

Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears

Andrés Ordiz · Ole-Gunnar Støen · Miguel Delibes · Jon E. Swenson

Received: 8 December 2009 / Accepted: 12 January 2011 / Published online: 6 February 2011
© Springer-Verlag 2011

Abstract Prey usually adjust anti-predator behavior to subtle variations in perceived risk. However, it is not clear whether adult large carnivores that are virtually free of natural predation adjust their behavior to subtle variations in human-derived risk, even when living in human-dominated landscapes. As a model, we studied resting-site selection by a large carnivore, the brown bear (*Ursus arctos*), under different spatial and temporal levels of human activity. We quantified horizontal and canopy cover at 440 bear beds and 439 random sites at different distances from human settlements, seasons, and times of the day. We hypothesized that beds would be more concealed than random sites and

that beds would be more concealed in relation to human-derived risk. Although human densities in Scandinavia are the lowest within bear ranges in Western Europe, we found an effect of human activity; bears chose beds with higher horizontal and canopy cover during the day (0700–1900 hours), especially when resting closer to human settlements, than at night (2200–0600 hours). In summer/fall (the berry season), with more intensive and dispersed human activity, including hunting, bears rested further from human settlements during the day than in spring (pre-berry season). Additionally, day beds in the summer/fall were the most concealed. Large carnivores often avoid humans at a landscape scale, but total avoidance in human-dominated areas is not possible. Apparently, bears adjust their behavior to avoid human encounters, which resembles the way prey avoid their predators. Bears responded to fine-scale variations in human-derived risk, both on a seasonal and a daily basis.

Communicated by Jean-Michel Gaillard.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-1920-5) contains supplementary material, which is available to authorized users.

A. Ordiz (✉) · O.-G. Støen · J. E. Swenson
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
Postbox 5003, 1432 Ås, Norway
e-mail: andres.ordiz@gmail.com

A. Ordiz · M. Delibes
Estación Biológica de Doñana,
Consejo Superior de Investigaciones Científicas,
Avenida Américo Vespucio s/n, Isla de la Cartuja,
41092 Sevilla, Spain

O.-G. Støen
Department of Animal Ecology,
Swedish University of Agricultural Sciences,
901 83 Umeå, Sweden

J. E. Swenson
Norwegian Institute for Nature Research,
7485 Trondheim, Norway

Keywords Concealment behavior · Disturbance · Predator avoidance · Predator–prey relationships · *Ursus arctos*

Introduction

In order to maximize their fitness, prey modify their habitat use and movement patterns in response to predators, as they must balance risks (mainly predation) and potential benefits (e.g., foraging; Lima and Dill 1990). In a humanized biosphere (e.g., Vitousek et al. 1986), man has become a universal predator. Human activity and developments induce mortality, and human recreation disturbs the dynamics or the eco-ethological characteristics of populations of many animal taxa (Blanc et al. 2006). Evolutionarily adaptive

behaviors have likely arisen after a long coexistence between predators and prey, and it has been argued that disturbance stimuli could even be analogous to predation risk from an evolutionary perspective (Frid and Dill 2002).

Species with large spatial requirements, such as large carnivores, use multiple-use landscapes at a large scale (Noss et al. 1996), and in human-dominated environments a very high proportion of their adult mortality is human-induced (Woodroffe and Ginsberg 1998). Thus, large carnivores may alter their behavior to reduce encounters with humans, e.g., by becoming more nocturnal, avoiding areas with high human activity, or hiding in dense vegetation (Boydston et al. 2003). It is well documented that prey can reduce their perceived risk and fear via behavioral and morphological modifications to the same degree that predator behavior can increase the perception of risk in prey (see Stankovich and Blumstein 2005), and prey are able to adjust their anti-predator behavior to fine-degree variations in the perceived risk (e.g., Martín and López 2004). However, it is not clear whether adult large carnivores that are virtually free of natural predation, therefore lack anti-predator behavior, and only recently (in an evolutionary perspective) have had to cope with humans, are able to flexibly adjust their behavior to subtle variations in human-derived risk.

To address this issue, we used the brown bear (*Ursus arctos*) as a model species. Bears are threatened by human-caused mortality, habitat fragmentation, and habitat loss, both in North America and Europe (e.g., Servheen et al. 1999). Brown bears need large areas of habitat with sufficient availability of food and cover to satisfy their lifetime requirements (e.g., Swenson et al. 2000). The persistence of brown bear populations depends on habitat quality, human density, and human behavior (e.g., Mattson et al. 1996). Indeed, brown bears tend to avoid human activity throughout their range (e.g., Mace et al. 1996). In a large area that included our study site, Nellemann et al. (2007) found that, for comparable habitat and terrain types, bear density increased substantially with increasing distance to towns and resorts. Bears also avoid humans by altering their temporal use of areas with high recreational activities (Rode et al. 2006a).

To avoid encounters, detection, and capture, prey have developed behavioral defenses against predators. As a metric of wariness, much attention has been paid to the distance at which an individual prey initiates flight when approached by a predator (e.g., Blumstein 2006). Other surrogates of perceived risk include the amount of activity in the presence versus absence of predators (Stoks et al. 2003), shifts in habitat choice (Kotler et al. 1991), frequency of vigilance or use of alarm signals (Blumstein 2007), and group size (Heard 1992). Most of these approaches are not strictly applicable for large carnivores,

which are usually scarce, solitary, elusive, and nocturnal. However, radio-tracking techniques can allow the identification of responses of large carnivores to human presence, because large carnivores usually avoid humans at a large scale. For example, the location of wolf (*Canis lupus*) breeding and rendezvous sites depends more on the distribution of villages and roads than on habitat types (Theuerkauf et al. 2003), and Scandinavian bears try to avoid large human settlements and resorts (Nellemann et al. 2007) and select winter dens where human disturbance could be minimized (Elfström et al. 2008).

However, total avoidance of people in human-dominated landscapes is not possible. Cover is a key habitat factor that may lower the risk of mortality by reducing the chance of detection and hindering attacks (Mysterud and Østbye 1999), and it is important for many animal groups, including carnivores. For instance, American black bears (*Ursus americanus*) select for a mosaic of habitat types that provide cover near food resources (Lyons et al. 2003); European badgers (*Meles meles*) need cover for the selection of diurnal resting dens, even in a highly protected national park where disturbance by people is expected to be low (Revilla et al. 2001); spotted hyenas (*Crocuta crocuta*) are able to persist in areas with increasing livestock pressure by relying on dense cover (Boydston et al. 2003); and the availability of cover for resting during daytime is probably the limiting habitat requirement for European lynx (*Lynx lynx*) in human-dominated areas (Sunde et al. 1998). Also, the availability of cover is important in determining how human activities influence brown bear habitat use (e.g., Suring et al. 2006). Bears may adapt to living in human-dominated landscapes by choosing denser habitat when closer to people. Bears in the Italian Alps avoid areas of major human activity and forage most intensively in areas with a high degree of cover (Preatoni et al. 2005).

Prey sensitivity to the risk of predation while resting is shown by the different tactics frequently used, e.g., hiding cryptically in the safest possible areas, orienting the detection senses toward the most likely direction of approach by a predator, or forming groups (see Semeniuk and Dill 2005). Improving our knowledge on animals' adaptive behaviors, such as foraging, patch use, and habitat selection, can be useful for conservation (Morris et al. 2009). For large carnivores, activities such as feeding (e.g., diet analyses) or movement (e.g., home-range estimations) are better documented than resting-site selection, although animals devote much time to resting. For instance, Scandinavian brown bears rest ~12 h a day, with a short (~3 h) resting period in the night and the longest (~9 h) in the day (Moe et al. 2007). Legal hunting, which takes place during the day, is the single most important cause of mortality for brown bears in Sweden, with human-caused mortality accounting for 86.5% of confirmed deaths of radio-marked

animals between 1984 and 2006 (Bischof et al. 2009). Thus, it can be expected that large carnivores are very selective when choosing their daily resting sites, which makes the study of this selection of prime importance for their ecology and conservation. Technical limitations have likely hindered such fine-scale studies until recently.

We have used GPS radio-tracking combined with fieldwork to estimate the “fear” (i.e., the perceived risk; sensu Stankovich and Blumstein 2005) of bears towards humans at a fine scale, by measuring the amount of concealment around their temporary resting sites (beds). We analyzed the concealment, i.e., horizontal and canopy cover, at beds of GPS-collared bears at different distances from human settlements, different times of the day, and in relation to seasonal shifts in human activities throughout the non-denning season. We aimed to understand the very fine-scale behavior and requirements of a large carnivore when choosing resting sites in relation to human-derived risk. If fine-scale adjustment in bed selection were a response to human-derived risk, we would expect to find that beds were (1) more concealed than random sites, (2) more concealed during the day, when humans are more active, than during the night, (3) more concealed close to human settlements than further away, and (4) more concealed in late summer-early fall (when human activity outdoors is most common and includes hunting) than in spring.

Materials and methods

Study species and study area

Brown bears are large but shy, and usually use cover when resting (Servheen et al. 1999). Here, we refer to resting as a daily process, as opposed to denning, which refers to winter hibernation. Although brown bears are primarily diurnal throughout their range in North America (Munro et al. 2006), they are often nocturnal where human activity is high, both in North America (e.g., Gibeau et al. 2002) and in Europe, where the highest activity levels occur during the crepuscular-nocturnal hours (Kaczensky et al. 2006). In Scandinavia, the brown bear has been hunted intensively for hundreds of years in an attempt to exterminate the species. Bears were protected from hunting on state land in Sweden in 1913, but hunting became legal again in 1943 and has been managed by quotas since 1981 (Swenson et al. 1995). The annual brown bear hunting season starts on 21 August in Sweden and bears are hunted for approximately 2 months or until quotas are filled. Hunting is allowed from 1 h after sunrise until 2 h before sunset. Small game hunting starts earlier in the summer (July and August) and moose hunting starts at the beginning of September and continues after the onset of bear winter denning.

The study was carried out in 2007 in Orsa Finnmark (Dalarna and Gävleborg counties, central Sweden) near the southernmost distribution of the Scandinavian brown bear population (61°N, 15°E). The 2,100-km² study area is covered with managed productive forest (80%), mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula* spp.), with gravel roads spread densely throughout the area. Heather (*Calluna vulgaris*), grasses, and berry-producing shrubs dominate the understory vegetation (see Elfström et al. 2008 for further details) and bogs and lakes occupy the remaining area. The human settlements consist of a few scattered small villages ($n = 24$) and few seasonally used single houses. In 2007, human density in the municipalities ranged from 4.1 to 7.1 inhabitants per km² (Statistics Sweden 2008); our study area is located at the lowest density range, with 2–150 inhabitants per settlement. Bear density is about 30 bears per 1,000 km² (Bellemain et al. 2005).

Selection of the resting sites visited in the field

Twenty-two bears (17 females and 5 males) were equipped with GPS-GSM collars (Vectronic Aerospace, Berlin, Germany). For details on capturing and marking, see Arnemo et al. (2006) and Arnemo and Fahlman (2007). By the time the fieldwork was done, these bears had been radio-tracked for 3.5 years on average (range 0.5–13 years). The collars were programmed to obtain a location every half hour, giving a maximum of 48 locations per 24 h. The coordinates and time were obtained by the NAVSTAR global positioning system (Rodgers et al. 1996). The locations were sent via SMS and downloaded to a 1:50,000 map in the ArcGIS (Geographic Information System) 9.0 software (2004; Environmental Systems Research Institute, Redlands, CA, USA). We defined a cluster as a minimum of three consecutive locations within a circle of 30-m radius, i.e., an area where the bear spent ≥ 1.5 h, suggesting resting behavior. We visited 518 clusters and recorded all bear signs within a 30-m radius set around the most central bear location of those composing the cluster. Most of the clusters (85%) contained at least one bear bed. To avoid doubts, a bed was defined as a bear bed (hereafter, bed) only if it contained bear hairs. No bed was visited twice by any bear. From late April to October (non-denning season; Friebe et al. 2001), we visited clusters corresponding to nocturnal and diurnal resting periods, ≥ 48 h after the bear used the area, and after we confirmed that no marked bear was there, to avoid disturbance.

Measurement of horizontal and canopy cover

We measured the concealment of the bed closest to the center of the cluster. A cover cylinder (60 cm high, 30 cm

wide; Ordiz et al. 2009) was placed in the bed and we walked in the four cardinal directions and one random direction to measure the sighting distances, i.e., the minimum distance required for the device to be completely hidden (Myserud and Østbye 1999). Thus, the shorter the sighting distance, the more horizontal cover the bed had. The average sighting distance value at beds was similar ($t = -0.36$, $n = 440$, $p = 0.72$) when obtained from the random (21.4 ± 13.8 m; mean \pm SD) and the four cardinal directions (21.2 ± 10.8 m). To compare bed site concealment with the surrounding habitat, we also measured sighting distance from a random direction at a randomly selected point 50 m from every bed, and used the measurements of cover from random directions at beds and random sites to compare them. Canopy openness was measured above both the beds and the randomly selected point with a densiometer (Lemmon 1956) held on top of the cylinder. The lower the canopy openness, the more canopy cover the bed had.

Temperature might influence the selection of bed sites (Myserud 1996). We installed a temperature logger (Easy Log OM-EL-USB1; Omega Engineering, Manchester, UK) at six permanent sites to record the temperature every 30 min during the field season. The loggers were placed in the main habitat types present in the study area, i.e., mature forest, intermediate-age forest, young forest, swamp forest, tree-rich bog, and clear cut (from Karlsson and Westman 1991). Finally, at each cluster, we measured the distance from the selected bed to the edge of the closest different main habitat type.

Statistical analyses

We used generalized linear regression models to analyze the difference between beds and random sites. Bed-site selection can be considered as a discrete choice between the observed bed site and the paired random site, as has been used to analyze bed selection by roe deer (Van Moorter et al. 2009). Manly et al. (2002, p. 152) proposed the analysis of the discrete-choice problem with a logistic regression using the difference in scores for the habitat variables between the selected and the paired site with a zero intercept. Secondly, only for places actually used by bears for resting (i.e., beds), we analyzed the effect of several variables on sighting distance (response variable for horizontal cover) and on canopy openness (response variable for canopy cover). Sighting distance and canopy openness were log-transformed to improve model performance, avoiding overdispersion of the deviance. The following list of variables included environmental aspects, animal-related variables, and human-related variables, which may help explain the selection of bed sites and their characteristics:

1. Day/night: the core resting periods previously defined for this bear population were 0000–0330 and 0900–1800 hours (Moe et al. 2007). For this study, we adjusted them to outdoor human-activity periods, thus considering beds from 0700 to 1900 hours as day beds; and from 2200 to 0600 hours as night beds. All times refer to GMT + 2 h.
2. Straight-line distance to the closest permanently inhabited human settlement.
3. Daylight length: minutes of daylight for every day within the study period (data from Astronomical Applications Dept, US Naval Observatory Washington, DC 20392-5420).
4. Sex: male ($n = 5$) or female ($n = 17$; only two females had cubs during the whole season).
5. Age: adult ($n = 18$ bears ≥ 4 years old) or subadult ($n = 4$ bears < 4 years old).
6. Temperature: we used an average daily value of the six temperature loggers, based on values recorded between 0100 and 0200 hours for night beds and between 1300 and 1400 hours for day beds, as predictor values to be compared with the concealment of every bed.
7. Season: spring (26 April–15 July) and summer/fall (16 July–11 October). Brown bear behavior, habitat use, and movement patterns change seasonally during the non-denning period (e.g., Mueller et al. 2004; Moe et al. 2007). The spring season includes the bear mating season (Dahle and Swenson 2003), and the summer/fall season is the period of hyperphagia, when bears eat copiously to gain fat reserves for winter denning (e.g., Farley and Robbins 1995). Also, there is higher human activity in the entire area during the summer/fall season (e.g., berry picking and hunting, including small game, moose *Alces alces* and bear hunting) than in the spring season. The boundary between seasons was set to 15 July, when berries began to be a main, consistent component of the bears' diet, based on visual inspection of scats in the field. This temporal division has been used in previous studies on this species, both in North America (e.g., Heard et al. 2008) and Europe (e.g., Moe et al. 2007 in our study area).

The most general models included all of the above variables and meaningful interactions among them. Because temperature and daylight length were highly correlated ($r = 0.87$), only daylight length was included in the final selection process, because it was a more explanatory variable in the analyses. In addition, daylight length was a relevant variable to include, because bear hunting is allowed only during the day (see “Materials and methods”). Thus, we chose this variable because of its capacity to reflect a potential effect of temperature and it also reflected the daily hunting interval quite closely. We performed and compared

generalized linear models with the Akaike Information Criterion (AIC; Akaike 1974). We used an information-theoretic approach and constructed candidate models that would predict each response variable. We compared the support for models according to differences in their AIC scores, and calculated Akaike model weights (Link and Barker 2006). We also included individual bear identification as a random effect in generalized linear mixed versions of the selected models for horizontal and canopy cover at beds. However, the variation explained by the random effect was negligible (as shown by likelihood ratio tests comparing the best model with and without random effect) and therefore was omitted from the final models. We used the statistical package R 2.11.0 (R Development Core Team 2009) in all statistical analyses.

Results

We analyzed the concealment around 440 beds (220 day beds and 220 night beds), and 439 random sites. The beds had been used by 22 different bears; 20 ± 13.6 (mean \pm SD) beds per individual. The mean distance from a bed to the closest different main habitat type was short, 10.7 ± 7.0 m.

In agreement with our predictions, both horizontal and vertical cover were denser (lower sighting distance and lower canopy openness, respectively) at beds (and especially day beds) than at random sites (Table 1; Fig. 1).

Horizontal cover at beds was denser during the day than at night, denser when closer to human settlements, denser with increasing daylight length, and denser during summer/fall (“berry season”). The interactions that persisted in the best model indicated that horizontal cover at beds was especially dense during the day in the summer/fall season, and only diminished far from settlements and with shorter (i.e., darker) days (see Table 1 and Appendix 1 in ESM). Canopy cover at beds was also denser in the summer/fall season, denser when closer to human settlements, diminished during the night far from settlements and also diminished during the night with increasing daylight length, and canopy cover diminished during the night in the summer/fall season.

Discussion

As we expected, we found (1) denser cover at beds than at random sites and (2) denser cover at day beds than at night beds. Day beds were better concealed in summer/fall, even though bears rested further from human settlements in that season (hypotheses 3 and 4), when there were more people and human activities in the study area, including hunting.

Despite the low human density in our area, humans had a clear effect on brown bear selection of cover at resting sites. Bears apparently detected shifts in human activities within very short temporal frames, both on a seasonal and a daily basis, hiding further away from settlements and in denser cover when the chance to meet humans was greater. Thus, bears appeared to be able to finely adjust their bed-site selection to the perceived human-derived risk, suggesting the evolution of fine-scale anti-predator behavior in this large carnivore. Day beds were especially well concealed during summer/fall, which would help bears avoid detection and the costs and risks of fleeing. Escape theory suggests that prey monitor approaching predators to assess predation risk and will escape only when the risk reaches some level in relation to the cost of escaping (Cooper 2008). If cover is far away, so that the chances of escaping are reduced, an animal may flee sooner than if cover is at hand (Ydenberg and Dill 1986), and escaping implies the loss of benefits that could be obtained by not fleeing, plus costs of emerging, e.g., energetic expenditure or risk of injury (Cooper and Frederick 2007). Thus, presumably bears select beds in a way that minimizes detection and the consequential need and costs of fleeing. The use of protective cover is commonly associated with high predation risk; hiding under vegetation may be especially adaptive during the day as a defense against visually oriented predators, and it is common that prey species that are exposed to visually oriented predators (e.g., birds of prey) use more open areas during the night than during the day (Moreno et al. 1996). Hunted brown bears appeared to show the same behavior. As humans are visually oriented predators, we would expect day beds to be as concealed as possible, as with ungulates selecting dense vegetation with limited visibility to conceal their fawns (Bongi et al. 2008).

In the summer/fall season, when human activity was more common, more dispersed, and more dangerous (hunting), bears seemed to increase their avoidance of encounters with people by increasing the distance of their beds to human settlements, by choosing denser horizontal and canopy cover, and, as previously documented in our study area, by becoming more active at night (Moe et al. 2007). Bears also used denser vegetation for both horizontal and canopy cover at day beds nearer human settlements. Interestingly, day/night did not mean light/dark at our boreal latitude (>9h of daylight change in the study period), but rather reflected outdoor human activity (day), including the hours of the day when hunting occurs, versus human resting periods (night). Mueller et al. (2004) also found that brown bears in Alberta, Canada, moved away from human development in periods of high human activity (0700–1800 hours) and were closer when human activity diminished (1800–0700 hours). In our case, daylight length, a surrogate of both temperature and the time of the day when

Table 1 List of candidate and selected models for bed/random site, horizontal cover at beds (sighting distance as response variable) and canopy cover at beds (canopy openness as response variable), respectively. We show AIC values, differences in AIC values between the best model (lowest AIC) and each candidate model (Δ AIC), and AIC weights (W_i)

Response variable: bed/random site ^a	AIC		
H_Diff:O_Diff + (H_Diff:O_Diff):Time	458.37		
Response variable: horizontal cover at beds (log sighting distance) ^b	AIC	Δ AIC	W_i
Time + S + log(D) + DL + Time:S + log(D):DL	813.83	0	0.35
Time + S + log(D) + DL + Time:S + log(D):DL + S:log(D)	814.23	0.40	0.28
Time + S + log(D) + DL + Time:S + Time:log(D) + log(D):DL + S:log(D)	815.28	1.45	0.17
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + log(D):DL + S:log(D)	816.82	2.98	0.08
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + log(D):DL + Time:log(D):S + S:log(D)	818.35	4.52	0.04
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + S:DL + log(D):DL + S:log(D)	818.76	4.93	0.03
Time + S + log(D) + DL	818.96	5.13	0.03
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + S:DL + log(D):DL + Time:log(D):S + S:log(D)	820.32	6.49	0.01
Time + S + log(D) + DL + Age	820.83	6.99	0.01
Time + S + log(D) + DL + Sex + Age	822.80	8.97	<0.01
Time + S + log(D) + DL + Sex + Age + Time:S + Time:log(D) + Time:DL + S:DL + log(D):DL + Time:log(D):S + S:log(D)	824.29	10.45	<0.01
Time + S + log(D) + DL + Sex + Age + Time:S + Time:log(D) + Time:DL + Time:Sex + Time:Age + S:DL + S:Sex + S:Age + log(D):DL + log(D):Sex + log(D):Age + Time:log(D):S + S:log(D)	832.63	18.80	<0.01
Response variable: canopy cover at beds (log canopy openness) ^b	AIC	Δ AIC	W_i
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL	1,390.13	0	0.46
Time + S + log(D) + DL + Age + Time:S + Time:log(D) + Time:DL + S:Age	1,391.33	1.19	0.25
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + log(D):DL + S:log(D)	1,392.48	2.35	0.14
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + S:DL + log(D):DL + S:log(D)	1,394.02	3.89	0.07
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + log(D):DL + Time:log(D):S + S:log(D)	1,394.48	4.35	0.05
Time + S + log(D) + DL + Time:S + Time:log(D) + Time:DL + S:DL + log(D):DL + Time:log(D):S + S:log(D)	1,396.02	5.89	0.02
Time + S + log(D) + DL + Time:S + Time:log(D) + log(D):DL + S:log(D)	1,400.37	10.24	<0.01
Time + S + log(D) + DL	1,401.87	11.74	<0.01
Time + S + log(D) + DL + Age	1,403.87	13.74	<0.01
Time + S + log(D) + DL + Sex + Age	1,404.83	14.69	<0.01
Time + S + log(D) + DL + Sex + Age + Time:S + Time:log(D) + Time:DL + Time:Sex + Time:Age + S:DL + S:Sex + S:Age + log(D):DL + log(D):Sex + log(D):Age + Time:log(D):S + S:log(D)	1,405.76	15.62	<0.01
Time + S + log(D) + DL + Time:S + log(D):DL + S:log(D)	1,406.04	15.90	<0.01

^a H_Diff difference in horizontal cover between a bed and the associated random site, O_Diff difference in openness between a bed and the associated random site, $time$ day/night

^b $Time$ day/night, S spring and summer/fall season, DL daylight length, D distance to human habitation, age adult/subadult

hunting occurred, and the human-associated variables (distance to human settlements and day/night) influenced bear selection of cover at beds the most.

Both horizontal and canopy cover were denser at beds than at random sites (only 50 m away from the beds), which suggests a very fine-scale habitat selection. In our area, the median habitat patch size is 22,500 m², which implies an average maximum exit distance of 85 m (Moe et al. 2007). Thus, a median habitat patch size would usually include the random sites 50 m from the beds, unless the beds were near

the edges of habitat patches. Bears were indeed quite close to habitat patch edges (10.7 ± 7.0 m to the next habitat type) and random sites at 50 m often fell in a different habitat patch. Thus, 50 m was a distance large enough to document such fine-scale selection by the bears. Indeed, bears use forest edges more than other large carnivores in Scandinavia (May et al. 2008), and Moe et al. (2007) found bear beds in dense habitats with more open surroundings. Likewise, Lyons et al. (2003) often located black bears near edges of closed canopy classes in North America. This

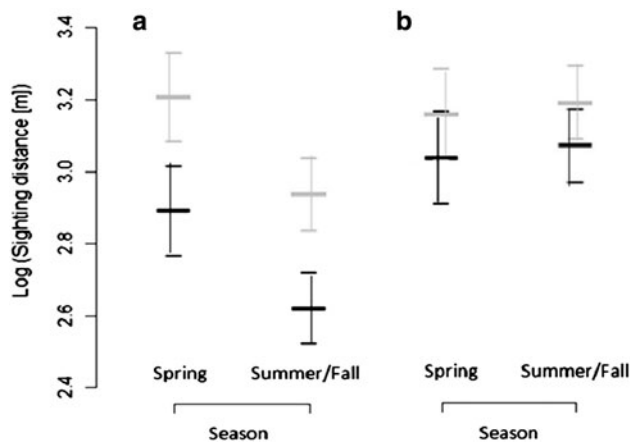


Fig. 1 The horizontal cover measured as sighting distance in meters (mean \pm SD) at brown bear (*Ursus arctos*) resting beds ($n = 440$; black) and random sites ($n = 439$; gray), at **a** day and **b** night, during the spring and the summer/fall seasons in Sweden

could be due to the denser protective cover at edges than in mature stands, which may protect the animals from olfactory predators (e.g., bear-hunting dogs), because turbulence and updrafts occur along edges and it has been reported that dogs have difficulty following scent when they cross from one habitat type to another (Conover 2007 and references therein).

Bear beds are one-use resting sites chosen for rest during some hours, either at night or during the day (see above). For prey species, predation risk varies in space and time, which may be the reason why refuges, such as dense vegetation, are used in a flexible way, depending on the presence/absence of predators (e.g., Sih 1992). Our fine-scale approach showed that bears are able to discriminate among different perceived risks. The presence of hunters (annually ~ 700 big-game hunters plus small-game hunters visit the 2,100-km² study area) and berry pickers likely explained the bears' choice of denser horizontal cover during the day and the larger distances to human settlements in the summer/fall season. The fact that horizontal cover at random sites associated with night beds did not differ between spring and summer/fall seasons, but random sites associated with day beds were more concealed in the summer/fall season (Fig. 1), emphasized that bears selected denser habitats, not just denser cover, at bed sites when human activity was more intense and dispersed. However, more openness at night might facilitate monitoring of a potential predator to determine its position and behavior to assess risk (Cooper 2008).

The distribution of bears in relation to disturbance has been reported to vary with sex, age, and social status; bears closer to large settlements and resorts (<10 km away) were on average 27–51% younger than in areas beyond (Nellemann et al. 2007). Sexual dimorphism and differing

reproductive tactics also led to sexual segregation in habitat use by bears in relation to human disturbance (Rode et al. 2006b). Female ungulates select habitats with more horizontal cover than males (Myserud and Østbye 1999). Beds of subadult bears appeared to have lower canopy cover than beds of adult bears during the summer/fall season, but our sample was biased towards adult bears (81%), and mainly females (77%), which may have affected the potential influence of sex and age. Intra-specific killing of subadult bears has been documented. In Scandinavia, 86% of known cases occurred during the spring, the mating season (Swenson et al. 2001), a pattern also observed in North America (Mattson et al. 1992). Taken together, our results rather suggest that bears prioritized human avoidance over bear avoidance, although it is probably easier for bears to avoid humans than other bears. The random effect (individual bear identification) did not appear to be necessary in the final models, suggesting a general, well-developed bear behavior to hide further away from human settlements during the day, also relying on dense horizontal cover.

Given the importance of storing fat during hyperphagia, the essential foraging season for successful bear hibernation and cub production (Farley and Robbins 1995), a large allocation in security may also imply foraging costs for the animals (Brown and Kotler 2004). An allocation in security may reduce time for foraging, which should be the main activity of brown bears during the hyperphagia season.

The results of our study, carried out at the lowest human density within the distribution of bears in Western Europe, stress the importance of cover for large carnivores and are relevant to reducing conflicts with people. As a management mitigation, people could be encouraged to avoid areas with dense vegetation or rugged terrain, i.e., areas with low accessibility for humans, which appear indispensable for the occurrence and survival of large carnivores (e.g., Naves et al. 2003; Fernández et al. 2006), to minimize potential interactions and as a safety measure for both large carnivores and humans.

We have documented that the brown bear, like any prey, is able to discriminate among subtle differences of potential risk from the human predator. Brown bears have coexisted with *Homo* spp. for at least 1 million years in Eurasia (e.g., Stiner 1999), but scarcely 10,000–20,000 years in North America. Thus, one would expect a greater antipredator (“antihuman”) behavior to have evolved in the Old World than in the New World. For instance, European brown bears show higher activity levels during the crepuscular-nocturnal hours than some North American populations (see “Materials and methods”). Nocturnal habits help bears avoid people and likely have allowed them to survive in areas with relatively high human densities, a pattern also observed when comparing Eurasian and North American wolves (Woodroffe 2000). Also, the careful avoidance of

people by Scandinavian bears, both on a daily and seasonal basis, depending on perceived risk, could be a result of the long-term human persecution that almost eradicated the species in Scandinavia by 1935 (Swenson et al. 1995) in addition to an effect of the current hunting regime.

Acknowledgements We appreciate the help provided in the field by volunteers and students of the Scandinavian Brown Bear Research Project, which is funded by the Swedish Environmental Protection Agency, Norwegian Directorate for Nature Management, Swedish Association for Hunting and Wildlife Management, WWF Sweden, Research Council of Norway, and the program “Adaptive management of fish and wildlife populations”. AO was funded by Fundación Oso de Asturias, funds provided by Hunosa and Sato. The manuscript greatly benefited from comments and advice by M. Basille, R. Bischof, J. Naves, S. Sæbø, G. Sonerud, P. Wegge, A. Zedrosser, and an anonymous reviewer.

Literature cited

- Akaike H (1974) A new look at the statistical model identification. *Trans Automat Contr* 19:716–723
- Arnemo J, Fahlman Å (2007) Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Norwegian School of Veterinary Science, Tromsø
- Arnemo JM, Ahlqvist P, Andersen R, Berntsen F, Ericsson G, Odden J, Brunberg S, Segerström P, Swenson JE (2006) Risk of anesthetic mortality in large free-ranging mammals: experiences from Scandinavia. *Wildl Biol* 12:109–113
- Bellemain E, Swenson JE, Tallmon O, Brunberg S, Taberlet P (2005) Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. *Conserv Biol* 19:150–161
- Bischof R, Swenson JE, Yoccoz NG, Mysterud A, Gimenez O (2009) The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *J Anim Ecol* 78:656–665
- Blanc R, Guillemain M, Mouronval J-B, Desmots D, Fritz H (2006) Effects of non-consumptive leisure disturbance to wildlife. *Rev Ecol (Terre Vie)* 61:117–133
- Blumstein DT (2006) Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim Behav* 71:389–399
- Blumstein DT (2007) The evolution, function, and meaning of marmot alarm communication. *Adv Study Behav* 37:371–400
- Bongi P, Ciuti S, Grignolio S, Del Frate M, Simi S, Gandelli D, Apollonio M (2008) Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. *J Zool* 276:242–251
- Boydston E, Kapheim K, Watts H, Szykman M, Holekamp K (2003) Altered behaviour in spotted hyenas associated with increased human activity. *Anim Conserv* 6:207–219
- Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 7:999–1014
- Conover MR (2007) *Predator–prey dynamics: the role of olfaction*. CRC Press, Boca Raton
- Cooper WE (2008) Visual monitoring of predators: occurrence, cost and benefit from escape. *Anim Behav* 76:1365–1372
- Cooper WE, Frederick WG (2007) Optimal flight initiation distance. *J Theor Biol* 244:59–67
- Dahle B, Swenson JE (2003) Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *J Anim Ecol* 72:660–667
- Elfström M, Swenson JE, Ball JP (2008) Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildl Biol* 14:176–187
- Farley SD, Robbins CT (1995) Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Can J Zool* 73:2216–2222
- Fernández N, Delibes M, Palomares F (2006) Landscape evaluation in conservation: molecular sampling and habitat modelling for the Iberian lynx. *Ecol Appl* 16:1037–1049
- Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. *Conserv Ecol* 6:11
- Friebe A, Swenson JE, Sandegren F (2001) Denning chronology of female brown bears in central Sweden. *Ursus* 12:37–46
- Gibeau ML, Clevenger AP, Herrero S, Wierzchowski J (2002) Grizzly bear response to human development and activities in the Bow River watershed, Alberta. *Can Biol Conserv* 103:227–236
- Heard DC (1992) The effect of wolf predation and snow cover on musk-ox group size. *Am Nat* 139:190–204
- Heard DC, Ciarnello LM, Seip DR (2008) Grizzly bear behavior and global positioning system collar fix rates. *J Wildl Manag* 72:596–602
- Kaczensky P, Huber D, Knauer F, Roth H, Wagner A, Kusak J (2006) Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *J Zool* 269:474–485
- Karlsson C, Westman SE (1991) *Skogsuppskattning, skogsinventering*, 2nd edn. Sollefteå, Sweden (in Swedish)
- Kotler BP, Brown J, Hasson O (1991) Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260
- Lemmon PE (1956) A spherical densiometer for estimating forest overstorey density. *For Sci* 2:314–320
- Lima SL, Dill LM (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Link WA, Barker RJ (2006) Model weights and the foundations of multimodel inference. *Ecology* 87:2626–2635
- Lyons AL, Gaines WL, Servheen C (2003) Black bear resource selection in the northeast Cascades, Washington. *Biol Conserv* 113:55–62
- Mace RD, Waller JS, Manley TL, Lyon LJ, Zuuring H (1996) Relationships among grizzly bears, roads and habitat in the Swan Mountains Montana. *J Appl Ecol* 33:1395–1404
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) *Resource selection by animals. Statistical design and analysis for field studies*, 2nd edn. Kluwer, Dordrecht, p 240
- Martín J, López P (2004) Iberian rock lizards (*Lacerta monticola*) assess short-term changes in predation risk level when deciding refuge use. *J Comp Psychol* 118:280–286
- Mattson DJ, Knight RR, Blanchard BM (1992) Cannibalism and predation on black bears by grizzly bears in the yellowstone ecosystem, 1975–1990. *J Mammal* 73:422–425
- Mattson DJ, Herrero S, Wright RG, Pease CM (1996) Science and management of Rocky Mountain grizzly bears. *Conserv Biol* 10:1013–1025
- May R, van Dijk J, Wabakken P, Swenson JE, Linnell JDC, Zimmermann B, Odden J, Pedersen HC, Andersen R, Landa A (2008) Habitat differentiation within the large-carnivore community of Norway’s multiple-use landscapes. *J Appl Ecol* 45:1382–1391
- Moe TF, Kindberg J, Jansson I, Swenson JE (2007) Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Can J Zool* 85:518–525
- Moreno S, Villafuerte R, Delibes M (1996) Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. *Can J Zool* 9:1656–1660
- Morris DW, Kotler BP, Brown JS, Sundararaj V, Ale SB (2009) Behavioral indicators for conserving mammal diversity. *Ann NY Acad Sci* 1162:334–356

- Mueller C, Herrero S, Gibeau ML (2004) Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15:35–47
- Munro RH, Nielsen SE, Price MH, Stenhouse GB, Boyce MS (2006) Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. *J Mammal* 87:1112–1121
- Mysterud A (1996) Bed-site selection by adult roe deer *Capreolus capreolus* in southern Norway during summer. *Wildl Biol* 2:101–106
- Mysterud A, Østbye E (1999) Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildl Soc Bull* 27:385–394
- Naves J, Wiegand T, Revilla E, Delibes M (2003) Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. *Conserv Biol* 17:1276–1289
- Nellemann C, Støen O-G, Kindberg J, Swenson JE, Vistnes I, Ericsson G, Katajisto J, Kaltenborne BP, Martin J, Ordiz A (2007) Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biol Conserv* 138:157–165
- Noss RF, Quigley HB, Hornocker MG, Merrill T, Paquet PC (1996) Conservation biology and carnivore conservation in the Rocky Mountains. *Conserv Biol* 10:949–963
- Ordiz A, Støen O-G, Langebro L, Brunberg S, Swenson JE (2009) A practical method for measuring horizontal cover. *Ursus* 20:109–113
- Preatoni D, Mustoni A, Martinoli E, Carlini B, Chiarenzi S, Chiozzini S, Van Dongen LA, Wauters A, Tosi G (2005) Conservation of brown bear in the Alps: space use and settlement behavior of reintroduced bears. *Acta Oecol* 28:189–197
- R Development Core Team (2009). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org>
- Revilla E, Palomares F, Fernández N (2001) Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area. *J Zool* 255:291–299
- Rode KD, Farley SD, Robbins CT (2006a) Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biol Conserv* 133:70–80
- Rode KD, Robbins CT, Farley SD (2006b) Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636–2646
- Rodgers AR, Rempel RS, Abraham KF (1996) A GPS-based telemetry system. *Wildl Soc Bull* 24:559–566
- Semeniuk CAD, Dill LM (2005) Cost/benefit analysis of group and solitary resting in the cowtail stingray, *Pastinachus sephen*. *Behav Ecol* 16:417–426
- Servheen C, Herrero H, Peyton B, IUCN/SSC Bear and Polar Bear Specialists Groups. (1999) Bears: Status survey and conservation action plan. IUCN, Switzerland
- Sih A (1992) Prey uncertainty and the balancing of antipredator and feeding needs. *Am Nat* 139:1052–1069
- Stankovich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. *Proc R Soc Lond B* 272:2627–2634
- Statistics Sweden (2008) Statistical database. Population statistics, 2007. <http://www.ssd.scb.se/databaser/makro/start.asp?lang=2>
- Stiner M (1999) Cave bear ecology and interactions with pleistocene humans. *Ursus* 11:41–58
- Stoks R, McPeck MA, Mitchell JL (2003) Evolution of prey behavior in response to changes in predation regime: damselflies in fish and dragonfly lakes. *Evolution* 57:574–585
- Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildl Biol* 4:177–183
- Suring H, Farley S, Hilderbrand G, Goldstein M, Howlin S, Erickson W (2006) Patterns of landscape use by female brown bears on the Kenai Peninsula, Alaska. *J Wildl Manag* 70:1580–1587
- Swenson JE, Wabakken P, Sandegren F, Bjärvall A, Franzén R, Söderberg A (1995) The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildl Biol* 1:11–25
- Swenson JE, Gerstl N, Dahle B, Zedrosser A (2000) Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe. Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), Nature and Environment, No. 114
- Swenson JE, Dahle B, Sandegren F (2001) Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12:81–92
- Theuerkauf J, Rouys S, Jedrzejewski W (2003) Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Can J Zool* 81:163–167
- Van Moorter B, Gaillard J-M, McLoughlin PD, Delorme D, Klein F, Boyce MS (2009) Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. *Oecologia* 159:669–678
- Vitousek PM, Ehrlich PR, Ehrlich AH, Matson PA (1986) Human appropriation of the products of photosynthesis. *Bioscience* 36:368–373
- Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. *Anim Conserv* 3:165–173
- Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128
- Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. *Adv Study Behav* 16:229–249