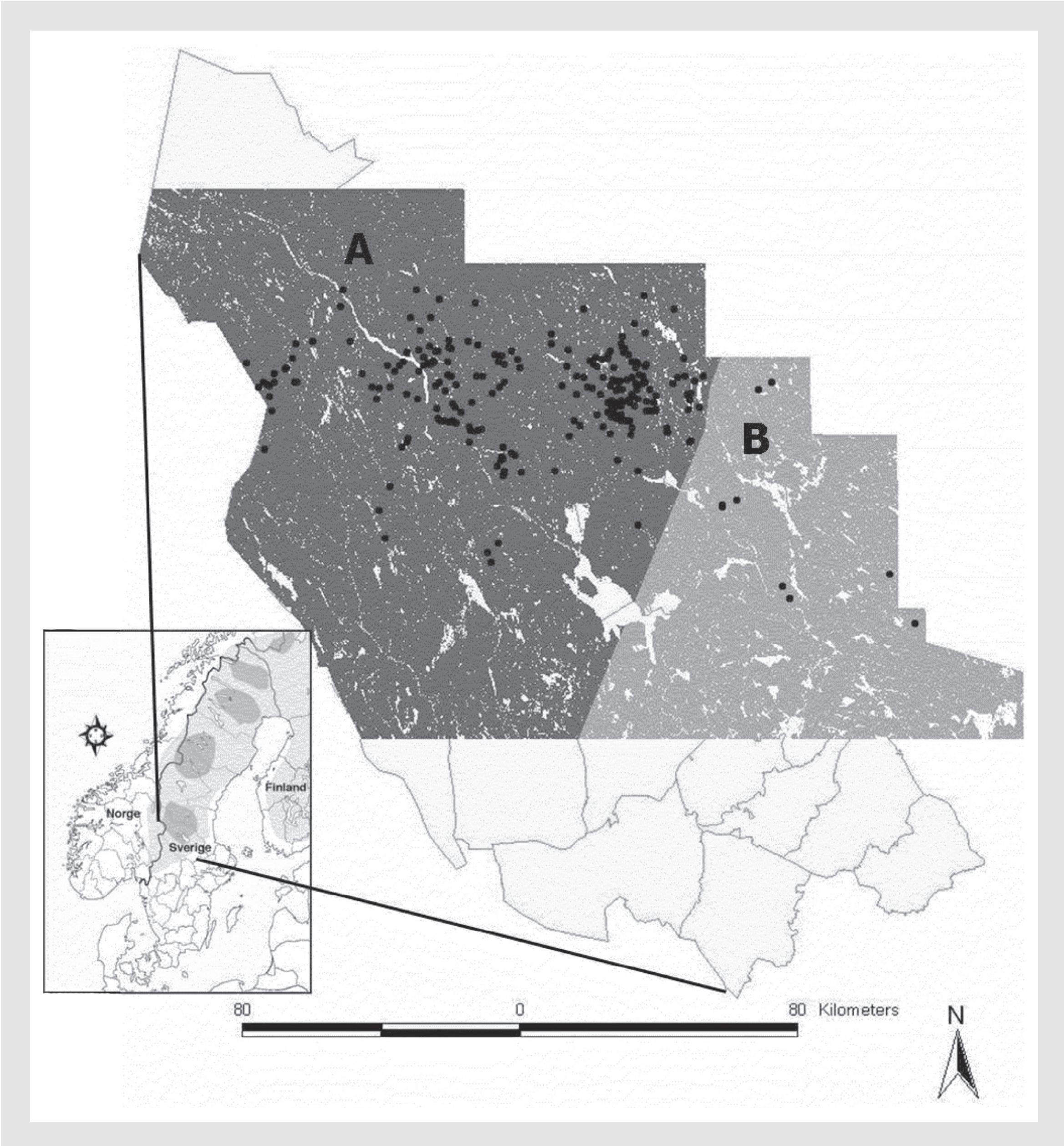

Figure 1. The study area for denning habitat selection by brown bears, situated in Dalarna and Gävleborg Counties in south-central Sweden. 'A' indicates western satellite scene coverage and 'B' indicates eastern satellite scene coverage, dark symbols represent brown bear dens. The insert map shows the distribution of brown bears, with darker areas showing areas of higher densities.

diverse with elevated terrain. In >90% of the study area, the slopes are <8°.

Structure of den data and denning anomalies

Radio-collared brown bears were separated into five different reproductive categories. Males ≥5 years of age were defined as adults (MA) and males <5 years of age were defined as subadults (MS). Females were defined as subadults (FS) until they had become reproductively active. Adult females were separated into lone females (FL), which were females that gave birth during denning (once they have started reproducing, very few females enter the den as non-pregnant or without cubs; the ones who did were

Table 1. Classified vegetation types in the satellite images that were used in the study of den site selection by brown bears in south-central Sweden, * indicates combined parameters.

Abbreviation	Habitat description, labelled according to Centrum för bildanalys (1998)		% coverage in total study area
A	HABITAT 1: WATER		7.1
B	HABITAT 2: CLOSED_ CANOPY_CONIFEROUS_FOREST (Older spruce *Picea abies* and pine *Pinus sylvestris*)		23.0
C	HABITAT 3: OPEN_CANOPY_CONIFEROUS_FOREST (Pine *P. sylvestris* with thin soil)		11.9
D	HABITAT 4: CONIFEROUS_FOREST_WITH_ UNDERSTORY_OF_VACCINIUM_TYPE		6.3
E	HABITAT 5: DECIDUOUS_FOREST		3.0
F	HABITAT 6:* YOUNG_FOREST HABITAT :* OVER-GROWN_CLEAR-CUT HABITAT :* NEW_CLEAR-CUT	Young forest and clear cut	16.7
G	HABITAT 7: PEAT		0.5
H	HABITAT 8:* FEN,_LOW_WATER_CONTENT HABITAT :* BOG,_LOW_WATER_CONTENT HABITAT :* FEN,_HIGH_WATER_CONTENT HABITAT :* BOG,_HIGH_WATER_CONTENT	Bogs	15.0
I	HABITAT 9: MOIST_SOIL_WITH_RICH_VEGETATION		3.8
J	HABITAT 10:* GRASS HABITAT :* EXPOSED_SOIL/FIELDS HABITAT :* FIELDS_AND_PASTURE	Open fields, grasses and pastures	7.3
K	HABITAT 11:* INDUSTRY_AND_BUILDINGS HABITAT :* RESIDENTIAL	Buildings	0.2
L	HABITAT 12: LICHEN-RICH_MOUNTAIN_BIRCH_FOREST		0.5
M	HABITAT 13: OTHER_MOUNTAIN_BIRCH_FOREST		1.0
N	HABITAT 14: LICHEN-RICH_ALPINE_TERRAIN		0.1
O	HABITAT 15: PERMANENT_SNOW-FIELDS		0.1
P	HABITAT 16: EXPOSED_BEDROCK_AND_GRAVEL_PITS		0.7
Q	HABITAT 17: ALPINE_MOOR		0.7
R	HABITAT 18: OPEN_CANOPY_MOUNTAIN_CONIFEROUS_FOREST_WITH_SHRUBS/LICHEN		2.4

excluded from our analysis), and females with cubs (FC), which were females that denned with cubs that became yearlings while in the den. Very few females entered the den with yearlings in this area.

Sample sizes for den characteristics varied because not all parameters were obtained for every den. Dens that were abandoned during the winter were analysed separately to contrast with successful dens. This treatment of abandoned dens further avoids differences resulting from hasty site selection (Kolenosky & Strathearn 1987). In one case a den was reused by the same bear in two successive years; we took a conservative approach and analysed it only once.

Unit of independence

Because a bear must select a den each year, each den has been treated as an independent unit or event, in agreement with similar studies (Schwartz et al. 1987, Hayes & Pelton 1994, Clark et al. 1995, Ball et al. 2001, Hightower et al. 2002). However, pooling data across individuals is justifiable only if the data do not show individual variation (Aebischer et al. 1993). To test if pooling data across individuals was justified, a Compositional Analysis (CA hereafter; Aebischer et al. 1993) was performed using only one den per individual, i.e. with individuals treated as the unit of independence, rather than dens. This allowed the comparison of the coefficient of variation (CV) between the two data sets, all bear dens with several dens for some individuals versus dens with one den per individual.

Telemetry and location of den sites

Bears were immobilised and fitted with radio-transmitters (Arnemo et al. 2006), after being darted from a helicopter with DAN-INJECT® equipment (DAN-INJECT AdS, Børkop, Denmark). Locations of dens were identified with telemetry by triangulation from the ground and by aerial telemetry during 1985-2003. Coordinates of the dens were obtained with Global Positioning System (GPS) units when they were visited on the ground.

Landscape features

The habitat variables analysed were determined from satellite images provided by the Administrative Board of Dalarna County. The satellite image was developed at 'Satellitbild i Kiruna', a satellite centre in Kiruna, Sweden, and was constructed from two Landsat TM scenes that covered the study area (see Fig. 1). We analysed only bear dens within five years of when the satellite image was taken to guard against any confounding effects of habitat change. The first satellite scene covered almost the entire study area and was taken in 1995. The second satellite scene covered the eastern portion of the study area and was taken in 1992. The eastern area did not include any dens older than 1990 so the dens in this scene ranged from 1990 until 1997.

Vegetation classification was conducted in 1998 at the Center for Image Analysis in Uppsala, Sweden. The two satellite scenes were treated and classified separately. The classification was based on both field observations and Geographical Sweden Data (GSD) map data in raster format with a scale of 1:50,000 for all classes except the habitat type called 'buildings' (Habitat K in Table 1), which was based on a scale of 1:250,000. When combining and resampling the different sources of map data at the Center for Image Analysis, a nearest neighbour technique was used, and to minimise differences between the two scenes when classifying, a maximum likelihood technique was used. The classification of vegetation types produced an initial total of 26 classes with a pixel resolution of 25×25 m. Due to different years between the two scenes, we combined time-sensitive classes, e.g. clearcuts. In some cases the classification was uncertain (Centrum för bildanalys 1998) so these classes were combined (see Table 1) for a conservative analysis.

The GIS analyses were performed in ArcView version 3.2a (ESRI 1996a), with extension software Spatial Analyst version 1.0 (ESRI 1996b) and Animal Movement version 1.1 (Hooge & Eichenlaub 1997). When defining the size of the available area for analysis, we considered the home range size of bears in order to not constrain the distribution of random points to a narrow area around the den, which might have caused the exclusion of available denning area (Aebischer et al. 1993). Dahle & Swenson (2003) reported a post-mating season home range size of 500 km^2 for male brown bears in central Sweden, which corresponds to a radius of 12.6 km. A 25-km radius was chosen as the available areas, which theoretically equals twice the radius of the average home range of a typical male Scandinavian brown bear. The 'available' area will thus very probably include the bear's entire home range, even when the den is situated on the periphery. Within each den's available area, 100 random points were generated with the only *a priori* requirement being that they were not allowed to be positioned in water. Then, buffer zones with a 500 m radius were created around the random points, extracting the vegetation from the underlying satellite theme. The mean values from the 100 random buffer zones were then compared with the buffer zone value from its corresponding den to enable statistical comparisons of use to availability. The random points and the position of its corresponding den were used to perform the same comparisons of use to availability for altitude data and nearest road distances. Altitude was extracted from a raster-based digital map with a pixel resolution of 50 m, which also made extraction of aspect and slope possible after surface analysis. Distances to roads were extracted from a vector-based digital road map, provided by the Administrative Board of Dalarna County, and separated into five different size classes (Table 2).

Compositional analyses of habitat selection

We used compositional analysis (CA; Aebischer et al. 1993) to test for significant deviations from random use and to rank the habitat classes from most to least used. In contrast to traditional methods of habitat selection analysis (e.g. χ^2), this multivariate technique allows for analysis of habitat selection proportions and does not violate unit-sum constraints or result in inappropriate sample-size pooling (Aebischer et al. 1993, Lyons et al. 2003). For these and a variety of other reasons, CA has become one of the most widely used habitat analysis procedures (Conner et al. 2003). Habitat selection is defined here as a difference between observed habitat utilisation and expected habitat utilisation, as determined from a null model (Aebischer et al. 1993,

Table 2. The five road classes used in the analysis of den site selection by brown bears in south-central Sweden.

Parameters	Type	Width	Road number	Category code (GSD)
Road_1	Paved national highway	5-7 m and > 7 m	E4 - 99	5211 and 5311
Road_2	Paved highway	5-7 m and > 7 m	100 - 499	5221 and 5321
Road_3	Paved smaller highway	5-7 m and > 7 m	> 500	5331 and 5231
Road_4	Gravel roads for residents	< 5 m	> 500	5431
Road_5	Gravelled forestry roads	< 5 m	-	5551

Conner et al. 2003). All recorded denning characteristics were compared among sex and age classes of bears. Before log-ratio transformation, all zero counts were replaced with 0.000001, which is one magnitude smaller than the smallest value observed in the data set, in agreement with Aebischer et al. (1993). Significant departure from random for each habitat type was evaluated using randomisation tests involving 999 permutations of the data with the minimum attainable P value of 0.001. The resultant ranking matrix of pair-wise habitat comparisons was used to rank relative habitat preferences (Aebischer et al. 1993). Habitats within a 25-km radius of the den were considered available denning habitat and habitat use was derived from dens. Compositional analyses were performed in SAS version 8.02 (SAS Institute 1989).

Statistical analyses

All statistical analyses except CA were performed using the program SPSS for Windows® version 12.0 (SPSS 2003). The Wilcoxon matched-pairs signed ranks test was used to compare used dens against their available sites (e.g. Ball et al. 2001, Rao et al. 2003). To evaluate differences among reproductive categories of bears and dependent variables, Kruskal-Wallis tests and Mann-Whitney U tests were used. A significance level of $\alpha = 0.05$ was accepted.

Results

In total, 250 dens from the period 1990-2000 were analysed using GIS (Table 3). Moderately young bears dominated the data set (mean age of 7.5 ± 5.7 SD years, range: 2-30).

Unit of independence

We performed an additional CA using one den from each of 65 individuals, as well as the CA using the entire set of 231 successful dens. Analysis of the CV between the two data sets showed no significant difference (Mann-Whitney U-test; $P = 0.61$), suggesting that pooling data across individuals was not a problem.

Compositional analysis of vegetation types

We considered the different reproductive categories of bears separately, but the overall conclusions were the same. A ranking matrix for all brown bear dens used for the entire winter, based on a pair-wise comparison of the habitat types ($N = 231$), showed the following ranking order of habitat types (from highest use to least use), with the triple sign ⋙ indicating a significant selection (at $P < 0.05$), relative to all other following habitat types (Table 4):

open canopy coniferous > lichen-rich alpine terrain > moist soil with rich vegetation ⋙ closed canopy coniferous > young forest & clear-cut > lichen-rich mountain-birch forest > coniferous with *Vaccinium* > open canopy mountain-coniferous > buildings > bogs > permanent snow-fields > open fields; grasses & pastures > alpine moor ⋙ alpine mountain-birch forest > water ⋙ deciduous forest > peat ⋙ exposed bedrock & gravel pits

Successful dens vs abandoned dens

Dens that were abandoned in winter had significantly higher proportions of the habitat types 'water' and 'moist soil with rich vegetation' within 25 km, compared to successful dens (Mann-Whitney U-test: $P = 0.021$ and 0.022, respectively; Table 5). No other significant differences were found (all comparisons: $P > 0.30$).

Denning in relation to topography

Bears selected denning habitat with significantly lower altitude, easterly aspect and steeper slope than available, based on the analysis of dens used all winter by all categories of bears combined (Table 6). Most categories of bears showed a similar pattern

Table 3. Number of brown bears with successful dens and brown bears that abandoned winter dens during 1990-2000 in south-central Sweden.

	Successful dennings		Abandoned dens		
Reproductive category	No of individuals	No of dens	No of individuals	No of dens	Rate of abandonment (%)
Males subadult (MS)	20	31	3	3	8.8
Males adult (MA)	13	30	0	0	0.0
Females subadult (FS)	25	59	2	2	3.3
Lone females (FL)	27	69	7	11	13.8
Females with cubs (FC)	20	42	3	3	6.7
Total	105	231	15	19	7.6

Table 4. A simplified ranking matrix for all brown bears denning for the entire winter in south-central Sweden, based on comparing proportional denning habitat use with proportions of total available denning habitat types. Each mean element in the matrix is replaced by its sign; a triple sign represents significant deviation from random at $P < 0.05$. See Table 1 for habitat abbreviations.

	Habitat types																		
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	Rank
A	-	---	---	---	+++	---	+++	---	---	---	---	---	-	---	---	+++	-	---	3
B	+++	-	---	+	+++	+	+++	+++	---	+++	+++	+	+++	-	+++	+++	+++	+	14
C	+++	+++	-	+++	+++	+++	+++	+++	+	+++	+++	+++	+++	+	+++	+++	+++	+++	17
D	+++	-	---	-	+++	-	+++	+	---	+	+	-	+++	---	+	+++	+++	+	11
E	---	---	---	---	-	---	+	---	---	---	---	---	---	---	---	+++	---	---	2
F	+++	-	---	+	+++	-	+++	+++	-	+++	+++	+	+++	-	+++	+++	+++	+	13
G	---	---	---	---	-	---	-	---	---	---	---	---	---	---	---	+++	---	---	1
H	+++	---	---	-	+++	---	+++	-	---	+	-	---	+++	---	+	+++	+	-	8
I	+++	+++	-	+++	+++	+	+++	+++	-	+++	+++	+	+++	-	+++	+++	+++	+++	15
J	+++	---	---	-	+++	---	+++	-	---	-	-	---	+++	---	-	+++	+	-	6
K	+++	---	---	-	+++	---	+++	+	---	+	-	-	+++	---	+	+++	+	-	9
L	+++	-	---	+	+++	-	+++	+++	-	+++	+	-	+++	---	+++	+++	+++	+	12
M	+	---	---	---	+++	---	+++	---	---	---	---	---	-	---	---	+++	---	---	4
N	+++	+	-	+++	+++	+	+++	+++	+	+++	+++	+++	+++	-	+++	+++	+++	+++	16
O	+++	---	---	-	+++	---	+++	-	---	+	-	---	+++	---	-	+++	+++	-	7
P	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	-	---	---	0
Q	+	---	---	---	+++	---	+++	-	---	-	-	---	+++	---	---	+++	-	-	5
R	+++	-	---	-	+++	-	+++	+	---	+	+	-	+++	---	+	+++	+	-	10

Ranking order of denning habitat types: C > N > I ⋙ B > F > L > D > R > K > H > O > J > Q ⋙ M > A > E > G ⋙ P

regarding altitude and aspect (see Table 6). However, adult males selected significantly flatter slopes, compared to available denning sites, than the selection exhibited by all bears. Subadult and lone females showed a significant selection for lower altitude, but, in contrast to the category of all bears, preferred flatter slopes. Females with cubs did not show any significant selection concerning elevation. Most importantly, bears that abandoned their dens during the winter had selected sites with significantly flatter slopes, compared to available denning sites, than the category of all successfully denning bears.

Denning in relation to roads

Successful dens of all bears combined were significantly farther from roads of classes 2, 3 and 4 (i.e. paved highways, smaller highways and gravel roads used by residents; see Table 2), than available denning sites. Conversely, bear dens were significantly closer to roads of classes 1 and 5 (paved national highways and forestry roads; see Table 2), compared to available denning sites (Fig. 2 and Table 7). These general patterns were found for all bear categories (see Table 7).

Table 5. Comparison of proportions of water and moist soil with rich vegetation at the landscape level for successful (N = 231) and abandoned (N = 19) brown bear dens in south-central Sweden, for all bear categories combined. Values are given as mean ± SD

Habitat type	Successful dens	Abandoned dens
Water	0.03 ± 0.05	0.04 ± 0.04
Moist soil with rich vegetation	0.07 ± 0.08	0.12 ± 0.12

Discussion

We tested whether the denning habitats used by brown bears mirrored the proportion of habitats available on a landscape scale and if not, which habitats were selected or avoided. Less important limiting factors may influence habitat selection patterns only at smaller scales of selection, e.g. within the home range (McLoughlin et al. 2002). Failure to view habitat selection as a hierarchical process may result in a narrow and possibly misleading notion of the importance of different habitats to animals (Aebischer et al. 1993, McLoughlin et al. 2002, Lyons et al. 2003).

A few previous studies (Schoen et al. 1987, Naves & Palomero 1993, Groff et al. 1998, Petram et al. 2004) also compared used and available denning sites. However, in some (Naves & Palomero 1993, Groff et al. 1998, Petram et al. 2004) there is at least a possibility of bias, because they identified denning sites by searching for dens rather than from

Table 6. Comparison of elevation (in m), aspect (in °) and slope (in °) for dens of brown bears in different categories compared with available habitat in south-central Sweden. * and ** indicate a significant difference at P<0.05 and 0.001, respectively, for Wilcoxon matched-pairs signed ranks test.

Bear category	N	Habitat type	Denning sites Mean±SD	Available sites Mean±SD	P
All bear categories, successful denning	231	Altitude**	499.7±121.2	521.0±109.4	0.000
		Aspect**	152.4±96.6	174.1±12.3	0.001
		Slope*	5.6±5.0	5.5±1.1	0.017
All bear categories, abandoned dens	19	Altitude	475.2±144.3	498.4±103.5	0.31
		Aspect	157.5±93.0	176.2±10.3	0.33
		Slope*	3.9±2.8	5.4±1.4	0.018
Subadult males, successful denning	31	Altitude	434.5±100.7	444.1±86.0	0.46
		Aspect*	115.4±77.6	169.1±10.9	0.002
		Slope*	6.5±4.3	4.6±0.8	0.040
Adult males, successful denning	30	Altitude	548.1±149.0	541.4±112.2	0.63
		Aspect	144.2±86.9	177.0±9.4	0.057
		Slope*	5.0±4.8	5.3±1.3	0.053
Subadult females, successful denning	59	Altitude**	478.0±118.6	512.0±103.4	0.001
		Aspect	164.6±95.9	176.0±11.5	0.34
		Slope*	4.6±3.5	5.6±0.9	0.005
Lone females, successful denning	69	Altitude*	512.7±110.0	540.8±111.5	0.005
		Aspect	161.6±104.7	173.3±12.5	0.32
		Slope*	5.5±5.6	5.6±1.1	0.019
Females with cubs, successful denning	42	Altitude	522.1±113.6	543.6±104.8	0.20
		Aspect	153.1±100.0	174.4±15.0	0.15
		Slope	6.6±6.2	5.8±1.1	0.96

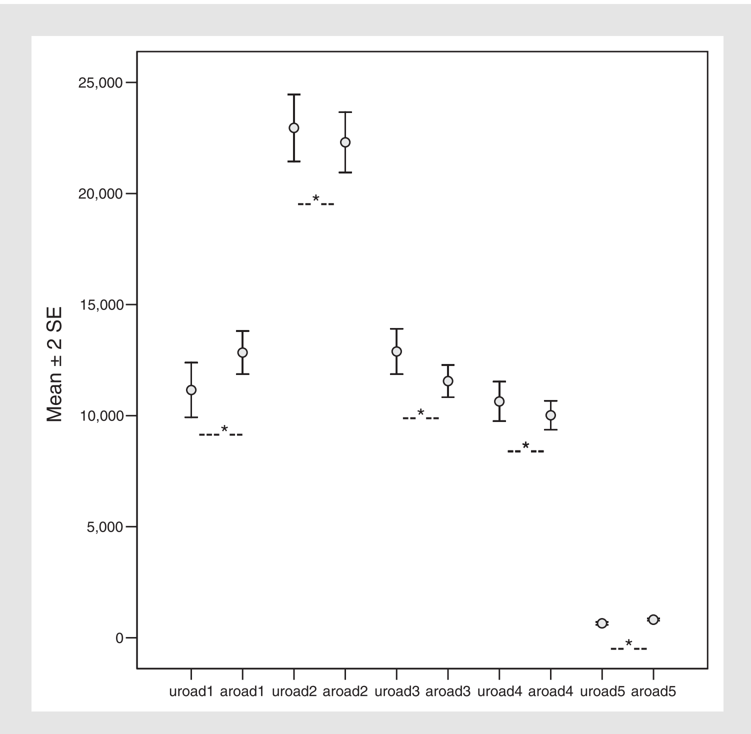

Figure 2. Comparison of nearest road distances to successful dens of brown bears and to available denning sites in south-central Sweden. On the X-axis: u-represents used distances and a-represents available distances, to the different road classes (see Table 2). * indicates a significant difference (Wilcoxon Matched-Pairs Signed Ranks test) between used dens and available denning sites within each road class. Bars represent standard errors.

following marked bears. To avoid any potential bias, we identified the denning sites actually used by bears by tracking radio-collared bears to their den, and then we compared them to available sites.

Our results suggest that pooling data across individuals, as we did, is justifiable (Aebischer et al. 1993) and has been done in similar studies (Schwartz et al. 1987, Clark et al. 1995, Ball et al. 2001, Hightower et al. 2002).

The compositional analysis showed that, at a landscape scale, Scandinavian brown bears showed distinct preferences in selection of denning habitats. The most selected denning habitat types seemed to provide bears with adequate understory vegetative cover, in agreement with Lecount (1983), who reported that dense vegetative cover and early development of spring forage was important for denning habitat selection by American black bears. According to Servheen & Klaver (1983), brown bears seek out iso-

Table 7. Comparisons of distances to roads (in m) for different brown bear categories in relation to availability in south-central Sweden. * and ** indicate a significant difference at P<0.05 and 0.001, respectively, for Wilcoxon matched-pairs signed ranks test. See Table 2 for definition of road classes.

Bear category	N	Road class	Denning sites Mean ± SD	Available sites Mean ± SD	P
All bear categories, successful denning	219	Road 1**	11150 ± 9110	12840 ± 7190	0.000
		Road 2**	22950 ± 11140	22300 ± 10040	0.001
		Road 3**	12890 ± 7560	11560 ± 5350	0.000
		Road 4*	10640 ± 6580	10020 ± 4810	0.004
		Road 5**	650 ± 470	820 ± 360	0.000
All bear categories, abandoned dens	19	Road 1	11130 ± 7940	12160 ± 6210	0.17
		Road 2*	27980 ± 9820	25790 ± 10490	0.004
		Road 3*	13140 ± 7630	10310 ± 5560	0.003
		Road 4	11950 ± 7300	10870 ± 5320	0.38
		Road 5	770 ± 630	780 ± 240	0.97
Subadult males, successful denning	31	Road 1*	9590 ± 6780	10930 ± 5280	0.002
		Road 2	19500 ± 10410	18250 ± 8380	0.060
		Road 3**	15180 ± 7790	13030 ± 5780	0.000
		Road 4*	10370 ± 4850	9060 ± 2990	0.011
		Road 5*	500 ± 320	660 ± 230	0.024
Adult males, successful denning	29	Road 1	16560 ± 10050	17330 ± 8710	0.41
		Road 2	25620 ± 10410	25540 ± 9910	0.16
		Road 3*	11850 ± 6520	10550 ± 4580	0.023
		Road 4	10330 ± 8170	10070 ± 6080	0.72
		Road 5	960 ± 700	840 ± 280	0.61
Subadult females, successful denning	58	Road 1**	9680 ± 8160	11810 ± 6090	0.000
		Road 2*	23670 ± 11570	22410 ± 10440	0.002
		Road 3*	13050 ± 7910	11710 ± 5410	0.002
		Road 4**	12510 ± 5930	11020 ± 4390	0.000
		Road 5*	650 ± 400	830 ± 450	0.006
Lone females, successful denning	63	Road 1**	11250 ± 9750	12910 ± 7410	0.000
		Road 2	21800 ± 11220	21780 ± 10110	0.78
		Road 3*	12340 ± 7410	11560 ± 5200	0.026
		Road 4	8840 ± 6830	9120 ± 4970	0.43
		Road 5**	590 ± 450	850 ± 340	0.000
Females with cubs, successful denning	38	Road 1*	10390 ± 9190	12430 ± 7380	0.051
		Road 2	24530 ± 11060	24620 ± 10020	0.67
		Road 3	12490 ± 7800	10890 ± 5700	0.060
		Road 4	11230 ± 6470	10720 ± 5060	0.29
		Road 5*	630 ± 420	850 ± 360	0.015

lated and remote areas that will accumulate enough snow to insulate them from cold winter temperatures, which may explain the selection of open canopy forests, providing a thicker snow cover and colder temperatures, rather than closed canopy forests. However, snow is probably less important for insulation where temperatures rarely fall below -20°C (Schoen et al. 1987). Instead, bears need dry sites where temperatures generally remain below 0°C and free-flowing surface water is rare (Schoen et al. 1987). We suggest that the avoidance of open fields, water and bogs may be to avoid wet soil conditions, with free-flowing surface water, which reduces the bears' insulation (Schoen et al. 1987). Smith et al. (1994) also reported avoidance of marshlands and grass-sedge openings by denning North American black bears, as did Beecham et al. (1983) and Schwartz et al. (1987). Our analysis thus supports the hypothesis that bears did indeed select denning habitat.

Overall, bears that abandoned their dens during winter selected habitats rather similar to those with successful denning sites. Habitats surrounding successful dens were less wet than abandoned dens (see Table 5), but the difference in the proportion of water was small (0.03 vs 0.04, respectively) so we are hesitant to emphasise it. Nevertheless, the potential importance of this variable is consistent with our other finding that bears which abandoned their dens during winter had used sites with flatter slopes which could result in running water entering the den. The role of water needs further study to determine how general a factor it may be. One explanation for finding rather small differences in habitat between successful and abandoned dens is that the major reason for den abandonment seems to be human disturbance. Swenson et al. (1997) found that at least 67% of abandoned dens had had human activity near them. Thus, habitat might play a secondary role, and the influence of human use of an area might be more important. Humans may have used flatter slopes preferentially in the winter, for example for snowmobiling, skiing or cutting timber.

Scandinavian brown bears showed distinct denning selection patterns concerning topography. Avoidance of denning on completely flat ground, i.e. sites not on slopes, has also been reported for American brown bears and may be due to a lack of ground insulation and potential flooding (Judd et al. 1986). In Spain, Naves & Palomero (1993) also reported a selection for steep slopes for denning, and argued that this may be because of a need for a safe refuge. Preferences for all aspects have been reported in various studies of American black and brown bears: Vroom et al. (1980), west; Judd et al. (1986), Mack (1990) and Smith et al. (1994), north; Kolenosky & Strathearn (1987), east; Schoen et al. (1987) and Miller (1990), south, although Van Daele et al. (1990) reported no preference in selection of aspect. Schoen et al. (1987) suggested that bears prefer slope exposures that accumulate the greatest snowpack, insulating the den. In China, Li et al. (1994) argued that eastern, southeastern and southern slopes could expose the den to more solar energy and reduce the influence of cold wind in winter. Whether or not Scandinavian dens with easterly aspects are provided the greatest snowpack requires further evaluation.

In our tests for any effect of roads and disturbance, avoidance of a road was revealed as a significantly longer distance from a road to an actual den than from random sites to a road, whereas selection was revealed by a significantly shorter distance. In selecting den sites, brown bears avoided roads that combined high traffic with ready access; they avoided denning near road classes 2, 3 and 4 (see Table 7), as has been documented for American brown bears (Kasworm & Manley 1990). These roads are of intermediate size (see Table 2), with relatively high traffic intensity and allow easy access for hunters, fishermen and others to walk into the forest and may represent a high disturbance potential for bears. In contrast, road classes 1 and 5, i.e. the largest and smallest types of road, respectively, were not avoided by bears. In fact, bears selected dens with shorter distances to these road types than was available (see Table 7). The largest road, class 1, is a national highway and, therefore, used only for high speed transportation and on these roads parking is almost completely prohibited. Thus this type of road evidently has a minor effect on denning bears, because people can not use the road for access to the area and the effects of vehicles which do not stop is likely trivial. Furthermore, the smallest road type, class 5, has almost no traffic during the denning period, because snow is not ploughed on these roads and thus this class of roads is likely to have only a very minor disturbance potential, again because it provides little access. As we found for class 1 and 5 roads, Clark et al. (1995) reported a tendency for American black bears to den near roads and also suggested the very low traffic intensity during winter to explain the behaviour. Kasworm & Manley (1990) stressed the importance of closed roads for bears to eliminate the disturbance potential. Analyses within each reproductive category concerning the nearest road distances showed the same pattern as for all bear categories (see Table 7), suggesting that on a landscape scale, there were no differences in road avoidance behaviour among sex and age categories of bears. Overall, our hypothesis that denning brown bears avoid roads in order to reduce disturbance potential was supported in that bears did avoid roads with high disturbance and they did not avoid roads with low disturbance.

Conclusions

Our analysis revealed that Scandinavian brown bears showed distinct selection for denning habitat and denning topography compared to availability. Furthermore, bears selected den sites with respect to disturbance. Specifically, although they denned near the roads with little disturbance (large highways where parking is prohibited, and very small roads which are not ploughed in winter), they avoided the three intermediate sizes of roads which are associated with much more disturbance.

Management implications

Our analysis of the denning selection of Scandinavian brown bears suggests that forest managers should try to preserve open canopy (Scots pine) forests and habitats with moist soil with rich vegetation. Furthermore, our analysis suggests that access by humans via roads is an important aspect for denning bears. In order to minimise disturbance to denning bears, the density of intermediate size roads should not be allowed to increase. If possible, many minor roads should be closed during winter in order to limit the access to the forest for hunters, fishermen and others, because bears seem to select denning sites where human disturbance can be avoided.

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