

Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*)

T.F. Moe, J. Kindberg, I. Jansson, and J.E. Swenson

Abstract: The goal of habitat selection studies is to identify important habitats for a particular species. However, most studies using radiotelemetry have focused on habitat-selection patterns using daytime positions only. We used 24 h data from six female brown bears (*Ursus arctos* L., 1758) equipped with GPS–GSM collars and activity loggers to analyse variations in habitat selection related to diel variations in activity (foraging and resting). We found that the bears rested mainly during the daylight hours and foraged mainly during the crepuscular and nocturnal hours. The bears selected habitats differently when they were resting than when they were foraging. We found no selection for tall coniferous forest using all data, but this habitat was selected by resting bears and avoided by foraging bears. Thus, for studies of habitat selection, our results show the importance of obtaining data from all 24 h and dividing these data into relevant categories based on the diel activity pattern of the studied species.

Résumé : Le but des études de sélection d'habitats est d'identifier les habitats qui ont de l'importance pour une espèce particulière. Cependant, la plupart des études basées sur la télémétrie se sont intéressées à la sélection d'habitats d'après les seules données de positionnement de jour. Nous avons utilisé des données récoltées sur 24 h chez des ours bruns (*Ursus arctos* L., 1758) munis de colliers GPS–GSM et d'enregistreurs d'activité afin d'analyser les changements dans la sélection d'habitat en fonction des variations journalières d'activité (recherche de nourriture et repos). Les ours se reposent surtout durant les heures de jour et recherchent leur nourriture principalement durant les heures du crépuscule et de la nuit. Les ours choisissent leurs habitats de façon différente pour le repos et pour la quête alimentaire. À l'étude de l'ensemble des données, nous ne trouvons aucune sélection pour les hautes forêts de conifères; cet habitat est cependant sélectionné par les ours au repos et évité par les ours en recherche de nourriture. Ainsi, en ce qui a trait à la sélection d'habitat, nos résultats démontrent l'importance d'obtenir des données sur l'ensemble des 24 h et de les répartir en catégories pertinentes en fonction des patrons d'activité journalière de l'espèce étudiée.

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Introduction

Habitat selection is an animal's disproportionate use of a habitat in relation to its availability, and can operate at different spatial and temporal scales (Johnson 1980; Schooley 1994; Myrsterud et al. 1999; Apps et al. 2004; Nielsen et al. 2004a). Throughout its life, an animal must satisfy its basic needs, such as food, cover, water, and pre-berry opportunities. Because usually no single habitat can satisfy all these needs adequately, the animal's habitat selection will reflect a trade-off among them. In the management of a species, it

is thus essential to know which habitats are used and why animals select some habitats over others (Manly et al. 2002).

The brown bear (*Ursus arctos* L., 1758) is an omnivorous animal with high energy requirements, spending most of its time foraging or resting (MacHutchon 2001). It is therefore important that the combination of habitats in a bear's home range covers all needs associated with these two activities. Rogers (1976, 1987) and Craighead et al. (1995) acknowledged that food availability is an important factor influencing survival and reproduction for bears, both at the individual and at the population level. Also McLoughlin et al. (2002) found that habitat selection was highly influenced by food availability for grizzly bears in the Canadian Arctic. The optimal brown bear habitat is probably a mix of open and forested habitats (Nielsen et al. 2004b), which might reflect a difference in habitats selected for resting and foraging. However, few previous studies have looked at brown bear habitat selection on such a fine scale, i.e., examining the selection of foraging and resting sites individually (but see Myrsterud 1983).

An animal's needs and behaviour change throughout the day. Studies on both brown bears (Servheen 1983; Belant and Follmann 2002; Nielsen et al. 2004a) and cervids (Myrsterud et al. 1999) have indicated that habitat selection also varies according to the time of day. Beyer and Hauffer (1994) stressed the need for habitat studies to consider a

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species' daily activity pattern. However, earlier habitat-selection studies have rarely taken this into account. Monitoring these finer spatiotemporal trends will be important in future studies for the conservation of animals, as it enables us to draw more biologically relevant conclusions (Johnson 1980; Beyer and Haufler 1994; Mysterud et al. 1999; Apps et al. 2004; Nielsen et al. 2004a).

Most previous habitat studies on large mammals have been conducted by equipping the animal with very high frequency (VHF) transmitters. Triangulation from the ground is labour intensive and has mainly been restricted to the daylight hours. With the introduction of GPS–GSM (global positioning system and global system for mobile communication) collars and the NAVSTAR GPS (satellites and ground receiving system), it is now possible to locate the animal's position with very high accuracy. Also, the collars can be programmed to produce a large amount of locations, independent of time and remoteness (Obbard et al. 1998; Arthur and Schwartz 1999). This new technology thus gives us the possibility of very small-scale habitat selection studies in both time and space (Rodgers et al. 1996; Adrados et al. 2003).

In this paper, we explore the habitat selection of six female brown bears in Sweden. They were all equipped with GPS–GSM collars, as well as activity loggers. From this we determined their coordinates and activity status (foraging or resting) at each site. Because the needs of a foraging bear (foods) are not the same as the needs of a resting bear (shelter), we expected (*i*) a difference in the habitat selection of foraging bears compared with those of resting bears. From this we also expected that (*ii*) the bears would forage and rest during different times of the day. As a result of the first two hypotheses, we also expected that (*iii*) the bears' habitat selection would vary on a diel scale. Finally, we conducted a 24 h habitat selection study, and based on the previous three hypotheses, we expected to find (*iv*) a difference between the diel habitat selection and the overall 24 h habitat selection.

Study area

The study was conducted in the counties of Dalarna and Gävleborg, Sweden (61°N, 15°E), an area near the southernmost distribution of the Scandinavian brown bear population. The area is mainly forested, 80% being covered by highly managed productive forest. Bogs and lakes cover the remaining area, and the human settlements consisted of a few scattered villages. The forest turnover time is 90–100 years, with <60% of the forest being older than 35 years (Swenson et al. 1999). Gravel roads crisscross the entire study area. Combined with the always-ongoing tree cutting, this makes the landscape a patchwork of different habitats with a median patch size of 22 500 m² (mean 80 600 m²). The terrain is gently undulating with altitudes ranging 200–700 m above sea level. No areas rise above the timberline. The dominating tree species is Scots pine (*Pinus sylvestris* L.), with Norway spruce (*Picea abies* (L.) Karst.), lodgepole pine (*Pinus contorta* Dougl. ex Loud., non-native), birches (genus *Betula* L.), and European aspen (*Populus tremula* L.) covering the remaining area. Important field-layer vegetations include myrtle blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), black crowberry

(*Empetrum nigrum* ssp. *hermaphroditum* (Lange ex Hagerup) Böcher), some forbs, and heather (*Calluna vulgaris* (L.) Hull). The ground layer consists of mostly lichens and mosses. The estimated winter population of moose (*Alces alces* (L., 1758)) was about 920 individuals per 1000 km² (Swenson et al. 2007) and the estimated brown bear population was about 30 bears per 1000 km² (Bellemain et al. 2005). Snow covers the ground from the end of October until early May and the mean temperature ranges from a minimum of –7 °C in January to 15 °C in July (Swenson et al. 1999).

Materials and methods

Data collection and GPS radiotelemetry

We studied six sexually mature female brown bears without cubs of the year, ranging 3–10 years old. All were equipped with GPS-Plus-3 collars, as well as activity loggers, VHF units, and GSM modems (VECTRONIC Aerospace GmbH, Berlin, Germany). For procedures on capture and marking, see Arnemo (2006). The coordinates and activity status ($N = 19\ 209$) of the bears were recorded every half hour (48 times a day) between 20 May and 24 August 2004. The coordinates and time of day were obtained by the NAVSTAR global positioning system (Rodgers et al. 1996). To correct for seasonal patterns in behaviour and diet (McLellan and Hovey 2001; McLoughlin et al. 2002), the study period was divided into the pre-berry (20 May – 6 July) (Dahle and Swenson 2003) and berry (16 July – 24 August) seasons, with a break between when berries started ripening.

The location error in this study was relatively small, at maximum approximately ± 10 m. One of the transmitters partly malfunctioned, resulting in a general loss of positions and (or) no positions at all for several days or weeks. Recognizing that this was a technical problem that would not lead to any habitat biases, we chose to include the available data from this bear in our analyses. A more serious problem was loss of data owing to a sporadic lack of contact between the GPS collars and the satellites. Several factors have been suggested as the cause of this, e.g., animal behaviour, the position of the antenna inside the collar, the number of satellites available, weather conditions, habitat density, and topography (Dussault et al. 1999; Bowman et al. 2000; Moen et al. 2001; D'Eon et al. 2002; Adrados et al. 2003). When studying habitat selection, this can be a serious problem, as it can lead to erroneous conclusions (D'Eon 2003). For example, loss of data in dense forests will underestimate this habitat. Although this study did not focus on habitat selection per se, we did examine the GPS-fix success rate and located what activity showed the lowest success rate.

Habitat description

Home-range habitats were defined using digital land-cover maps from the Swedish land-cover data (SMD – Svenska Marktäcke data; Engberg 2002). These maps were made from satellite images and field inventories during 1999 and 2002. The recorded habitat-patch sizes ranged 10 000 – 250 000 m² (depending on class) and the patch unit (pixel) of the map was 25 m \times 25 m.

Home ranges were defined by creating a 100% minimum convex polygon for each bear per season using ArcView[®]

Table 1. Habitat categories within the home ranges of six female brown bears (*Ursus arctos*) in Dalarna, Sweden, 2004.

Habitat class	Habitat description	SMD classes
Clearcut	Clearcut: without trees; shrub and tree heights <2 m	54
Young forest	Previous clearcut: tree height 2–5 m; canopy cover >30%	55
Short conifers	Short conifers: tree height 5–15 m; canopy cover >30%	44
Tall conifers	Tall conifers: tree height >15 m; canopy cover >30%	45
Poor conifers	As with short and tall conifers, but on lichen-dominated ground	43
Mixed forest	Tree height >5 m; canopy cover >30%, of which coniferous trees constitute <75%	40, 48
Forested bog	As with short and tall conifers and with mixed forest, but on boggy ground	41, 46, 49
Open bog	Bogs where shrubs and trees cover <30%	71, 72
Other	Human settlements, human-influenced areas, forests on open bedrock, open water, and water courses	5, 6, 10, 30, 32, 42, 47, 50, 80, 81, 82

Note: SMD (Svenska Marktäckedata) habitat classes are from the Swedish land-cover data (Engberg 2003).

version 3.3 (Environmental Systems Research Institute, Inc. 2002) with the Animal Movement extension (Hooge and Eichenlaub 1997). Home-range habitats were extracted using ArcGIS® version 9.0 (Environmental Systems Research Institute, Inc. 2004). We defined available habitat as the overall habitat proportions within these home ranges, and combined some of the SMD habitat classes (Table 1) (Engberg 2003) to improve the power of the tests and decrease the probability of obtaining classes with less than five expected observations (Neu et al. 1974; Manly et al. 2002; Nakagawa 2004). Habitat classes seldom used by the bears were not excluded but were combined into the group “other”. This was to avoid selection of the remaining habitats, as a result of changing the total availability pool (Johnson 1980; Manly et al. 2002). All habitat classes in Table 1 were available within each home range.

Activity sensors

Five of the bears had activity loggers that recorded an activity index between 0 and 510 every 5 min. The activity index was an indication of the bear’s head movement in two directions during these 5 min. The activity index of a bear at a site was the mean of the six recordings during the 30 min interval surrounding the time of the GPS fix. Based on the recommendations of Gervasi et al. (2006), we defined all periods where the bears showed a mean activity of <50 as passive periods and of ≥50 as active periods.

Statistics

Because our study included only six bears and three of these were related (mother and two independent daughters), we chose to use χ^2 goodness-of-fit tests, with individual observations as sample units and not the individual bear. Although this method has been criticized (Aebischer et al. 1993; Alldredge and Griswold 2006; Thomas and Taylor 2006), we felt that the method was justified because our primary goal was to compare habitat use in different periods of the day. To determine whether habitat use was spatially autocorrelated owing to restraints on bear movement, we also analysed the movement of the bears (calculated as the straight-line distance between subsequent GPS positions) to find their ability to move between the different habitat patches within the scope of two preceding observations. The χ^2 tests were performed with MINITAB® version 13.0 (Minitab Inc. 2000), and when they showed that the bears used their home-range habitats nonrandomly ($P \leq 0.05$), we

used the method described by Krebs (1999; pp. 480–481) to determine which habitats were selected or avoided. A selection index was the proportion of habitat used divided by the proportion available, with a value of 1 indicating no selection, indices significantly <1 indicating habitat avoidance, and indices significantly >1 indicating habitat selection. Running several tests on the same sample and using nonindependent habitat availability measures (risking unit – sum constraints) increased the risk of making type I errors (Aebischer et al. 1993; Manly et al. 2002; Nakagawa 2004). To reduce this probability, we performed a Bonferroni adjustment when calculating the 95% confidence intervals (α level/ n = 0.05/9). We considered two categories to be significantly different from each other when their confidence intervals did not overlap. This was a conservative assumption (Krebs 1999) and it might have decreased the power of our tests (Nakagawa 2004). However, the main goal of this study was to show the different habitat-selection patterns of studies using different temporal scales. Since all our tests were run using this same method, an absolute accuracy of which habitats were significantly selected or avoided was not necessary to adequately test our hypotheses.

Results

Methodology

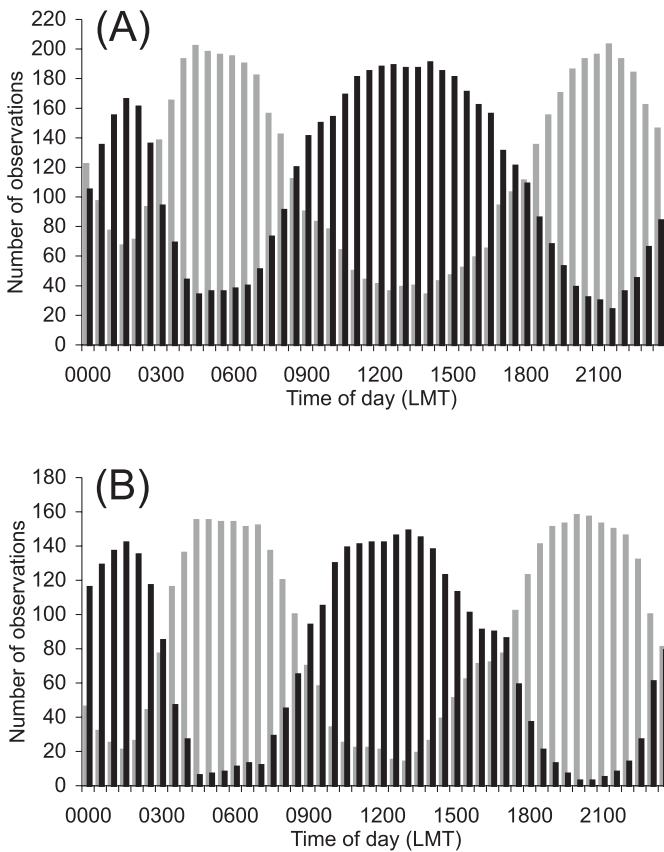
A median patch size of 22 500 m² gave an average maximum exit distance of 85 m; 160 m calculated from the mean (80 600 m²). To determine whether the bears were actually able to move between the habitats within the 30 min available between each GPS fix, we calculated their straight-line movement in metres per 30 min. Pooling the seasons and using all sites where the bears had been active (mean activity ≥50), the median movement was 361 m/30 min (N = 8948, quartile 1 = 180, quartile 3 = 604) and the maximum distance walked in 30 min was 2551 m. Less than 0.1% of the habitat patches exceeded 2 km across.

The GPS-fix success rate was 76% for the two seasons pooled. Of the failed fix attempts, 78% occurred when the bears were passive.

Diel activity periods

The activity periods were based on the mean activity levels of each half-hour interval. We divided the day into four separate activity periods, defined by the mean activity of the

Fig. 1. Mean activity for each half-hour period (local mean time) during a diel cycle for five female brown bears (*Ursus arctos*) in Dalarna, Sweden, during the (A) pre-berry and (B) berry seasons of 2004. Shaded bars are active periods (mean activity ≥ 50 ; $N_{\text{pre-berry}} = 5692$; $N_{\text{berry}} = 4246$) and solid bars are passive periods (mean activity < 50 ; $N_{\text{pre-berry}} = 5285$; $N_{\text{berry}} = 3543$).



bears during the two seasons (Fig. 1) — (1) night rest (NR): 0030–0259 pre-berry season, 0000–0329 berry season; (2) early-day activity (EDA): 0300–0829 pre-berry season, 0330–0859 berry season; (3) day rest (DR): 0830–1759 pre-berry season, 0900–1729 berry season; (4) late-day activity (LDA): 1800–0029 pre-berry season, 1730–2359 berry season.

Diel habitat selection in relation to diel activity periods

There was a significant difference in use of habitats during the different activity periods for both seasons (pre-berry: $\chi^2_{[24]} = 508.9$, $p < 0.001$; berry: $\chi^2_{[24]} = 174.9$, $p < 0.001$; Fig. 2). Poor conifers, open bog, and other habitats were almost always avoided, whereas young forest was always selected. But these four habitats were significantly more avoided (less selected) by resting than by foraging bears (except young forest during the berry season). Tall conifers, mixed forest, and forested bog were generally more selected by resting than by foraging bears. Short conifers were selected only by resting bears during the pre-berry season, but also by foraging bears during the berry season. Clearcut was avoided by both resting and foraging bears during the berry season, but significantly more so by resting bears. During the pre-berry season, clearcut was a selected habitat for foraging but not for resting.

Overall 24 h habitat selection compared with diel habitat selection

We also conducted an overall 24 h habitat-selection study to determine whether this gave the same results as dividing the habitat selection according to diel activity. The 24 h study showed that bears used the available habitats nonrandomly during both seasons (pre-berry: $\chi^2_{[8]} = 1\,281.7$, $p < 0.001$; berry: $\chi^2_{[8]} = 972.8$, $p < 0.001$; Table 2). As the bears selected habitats differently when they were foraging than when they were resting (Fig. 2), there were bound to be differences between the diel habitat selection and the 24 h habitat selection. During the pre-berry season, there seemed to be a general selection of short conifers and mixed forest based on the 24 h habitat selection, but these habitats were not selected during the active periods. Clearcuts also seemed to be selected based on the 24 h habitat selection, but they were not selected during the day-rest period. Tall conifers seemed to be avoided from the 24 h habitat selection, but they were selected during the day-rest period. Tall conifers were also selected during the day-rest period of the berry season, but it was not a selected habitat based on the 24 h habitat selection of the berry season.

Discussion

As hypothesized, we found that the habitat selection of female Scandinavian brown bears varied greatly throughout the day and that this variation was related to differences in habitat selection of foraging bears than of resting bears (Figs. 1, 2). Also, some habitats that seemed to be avoided from the overall (24 h) habitat selection (Table 2) were actually selected habitats by resting bears during the day-rest period (Fig. 2). Results of habitat-selection studies where traditional VHF radiotransmitters have been used might thus not be comparable with those based on the newer GPS radiotransmitters, as the former mainly used daytime positions, whereas the latter are based on positions from all 24 h. Also, studies using observations from all 24 h might in fact not be able to show habitats that are important only during a particular time of day. Based on our findings, it is obvious that understanding how animals select habitats differently according to their needs for food and shelter is crucial for the management of any species with diel behavioural differences.

Methodology

We wanted to determine whether using positions 30 m apart would cause a problem of spatial autocorrelation (Neu et al. 1974; Aebischer et al. 1993). To do this, we explored the bears' movement between subsequent GPS fixes and compared it with the average distances within the habitats of this patchy area. The average maximum exit distance of a patch was 85 m, with $< 0.1\%$ of the habitat patches exceeding 2 km across. Considering that the bears walked a median straight-line distance of 361 m during the time available, and sometimes as much as 2.5 km, the bears should be able to walk both out of and into all available habitats between each subsequent GPS fix, thus decreasing the problem of spatial autocorrelation.

The average success rate for GPS fixes was 76%, which was dependent on the activity of the bear. Almost 80% of

Fig. 2. Selection indices ($\pm 95\%$ confidence intervals) of habitats used during different activity periods by six female brown bears in Dalsarna, Sweden, during the (A) pre-berry ($N = 10881$) and (B) berry ($N = 6585$) seasons. There were no observations in the habitat category “other” during day rest in the berry season.

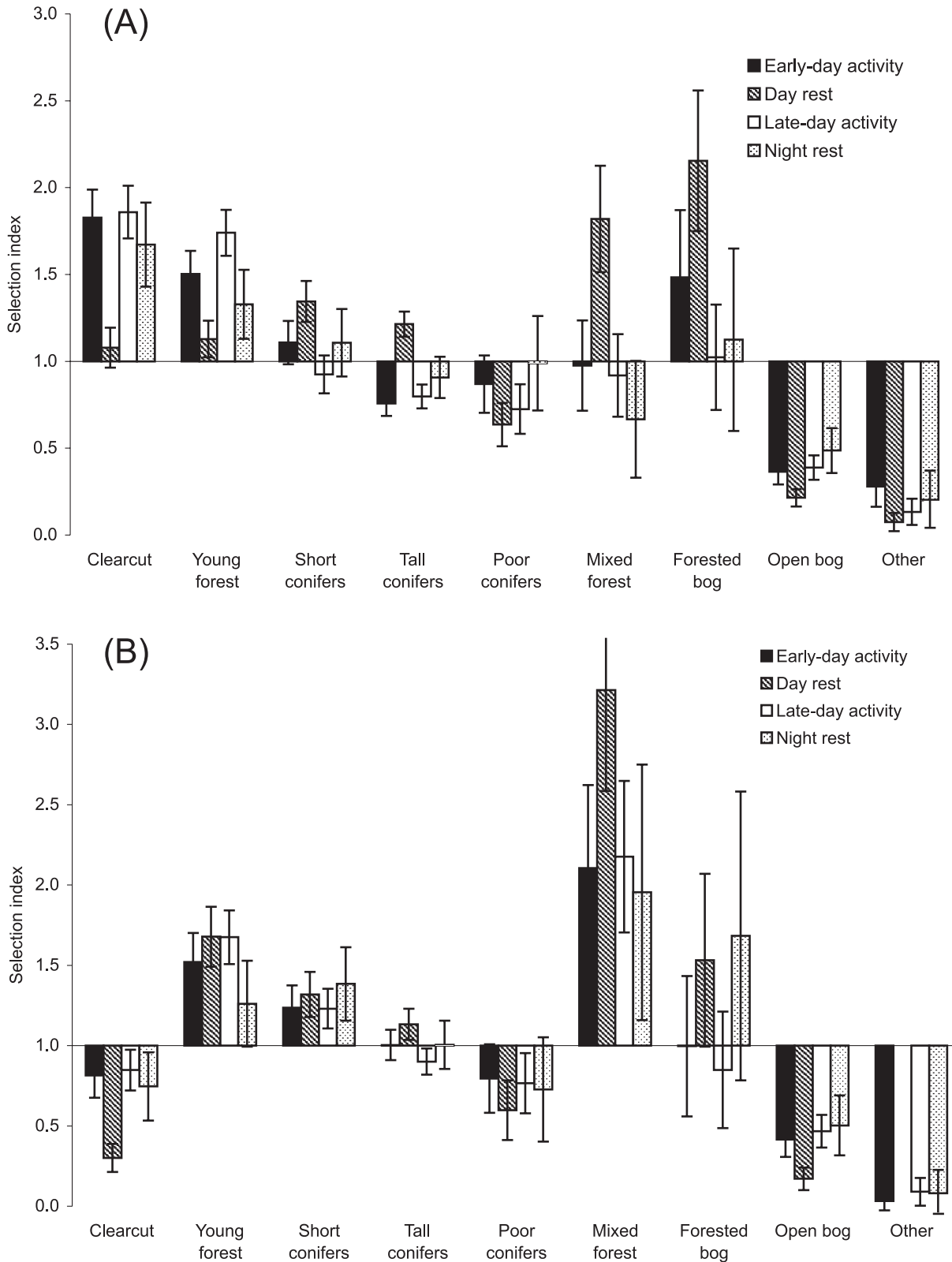


Table 2. Combined results regarding available and used habitats, number of observations, and 24 h habitat selection for six female brown bears in Dalarna, Sweden, 2004.

Habitat	Pre-berry season					Berry season				
	Available (%)	Bear use (%)	<i>N</i>	Selection index	Confidence interval	Available (%)	Bear use (%)	<i>N</i>	Selection index	Confidence interval
Clearcut	12.5	19.6	2130	1.566 ⁺	1.489, 1.664	13.5	9.2	603	0.677 ⁻	0.610, 0.743
Young forest	14.9	21.3	2313	1.427 ⁺	1.360, 1.494	13.4	21.2	1397	1.589 ⁺	1.493, 1.685
Short conifers	13.8	15.7	1703	1.134 ⁺	1.070, 1.199	18.0	23.0	1513	1.274 ⁺	1.200, 1.347
Tall conifers	26.9	25.3	2752	0.940 ⁻	0.901, 0.980	28.9	29.0	1910	1.004	0.955, 1.053
Poor conifers	6.9	5.2	571	0.761 ⁻	0.682, 0.840	6.0	4.3	285	0.723 ⁻	0.617, 0.830
Mixed forest	3.2	3.9	422	1.212 ⁺	1.065, 1.360	2.7	6.4	423	2.419 ⁺	2.129, 2.709
Forested bog	2.2	3.4	368	1.538 ⁺	1.337, 1.738	1.8	2.1	141	1.168	0.920, 1.416
Open bog	14.9	5.0	541	0.334 ⁻	0.298, 0.369	12.3	4.6	303	0.375 ⁻	0.322, 0.429
Other	4.6	0.7	78	0.153 ⁻	0.109, 0.196	3.5	0.2	11	0.048 ⁻	0.011, 0.085

Note: Selection index (\pm confidence intervals) values <1 indicate avoidance, whereas values >1 indicate selection, with significant positive and negative selections ($P < 0.05$) marked.

the failed fixes occurred when the bears were passive. The success rate has also been found to be behaviour-dependent in white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) (Bowman et al. 2000). The difference in fix rate between behaviours is probably due to one or both of two factors. First is the position of the antenna inside the collar. Resting bears might lie on their side or near a rock or other object. This might prevent the transmitter from having a clear line of contact with the satellites and might lead to an undersampling of resting sites. This should, however, not be a great problem, as we divided habitat selection into periods of resting and foraging. Second is the habitat choice of passive versus active bears. Resting bears seem to select denser habitats, and Dussault et al. (1999) and D'Eon et al. (2002) have found that a higher percentage of canopy cover and mature stands limit the transmitter's ability to contact the satellites. This problem should also be evened out more when segregating between habitat selection of foraging bears than of resting bears. But it might still have led to an undersampling of sites in denser habitats.

Diel activity periods

From the activity data, we found that the bears rested and were active at particular times of the day (Fig. 1). Resting was mainly restricted to the daylight hours, whereas activity was restricted to the crepuscular and nocturnal hours. This corresponded well with the findings of Kaczensky et al. (2006) for adult brown bears in Slovenia and Croatia. Gervasi et al. (2006) found that one could differentiate between resting and active bears from the activity data, but could not differentiate between foraging and other active behaviours. To examine whether the habitats used during the active periods of the day were important foraging habitats, our field crew visited 1051 randomly selected bear sites to look for any sign of foraging (data not shown). Confirming the study of Gervasi et al. (2006), we found that the bears avoided foraging during the day-rest period and that there were significant signs of foraging during the late active period of the pre-berry season. We did not find signs of foraging for the remaining active periods, but this lack of foraging signs did not necessarily reflect an actual lack of foraging during these periods, because of the difficulty of finding any sign of foraging on berries. Johansen (1997) found that almost

50% of the bears' assimilated energy came from berries in this area, and MacHutchon (2001) argued that brown bears spend most of their active time foraging.

Thus, the bears seemed to be resting mainly during the day-rest period and foraging mainly during the crepuscular and nocturnal hours. Traditionally, habitat studies of brown bears have been conducted without the use of GIS or GPS, and locating bears equipped with VHF radiotransmitters has mainly been restricted to the daylight hours. Given that foraging and resting bears select habitats differently, our results reveal that this procedure might have induced serious biases to these studies, as they might have included primarily resting habitats.

Diel habitat selection in relation to diel activity periods

There were large differences between the habitats selected during the resting compared with the active periods of the day (Fig. 2). Generally, resting bears seemed to avoid open habitats more than foraging bears. This was particularly obvious for clearcuts during both seasons. Also, tall conifer was an avoided habitat during most active periods, but it was in fact a selected habitat during the day-rest period. Servheen (1983) observed a similar trend for bears feeding on agricultural lands in Montana; they avoided using this open habitat during the daylight hours, but foraged there during the night. The same was true for the bears Nielsen et al. (2004a) studied in Alberta, which used clearcuts more often during the crepuscular and nocturnal hours than during the daylight hours. Horner and Powell (1990) studied habitat use in relation to activity of black bears (*Ursus americanus* Pallas, 1780) in North Carolina and differentiated between moving, foraging, and resting bears. In contrast to our findings, their results suggested no differences in habitat use between these activities. However, their analyses only included the most frequently used sites. Also, their method of defining resting and foraging activities from collar activity sensor levels was not verified with field observations. Gervasi et al. (2006) found that, although it was possible to differentiate between active and passive status of brown bears equipped with activity sensors, it was not possible to differentiate among active behaviours such as walking and foraging. From our results, we can conclude that if the objective is to study all habitats that are important for an animal, then it is crucial to include observations from all 24 h of the day.

We divided the day into categories based on diel activity rather than activity per se. But we also tested the habitats selected by active (activity level ≥ 50) versus passive (activity level < 50) bears regardless of time of day (data not shown), and the same pattern emerged as in Fig. 2. There were two main reasons why we chose to divide the categories according to the time of day. First, we wanted to examine whether studies based on observations from different times of the day were comparable, and our results clearly show that this might not be the case. Second, finding a diel regular activity pattern could be useful for future studies. According to our results, it should now be possible to program collars to take coordinates more often or seldom at particular times of the day based on animal behavioural patterns. For instance, in studies focusing on foraging bears it would be possible to decrease the interval between subsequent GPS-fix attempts (or stop altogether) during the daylight hours. This would increase the longevity of the batteries and thus save both money and animal stress as a result of being captured less often.

Overall 24 h habitat selection compared with diel habitat selection

Comparing our findings of the bears' 24 h habitat selection (Table 2) with diel habitat selection (Fig. 2) revealed another important pattern. Based on the 24 h habitat selection, clear-cut appeared to be highly selected during the pre-berry season. However, the bears did not select this habitat when they were resting (Fig. 2). From the 24 h habitat selection, it also appeared that the bears avoided or did not select tall conifers. However, they significantly selected this habitat when resting. These findings show the serious biases that can result from drawing conclusions based on the bears' 24 h habitat selection. Beyer and Haufler (1994) and Belant and Follmann (2002) emphasized the problems of using only observations from a particular time of day. But as we have seen, it can be equally erroneous to use overall 24 h data sets too. This becomes especially evident when dealing with habitats that are chosen differently for foraging and resting activities, as opposite selections might lead to an average of no selection at all. If the main goal of habitat-selection studies is to find which habitats are important to bears, then it is crucial to differentiate between foraging and resting habitat selections.

To our knowledge, this study is the first to document regular diel differences in habitat selection of resting compared with foraging brown bears. Studies of diel activities (MacHutchon 2001; Klinka and Reimchen 2002; Kaczensky et al. 2006) and diel habitat selection (Beyer and Haufler 1994; Belant and Follmann 2002; Mueller et al. 2004; Nielsen et al. 2004a) have been conducted separately, but never combined and in relation to foraging and resting behaviours. Based on our results, we strongly recommend using data from all 24 h when studying habitat selection. It is also crucial that these data are divided into relevant categories based on the diel behaviour of the particular animal being studied.

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