

Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*)

Jodie Martin, Mathieu Basille, Bram Van Moorter, Jonas Kindberg, Dominique Allainé, and Jon E. Swenson

Abstract: In human-dominated landscapes, species with large spatial requirements, such as large carnivores, have to deal with human infrastructure and activities within their home ranges. This is the case for the brown bear (*Ursus arctos* L., 1758) in Scandinavia, which is colonizing more human-dominated landscapes, leading inevitably to an overlap between their home ranges and anthropogenic structures. In this study, we investigated fine-scale habitat selection by brown bears to examine how they deal with this potential disturbance. Using Global Positioning System (GPS) data, we studied (i) habitat selection of female brown bears within their home range and (ii) the influence of diurnal variation in human disturbance on fine-scale habitat use. As expected, females selected habitats within their home range that provided abundant food resources and minimized human-caused disturbance. In addition, our temporal analysis of habitat selection revealed an avoidance of disturbed areas and a selection of slopes by bears during periods of highest human activities, i.e., during daylight hours. We clearly demonstrate the importance of considering the fluctuations in human activity when studying habitat selection, especially at fine spatial scales. Failing to do so may considerably reduce the power to detect important fine-scale habitat-selection behaviors.

Résumé : Dans les paysages dominés par l'homme, les espèces qui requièrent de grands espaces, tels que les grands carnivores, doivent gérer la présence d'infrastructures et d'activités humaines dans leurs domaines vitaux. C'est le cas de l'ours brun (*Ursus arctos* L., 1758) en Scandinavie, qui colonise de plus en plus les paysages dominés par l'homme, ce qui conduit inévitablement à un chevauchement des domaines vitaux des ours et des infrastructures humaines. Dans cette étude, nous avons analysé la sélection de l'habitat par l'ours brun à fine échelle spatiale afin de comprendre comment les ours gèrent cette perturbation potentielle. Nous avons utilisé des données de localisation GPS pour étudier (i) la sélection de l'habitat par les femelles dans leur domaine vital et (ii) l'influence des variations journalières des activités humaines sur la sélection de l'habitat à fine échelle. Les femelles sélectionnent dans leur domaines vitaux les habitats riches en ressources alimentaires et minimisent les perturbations dues à l'homme. De plus, l'analyse temporelle de la sélection de l'habitat révèle un évitement des zones perturbées et une sélection des zones pentues durant les périodes d'activité humaine élevée, c'est-à-dire durant la journée. Nous démontrons clairement l'importance de considérer les fluctuations possibles de l'activité humaine dans les études de sélection de l'habitat. Ne pas en tenir compte peut réduire considérablement le pouvoir de détection d'importants comportements de sélection de l'habitat à fine échelle.

Introduction

Studies assessing habitat selection often only consider spatial components, though the temporal component also may be important. First, an animal's requirements may vary according to season, reproductive status, time of day, etc.,

which can lead to differential selection of habitat components. Second, the animal's environment itself may change (e.g., seasonal variation), which can induce changes in individual distribution. Although the influence of large-scale changes in environment on individual space occupancy has been well studied, short-term changes (e.g., daily variations)

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J. Martin.¹ Université de Lyon, F-69000, Lyon; Université Lyon 1; Centre national de la recherche scientifique (CNRS), Unité mixte de recherche (UMR) 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France; Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway; Office National de la Chasse et de la Faune Sauvage, 85 bis avenue de Wagram, BP 236, F-75822 Paris CEDEX 17, France.

M. Basille. Université de Lyon, F-69000, Lyon; Université Lyon 1; Centre national de la recherche scientifique (CNRS), Unité mixte de recherche (UMR) 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France; Centre for Conservation Biology, Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

B. Van Moorter. Centre for Conservation Biology, Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

J. Kindberg. Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.

D. Allainé. Université de Lyon, F-69000, Lyon; Université Lyon 1; Centre national de la recherche scientifique (CNRS), Unité mixte de recherche (UMR) 5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France.

J.E. Swenson. Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway; Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway.

¹Corresponding author (e-mail: jodie.martin@univ-lyon1.fr).

that may influence animal behavior at fine scales have rarely been investigated (but see Paukert and Willis 2002). Typically, human activity varies throughout the day, being high during daylight and lower during the night. For species sensitive to human disturbance, i.e., “any human activity that changes the contemporaneous behavior or physiology of one or more individuals” (Nisbet 2000), variation in disturbance may lead to temporal changes in their habitat selection. Failure to detect selection for a particular habitat component at a fine scale may be due to temporal changes in the habitat-selection process caused by either changing environmental conditions or changing internal states (e.g., Moe et al. 2007).

This is particularly true for species that live in human-dominated landscapes and have large home ranges that often overlap with human infrastructure, such as large carnivores in Europe. Therefore, they should adapt their habitat use to cope with both acquiring their requirements (food, resting site, etc.) and avoiding human disturbance. The brown bear (*Ursus arctos* L., 1758) is such a species. After centuries of persecution, the Scandinavian population of brown bears has grown to a substantial size during the 20th century (>3000 individuals throughout Scandinavia; Kindberg et al. 2009). Consequently, although bears avoid high human density and infrastructures at the landscape level (Katajisto 2006; Nellemann et al. 2007), the still-increasing population is expanding its distribution and colonizing more human-dominated landscapes, with large networks of roads, higher human densities, and concentrations of recreational cabins (Statistics Sweden 2003). As such, their home ranges inevitably encompass anthropogenic structures. Because bear mortality is mainly human-caused (Wiegand et al. 1998; Woodroffe and Ginsberg 1998; Bischof et al. 2009), bears should perceive anthropogenic structures and human activity as a threat. For example, Nellemann et al. (2007) reported a positive correlation between terrain use by bears and distances to recreational cabins and settlements in south-central Sweden. These cabins are primarily used for outdoor activities (e.g., hunting and fishing), thus associated with increased human activity in the forest (facilitated by the road network), especially during summer and autumn. Furthermore, small-scale studies confirm the avoidance of human presence by bears, as they usually flee upon approach (Rode et al. 2006). Therefore, even at small scales, bears should trade their vital requirements for the avoidance of human activity. They can do so in two ways. First, bears can preferentially use safer parts of their home range where human disturbance is low. Second, they can use areas with human presence, but temporally avoid human activity.

In this study, we investigated how the possible variation of human activity may influence habitat use at the home-range scale by female Scandinavian brown bears during their activity season, where habitat is defined broadly as the characteristics (physical and biological) suitable for animal's occupancy (Hall et al. 1997). Specifically, we described habitat selection by female bears as a first step. Then, we investigated how females behave to higher human disturbance. We analyzed how the level of disturbance within their home range affected habitat selection by females and tested the prediction that females having home ranges with more anthropogenic structures should avoid risky areas (predic-

tion 1). We also tested the prediction that females temporally avoid human activity (prediction 2). In particular, slopes can provide increased security for bears (Apps et al. 2004; Nellemann et al. 2007) by increasing the detection range, owing to increased visibility and more olfactory information delivered by the wind (S. Brunberg, personal communication (2006)). Therefore, we expected selection of steeper slopes during daylight hours. Finally, we expected a stronger day–night variation in the use of slopes and disturbed areas when there was more human activity in female home ranges.

Materials and methods

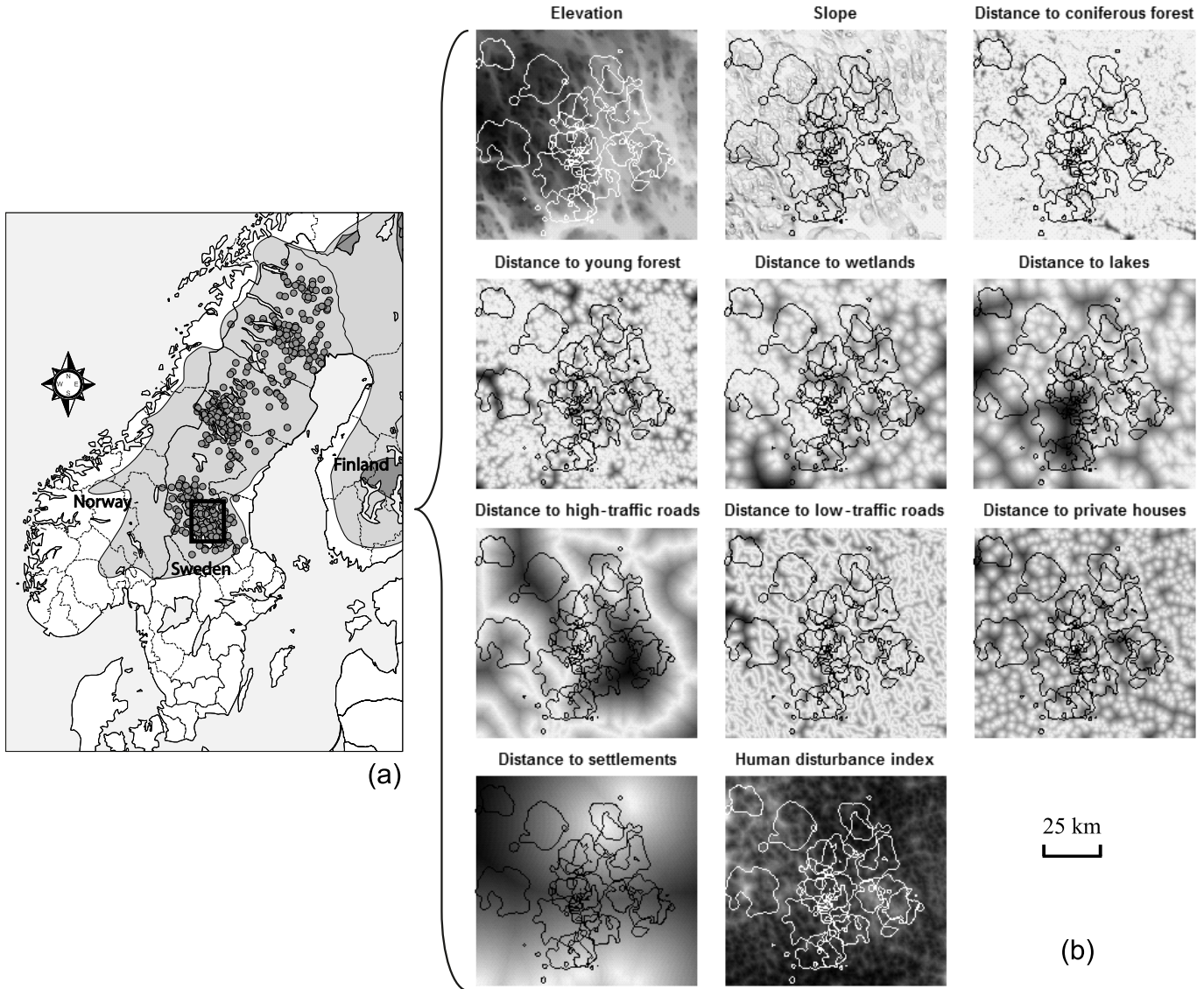
Study area

The study was conducted in the southernmost reproductive area of the Scandinavian population of brown bears in Dalarna and Gävleborg counties, south-central Sweden (61°N, 15°E; Fig. 1a) and covers 5802 km². The study area consists primarily of intensively managed coniferous forest (80%) in stands of different ages, ranging from recent clearcuts to 90- to 100-year-old trees (Swenson et al. 1999). The other main land cover types are lakes and bogs. The terrain is hilly and the altitude increases gradually from 175 m above sea level (a.s.l.) in the southeast to 725 m a.s.l. in the northwest. In the study area, human settlements are concentrated in the north and south, with only few high-traffic roads (i.e., main public roads; 0.14 km/km²). However, isolated houses (mainly cabins) and both paved and gravel roads with low-traffic volumes (e.g., roads used for forestry, or roads to private property, with very little traffic compared with high-traffic roads) are distributed throughout the study area (0.3 and 0.7 km/km² for cabins and low-traffic roads, respectively; Fig. 1b).

Individual tracking data

We used relocations of 23 independent lone adult female brown bears (3–14 years old) from May to September in 2006 (2 females), 2007 (9 females), and 2008 (12 females). We only used females in this study, because female survival and reproduction are the most important vital rates for population growth. Females were tranquilized from a helicopter using a remote drug delivery system (Dan-inject[®], Børkop, Denmark) shortly after den emergence in mid-April. For more details on drug protocols, see Arnemo (2005) and Arnemo et al. (2006). During immobilization, females were equipped with Global Positioning System (GPS) – Groupe Spécial Mobile (GSM) collars (Vectronic[®], Starkville, Mississippi, USA) scheduled to take a fix every 30 min (i.e., 48 relocations/day). Location errors are inherent with this kind of data and potentially can induce bias in habitat analysis. We therefore eliminated potentially large location errors by data screening based on two-dimensional (2D) and three-dimensional (3D) fixes in relation to the positional dilution of precision (PDOP) (Lewis et al. 2007); 3D positions having a PDOP > 15 and 2D positions having a PDOP > 5 were removed. Because of missing data and large error positions, we obtained 80% of the theoretical number of fixes, on average ($N = 125\,197$ cumulated relocations for all the 23 females). With this high success rate, we ex-

Fig. 1. The study area in Scandinavia and environmental variables under study. (a) Distribution of brown bears (*Ursus arctos*) (light gray) and locations of hunter-killed female brown bears (gray circles); the black rectangle represents the study area. (b) Map of environmental variables within the study area and representation of the home ranges of 23 females using 95% kernel. Elevation, slope, and human disturbance index are represented by their real values; the other maps represent distances to environmental attributes (coniferous forests, young forests, wetlands, lakes, high-traffic roads, low-traffic roads, private houses, and settlements). The darker the colour, the higher the value of each environmental attribute.



pected bias in habitat-selection estimates owing to habitat-specific detection rate to be low (Frair et al. 2004). Moreover, the main focus of our study is on the comparison of habitat use between time periods and individuals and we do not expect habitat-specific detection rate to be time- or individual-dependent. Therefore, our results should not be affected by a potential bias in habitat-selection estimates. As we used a spatial resolution of 200 m × 200 m, the remnant GPS error (±10 m) became negligible.

Environmental data

The environmental data for the study area were available with a spatial resolution of 200 m × 200 m pixels; each pixel was characterized by seven variables related to topog-

raphy, vegetation, and human disturbance (Table 1). A digital elevation model was available for the entire study area (GSD-Höjddkurvor, 25 m intervals ekvidistans Lantmäteriet, Sweden) and was also used to derive slope. The CORINE Land Cover map (CLC00) was used to define six vegetation types and distances to each of these types. Maps of distances to anthropogenic structures (low- and high-traffic roads, houses, and settlements) were derived from digital data of Sweden (GSD-Översiktskartan, Lantmäteriet, Sweden). Environmental variables were checked for collinearity prior to habitat-use analysis.

To assess the potential influence of human disturbance on habitat selection during the day, we computed a human disturbance index, based on distances to anthropogenic struc-

Table 1. Description, proportion, and label of the different habitat variables used in the analyses of habitat selection by female brown bears (*Ursus arctos*) in south-central Sweden.

Habitat variable	Description	Label
Distance to vegetation type		
Coniferous forest (66%)	Mainly Scots pines (<i>Pinus sylvestris</i> L.) and Norway Spruce (<i>Picea abies</i> (L.) Karst.)	D_Conif
Regenerating forest (19%)	Young-aged stands of forests, from clearcut to young forest	D_Reg_for
Wetlands (7%)	Mainly peat bogs (99.5%)	D_Wet
Water (5%)	Mainly water bodies (98%)	D_Lake
Elevation	Digital elevation data (m)	Elev
Slope	Slope (°), derived from the digital elevation model	Slope
Distance to high-traffic roads	Linear distance to public roads (km)	D_high_traffic
Distance to low-traffic roads	Linear distance to private roads (km)	D_low_traffic
Distance to houses	Linear distance to houses (km)	D_houses
Distance to settlements	Linear distance to human settlements (i.e., small villages) (km)	D_settle

tures (low- and high-traffic roads, houses, and settlements). The first axis of a principal component analysis (PCA) computed on the four variables was used as a synthetic index of human disturbance. Negative values corresponded to low disturbance, whereas positive values corresponded to high disturbance. ArcView version 3.2a (ESRI 1996) was used to prepare environmental data.

Data analyses

Habitat selection within home ranges

First, we explored habitat selection within the home ranges of female brown bears using K-select (Calenge et al. 2005). For each animal, the strength of habitat selection was assessed using marginality, i.e., the difference between the mean environmental conditions encountered in the home range (estimated using the classical method of minimum convex polygon (Mohr 1947) with the 5% outermost relocations excluded), and the mean conditions used by each individual, based directly on the relocations. K-select is similar to a PCA on the marginality vectors and returns a linear combination of the environmental variables that maximizes the mean marginality, thus extracting the relevant part of the habitat selection. If all animals have the same pattern of habitat requirements, all their marginality vectors will be oriented in the same direction and the mean marginality explained by the first axis will be high. The marginality explained by the first axis decreases as the variability in habitat use by individuals increases. For details on mathematical procedures of K-select see Calenge et al. (2005).

K-select was the basis for a more thorough investigation of the most important variables highlighted by the analysis. Using several univariate linear regressions, we analyzed the relationship between the degree of disturbance in individual home ranges (independent variable; estimated with the human disturbance index, which is described above) and the habitat selection within home ranges (dependent variable). All analyses were carried out using R (R Development Core Team 2007) and the package “adehabitat” (Calenge 2006).

Effects of diurnal changes in human activities on fine-scale habitat selection

We expected fine-scale habitat selection to depend on the changes in human outdoor activity during the 24 h period,

so we investigated individual variations in fine-scale selection of disturbance throughout the day. In particular, we looked at changes in use of slopes and areas with human disturbance during the day by females, as a function of the human activity in their home range. Females that had a negative mean index of human activity in their home range were considered to have a low degree of disturbance and those with a positive index were considered to have a high degree of disturbance. Data on use of disturbed areas were centered in each group (high and low degrees of disturbance in home ranges) by removing the means to take into account the differential quantity of disturbance in each group. There was no correlation between the human disturbance index and the degree of slopes in the home ranges (Pearson's correlation, $\rho = 0.03$, $p = 0.13$).

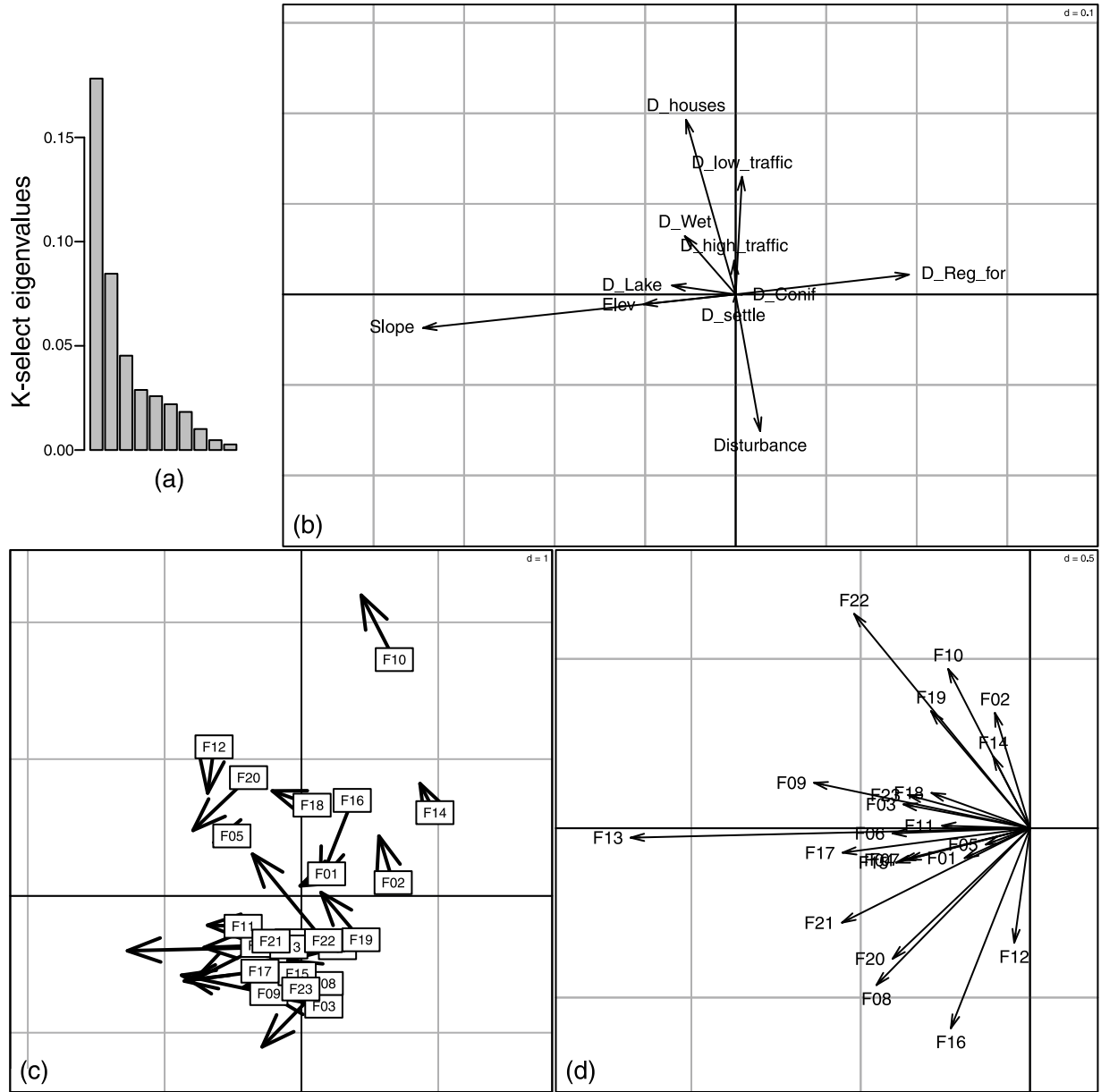
Results

Habitat selection within home ranges

The two first axes of K-select accounted for 61% of the marginality of individuals (Fig. 2a) and were retained in the analysis. There was a common pattern of habitat selection within home ranges; all females selected steeper slopes and shorter distances to young forests (as shown on the first axis; Figs. 2c, 2d; Table 2). However, a high variability in habitat selection in relation to anthropogenic structures (distance to houses and distance to low-traffic roads) was found on the second axis; females F16, F20, F08, and F12 selected areas particularly close to houses and private roads, whereas females F22, F10, F02, F19, and F14 selected areas farther from houses and low-traffic roads. As there was no significant correlation between forest type and slope (even using only the relocations of females), female bears did not select steeper slopes owing to selecting forest type.

Human disturbance within the home ranges was positively correlated with the strength of selection (length of marginality vectors) for slopes, meaning that females with more human disturbance within their home range (higher value of disturbance index) showed greater selection for steeper slopes (lower values of marginality; Fig. 3c; $F_{[1,21]} = 11.67$, $p = 0.002$). Surprisingly, there was no relationship between disturbance in the home range and selection for either undisturbed areas or regenerating forests (Figs. 3a, 3b; $F_{[1,21]} = 0.3$, $p = 0.6$ and $F_{[1,21]} = 0.8$, $p = 0.7$, respectively).

Fig. 2. Habitat selection of 23 female brown bears (*Ursus arctos*) (F01–F23) in south-central Sweden within their home ranges. (a) Bar chart of the K-select eigenvalues, measuring the mean marginality explained by each factorial axis. (b) Variable loadings on the two first factorial axes (axis 1: x axis; axis 2: y axis). (c) The marginality vectors of individuals on the first factorial plane. Labels are placed on the mean home-range composition, whereas the ends of the arrows correspond to the mean characteristics of the habitat on the relocations of individuals. (d) The marginality vectors of individuals after recentering on each individual home-range composition (i.e., the origin of the vector) given in the figures, which is axis 1 and axis 2.



Effects of diurnal changes in human activities on fine-scale habitat selection

The females varied the use of disturbed areas and slopes during the day (Figs. 4a, 4b). They were located on steeper slopes and in less disturbed areas during the main periods of human activity (i.e., daylight hours). Our results also revealed that females experiencing a higher degree of disturbance in their home range showed more variability in the use of slopes (Fig. 4a) during the day. Unexpectedly, we found a trend toward the reverse pattern on the use of disturbed areas. Although the standard errors of both groups of fe-

males often overlapped, females with lower degrees of disturbance tended to show more pronounced diurnal patterns (Fig. 4b) and females with less disturbance in their home range tend to show stronger differences in their avoidance of disturbance between day and night.

Discussion

Our analysis of habitat use by female brown bears revealed a common pattern of selection for steep slopes and regenerating forest. Several important food items in the diet

Table 2. Scores of variables on the three axes of the K-select analysis regarding habitat selection of female brown bears (*Ursus arctos*) in south-central Sweden.

Habitat variable	Axis		
	1	2	3
Elevation	-0.102	0.011	-0.027
Slope	-0.345	0.037	-0.088
D_Conif	0.007	-0.001	0.056
D_Reg_for	0.191	-0.022	-0.156
D_Wet	-0.056	-0.064	0.053
D_lake	-0.070	-0.016	-0.020
Disturbance	0.027	-0.151	-0.008
D_High_traffic	-0.002	-0.037	0.009
D_low_traffic	-0.007	-0.130	-0.065
D_houses	-0.055	-0.193	0.019
D_settle	-0.003	-0.008	0.038

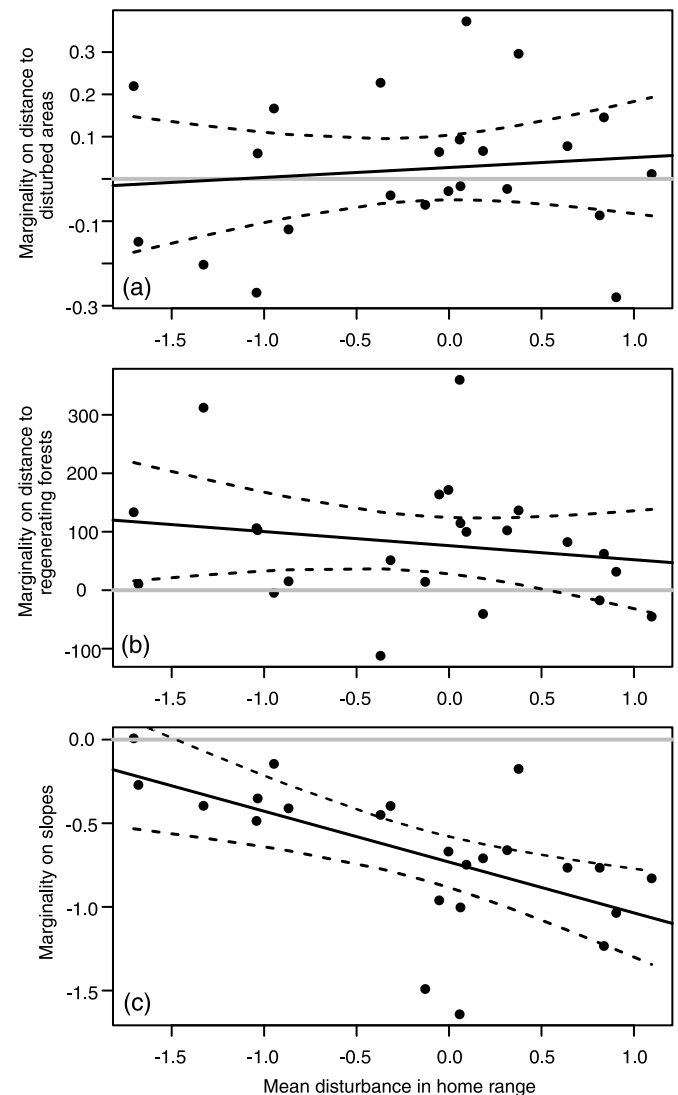
Note: The higher the absolute value, the higher the contribution of the variable on the axis. For definitions of the habitat variables refer to Table 1.

of Scandinavian brown bears occur in regenerating forests, such as numerous species of ants (Rolstad et al. 1998, 2000), more diverse and abundant herbaceous materials (Apps et al. 2004; Nielsen et al. 2004), and promote grasses, herbs, and crowberries (genus *Empetrum* L.) (Rolstad et al. 2000; Mallik 2003). In addition, moose (*Alces alces* (L., 1758)), whose calves are predated by bears (Swenson et al. 2007), forage preferably in regenerating forest stands and clearcuts (Edenius et al. 2002; Nikula et al. 2004; Cassing et al. 2006). Our results indicate that females select forest stands that provide food resources within their home range.

As expected, females also preferentially used areas offering a higher relative security (steeper slopes). But, contrary to our expectations, we did not find any direct avoidance of anthropogenic infrastructures when considering only the spatial component of habitat selection (Figs. 2, 3a). However, the strength of the selection for slopes varied greatly according to the degree of human disturbance in the home range (Fig. 3c), suggesting a behavioral response by bears to human disturbance. Bears used steeper slopes when their home range was located in an area with higher human disturbance, probably owing to the need for increased security (Nielsen et al. 2004). Thus, females without the possibility of establishing their home range in less disturbed areas may compensate by adjusting their habitat selection to a finer spatial scale, showing greater selection for steeper slopes. However, selection of disturbed areas did not vary with disturbance in home ranges, suggesting a random use of these disturbed areas.

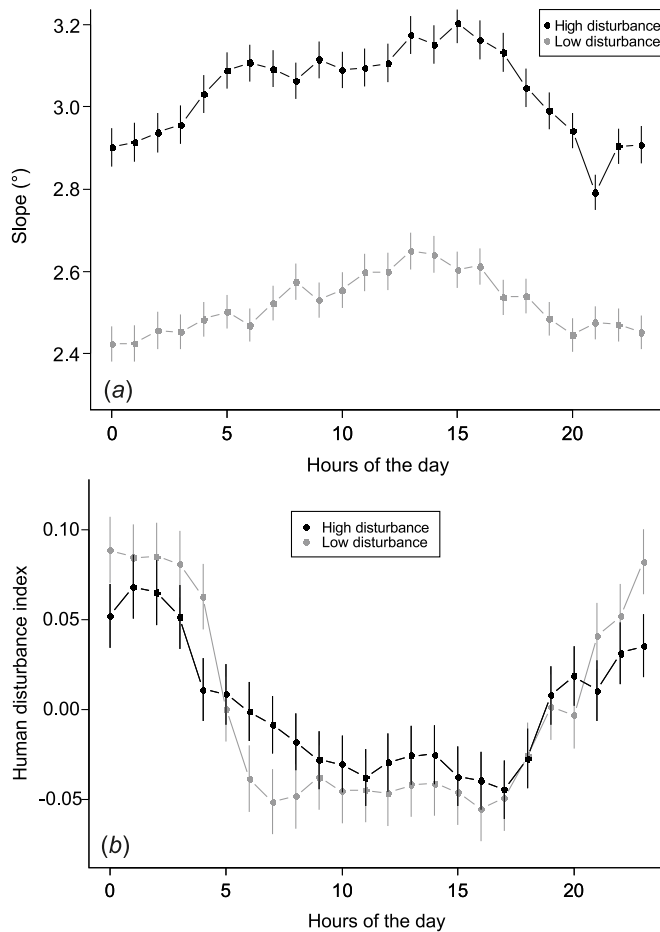
The use of high-frequency GPS tracking data also allowed us to investigate the temporal component of habitat selection, revealing a risk-avoidance strategy by females within their home ranges. We documented an avoidance of disturbed areas during the hours of higher human activity (Fig. 4b), supporting our prediction 2. In addition, bears selected steeper slopes during that same period of the day (Fig. 4a). This result is consistent with those of Hebblewhite and Merrill (2008), who found that gray wolves (*Canis lupus* L., 1758) showed a spatio-temporal avoidance of human activity during daylight with increased human density.

Fig. 3. Relationship between degree of disturbance in the home ranges (x axis) of 23 Scandinavian female brown bears (*Ursus arctos*) and their selection of disturbed areas (a), regenerating forests (b), and slopes (c). Selection for these factors was estimated using marginality, i.e., difference between the mean home-range composition and the mean characteristics at the relocations of each individual. Each circle represents one female. Gray horizontal lines represent a random selection (marginality of 0). As we studied distance to regenerating forests and distance to disturbed areas, positive values in a and b correspond to selection and negative values correspond to avoidance. In contrast to a and b, positive values in c correspond to avoidance and negative values to selection. There was a significant negative linear relationship between degree of disturbance in home range and selection of steep slopes (solid black line in c). The broken black lines are 95% confidence intervals.



Graham et al. (2009) also reported that African elephants (*Loxodonta africana* (Blumenbach, 1797)) altered their behavior in human-dominated landscapes in response to perceived risk. This allows animals to adapt to local risk conditions while exploiting habitats that provide food resource as much as possible by contracting or expanding their

Fig. 4. Variability in the use of slopes (a) and disturbed areas (b) by 23 Scandinavian female brown bears (*Ursus arctos*) during the day. Values are mean \pm SE. Black circles represent females with higher degrees of disturbance in their home range, whereas gray circles represent females with lower degrees of disturbance in their home range.



home range according to varying environmental risk. Roever et al. (2008) found that roadsides may provide more food for bears, which could explain why bears used areas closer to anthropogenic structures at night (roadsides for vegetation and ants, and houses and settlements for garbage).

Interestingly, the temporal pattern of use of slopes was more pronounced for females with higher degrees of disturbance in their home ranges (Fig. 4a), and they were located on steeper slopes, suggesting a stronger response to human activity. Nevertheless, contrary to our expectations, we found a trend toward the opposite pattern for the use of disturbed areas, with females in low-disturbed home ranges showing a higher differential use of disturbed areas during the day (Fig. 4b). We speculate that females in home ranges with more human infrastructure may exhibit some level of habituation. Although they also tended to use less disturbed areas during the day, they may tolerate to be closer to disturbed areas compared with females that have less human infrastructures in their home range.

Conservation implications

The importance of human disturbance for the occurrence of brown bears in Scandinavia differs with spatio-temporal scale. At the landscape scale (or population level), bears occur in areas with lower human density (Katajisto 2006; Nellemann et al. 2007). However, nearly the entire Scandinavian landscape is affected by human presence. Hence, bears cannot avoid some overlap between their home range and human infrastructures or activities. Female bears apparently deal with this constraint in two ways. First, they select slopes, which are more secure areas. This behavior is more pronounced when there is more disturbance by humans. Second, although females do not always avoid areas with human activity, they use these areas when human activity is low. Thus, there is a spatio-temporal avoidance of disturbed areas by bears.

In addition, our results suggest some habituation to human presence (Herrero et al. 2005). The predictability of human activity may provide sufficient alternative time to access resources (Rode et al. 2006). Bears can avoid human presence by staying far from human infrastructures during times of high human activity (Rode et al. 2006) and approach these areas during the night. Human infrastructures may even be an attractive feature in the landscape once females no longer fear them, because they may provide access to food or reduced intraspecific competition (Olson et al. 1997; Tollefson et al. 2005), which may explain why females are closer to human infrastructures during night hours.

Our results demonstrated the importance of investigating temporal variation in habitat-selection behavior. Temporal variation in environments and individual requirements is an important component of habitat selection. Failure to consider variation in habitat selection throughout the day would have led to misleading conclusions about the influence of human infrastructures and activity on habitat selection by bears.

Further research should be oriented toward the ultimate consequences of these spatio-temporal variations in habitat selection for population dynamics. Indeed, the adaptive nature of this behavior could be determined by linking the differential use of disturbed areas within individual home ranges (according to the degree of disturbance) with the reproductive success of females.

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