Therese Fosholt Moe

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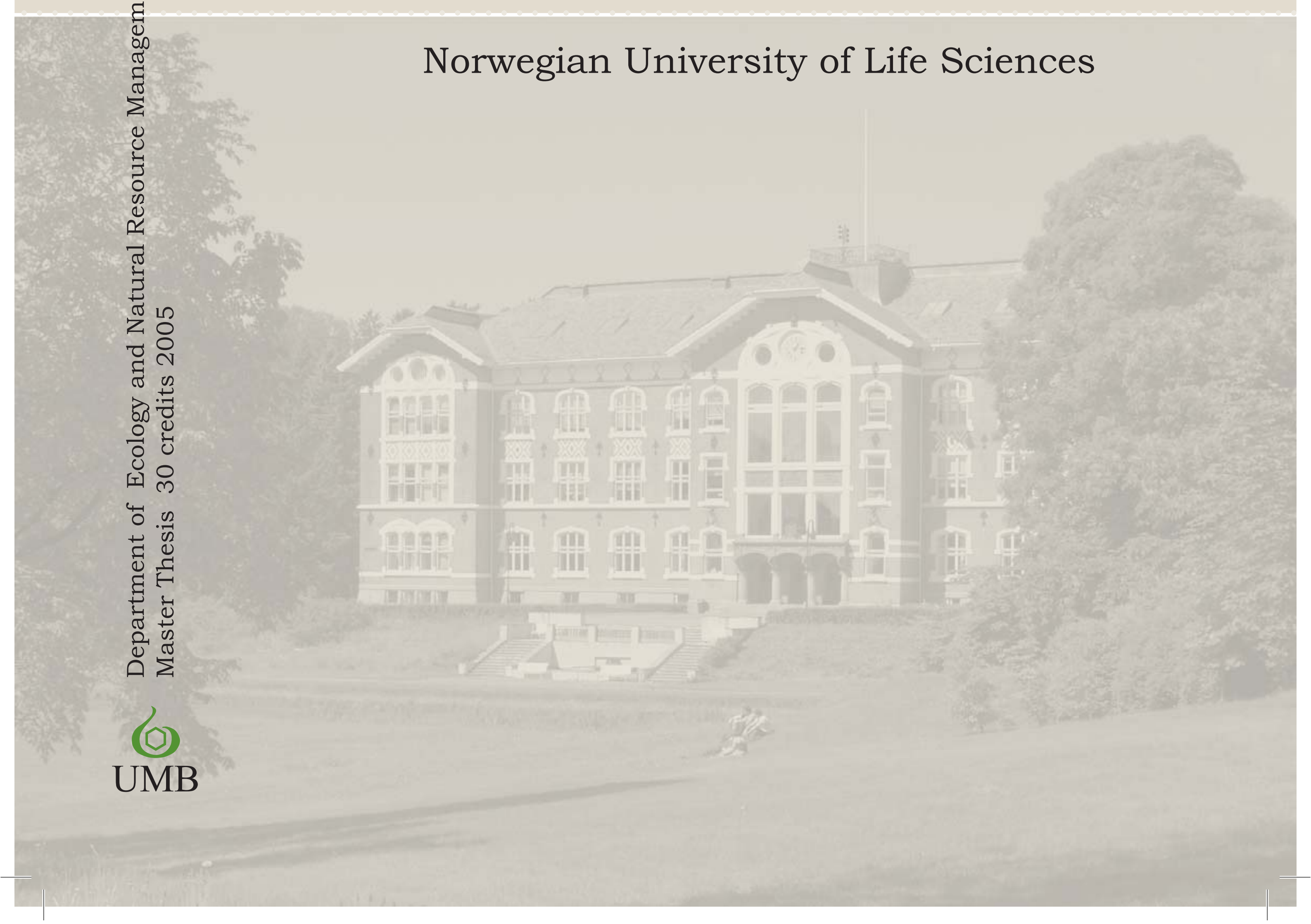
Norwegian University of Life Sciences



Department of Ecology and Natural Resource Management
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UMB

Diel variation in habitat selection of female Scandinavian brown bears (*Ursus arctos*) in relation to foraging and resting behaviour

Døgnvariasjoner i habitatseleksjon hos skandinaviske brunbjørnbinner (*Ursus arctos*) i forhold til furasjering og hvile

Therese Fosholt Moe

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Institutt for Naturforvaltning
Universitet for Miljø- og Biovitenskap

PREFACE

It has been both a pleasure and an extraordinary learning experience to be a part of the Scandinavian Brown Bear Research Project, and I send a thousand thanks to both Jon E. Swenson and Sven Brunberg for giving me this opportunity! I also want to thank Jon for all encouragement and help during the process of writing my thesis.

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Ås, 19.oktober 2005

Therese Fosholt Moe

ABSTRACT

The goal of habitat selection studies should be to find which habitats are ecologically important for the studied species. However, most previous studies on large mammals have focused on overall habitat selection patterns using only daytime positions. I have used 24-hour data from six female Scandinavian brown bears (*Ursus arctos*) equipped with GPS-GSM-collars, with activity loggers. I combined these data with data from field studies, to analyze diel variations in habitat selection related to diel variations in activity (foraging and resting). The bears foraged primarily during the crepuscular/nocturnal hours. During the mating season, they selected mostly clearcuts, young forests and forest-covered bogs for foraging, and young forests, short coniferous forests and mixed forests were selected during the berry season. Also, tall coniferous forests were used extensively, especially during the berry season. The habitats selected for foraging seemed to follow the seasonal differences in food availability rather than the potential cover provided by the different habitats. The main resting period was during the daylight hours, and the bears selected young forests, short and tall coniferous forests, mixed forests and forest-covered bogs for this activity during both seasons. Tall coniferous forest was the most widely used habitat. The habitats selected for resting seemed to be more dependent on the cover provided than the foods available. Poor coniferous forests, nonforested bogs and “Other habitats” were avoided for both activities. As activity depended on the time of day, my findings show the importance of obtaining data from all 24 hours. Also, as the habitat selection depended on the activity, my data show the importance of dividing these data into relevant categories based on the diel activity pattern of the studied species.

SAMMENDRAG

Det overordnede målet med ethvert habitatseleksjonsstudium bør være å finne hvilke habitater som har en økologisk viktig funksjon for den studerte arten. De fleste tidligere habitatseleksjonsstudier har imidlertid kun brukt observasjoner fra dagtid, og de har heller ikke tatt hensyn til eventuelle variasjoner som følge av ulike habitatvalg ved forskjellige aktiviteter. I dette studiet har jeg samlet data fra seks skandinaviske brunbjørnbinner (*Ursus arctos*) gjennom 86 døgn. De var utstyrt med GPS-GSM-sendere samt aktivitetssensorer. Jeg har brukt data fra disse, kombinert med feltdata, for å analysere døgnvariasjoner i bjørnenes habitatseleksjon og aktiviteter (furasjere og hvile). Bjørnene furasjerte hovedsakelig grytidlig om morgenen og om kvelden. I parringssesongen var hogstflater, ungskog og skogkledde myrer mest selektert, mens i bærsesongen var ungskog, middels gammel skog og blandingsskog mest selektert. Bjørnene brukte også hogstklar skog i stor grad, særlig i bærsesongen. Habitatene der bjørnene furasjerte så ut til å være valgt på grunn av mattilbudet heller enn på grunn av potensielt skjul. Den viktigste hvileperioden var om dagen, og bjørnene selekterte ungskog, middels gammel og hogstklar barskog, blandingsskog og skogkledde myrer når de hvilte. Hogstklar barskog var det mest brukte hvilehabitatet. Hvilehabitatene så ut til å være valgt på grunn av potensielt skjul heller enn på grunn av mattilbud. Bjørnene unngikk fattig barskog, åpen myr og ”andre habitater” både når de furasjerte og når de hvilte. Mine data har vist at aktiviteten er avhengig av tiden på døgnet, og at habitatseleksjonen er avhengig av aktiviteten. Konsekvensene av dette er at for å trekke økologisk relevante konklusjoner må man samle data fra hele døgnet og dele disse inn i kategorier basert på døgnlige variasjoner i aktivitetsmønsteret hos arten man studerer.

INTRODUCTION

Habitat selection is defined as an animal's disproportionate use of a habitat in relation to its availability (Johnson 1980), a selection that can operate at different spatial and temporal scales (Johnson 1980; Mysterud et al. 1999; Apps et al. 2004; Nielsen et al. 2004*a*). This habitat selection probably reflects the animal's different behaviors. Throughout its life, an animal must satisfy its basic needs, such as food, cover, water, and mating opportunities. As 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 what kinds of habitats are used and why animals select some habitats over others (Manly et al. 2002).

The brown bear (*Ursus arctos*) is an omnivorous animal with high energy requirements, and it spends 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 the availability of food is an important ecological factor for bears, both at the individual and at the population level, influencing survival and reproduction. And McLoughlin et al. (2002) found that habitat selection was highly influenced by food availability in grizzly bears (*U. a. horribilis*) in the Canadian Arctic. However, Jansson (2005) argued that the selection of resting habitats was more important than the selection of foraging habitats for brown bears (*U. a. arctos*) in Scandinavia. It is believed that the optimal brown bear habitat is a mix of open and forested habitats (Nielsen et al. 2004*b*), and this might reflect a difference in habitats selected for resting and habitats selected for foraging. However, no previous studies have looked at brown bear habitat selection on such a fine scale, i.e. examining the use of foraging and resting sites individually.

An animal's needs change throughout time, and so probably does its behavior. Food availability might change between years, and many animals, including bears, are capable of switching between the most abundant foods (Schooley 1994; Swenson et al. 1999). Also, because the diet changes between seasons, seasonal differences in the bears' habitat selection would be expected. This has been found in many studies in North America (e.g. Servheen 1983; Waller & Mace 1997; Heyden & Meslow 1999; McLellan & Hovey 2001; Stratman et al. 2001; Belant & Follmann 2002; McLoughlin et al. 2002). Studies on both brown bears (Servheen 1983; Belant & Follmann 2002; Nielsen et al. 2004*a*) and cervids (Mysterud et al. 1999) indicate that habitat selection also varies according to the time of day. Beyer & Haufler

(1994) also recognized the need for habitat studies to consider a 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 & Haufler 1994; Mysterud et al. 1999; Apps et al. 2004; Nielsen et al. 2004*a*).

Most previous habitat studies on large mammals have been conducted by equipping the animal with very high frequency (VHF) transmitters. Location of the animal has then been from the ground or from aircraft and mainly during the daylight hours. Triangulation from the ground is labor intensive, whereas using aircraft is expensive. The resulting observations are infrequent, weather dependent and not very accurate (White & Garrot 1990). With the introduction of GPS-GSM-collars (Global Positioning System and Global System for Mobile communication) and the NAVSTAR GPS (satellites and ground receiving system), a new era in the study of habitat selection is beginning (Rodgers et al. 1996). Via contact with the NAVSTAR satellites, the GPS-GSM-collars can locate the animal's position with very high accuracy. Because the coordinates are sent via SMS (Short Message Service), receiving the animals' locations also is independent of human effort. And the collars can be programmed to produce a large amount of locations, independent of time and remoteness (Obbard et al. 1998, Arthur & Schwartz 1999). This new technology thus gives us the possibility of very small-scale habitat selection studies in both time and place (Rodgers et al. 1996; Adrados et al.2003).

In this paper, I explore the habitat selection of six female brown bears in Sweden. They were all equipped with GPS-GSM-collars including activity loggers. From this I determined their activity status (active/passive) at each position, and I also conducted field studies to examine their behaviors (foraging/resting). My main hypothesis was that the bears would use their habitats nonrandomly as a result of different habitats covering different needs. Secondly, as the needs of a foraging bear (foods) are not the same as the needs of a resting bear (shelter), I expected a difference in the habitat selection of foraging compared to resting bears. Thirdly, I expected the bears' resting and foraging behaviors to vary throughout the day, and thus also expected to find a diel variation in their habitat selection pattern.

STUDY AREA

The study was conducted in the counties of Dalarna and Gavleborg, Sweden (61°N, 15°E), an area near the southernmost distribution of the Scandinavian brown bear populations (Fig. 1). The area is mainly forested, 80% being covered by highly managed productive forest. Bogs and lakes cover the remaining area, and the human settlements are no more than a few scattered villages. The forest turnover time is 90-100 years, and clearcuts constitute approximately 8% of this area. Less than 60% of the forest is 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 m^2. The terrain is gently undulating with altitudes ranging from 200 to 700 m above sea level. No areas rise above the timberline. The dominating tree species is Scots pine (*Pinus sylvestris*), with Norway spruce (*Picea abies*), lodgepole pine (*Pinus contorta*, non-native), birches (*Betula* spp.) and aspen (*Populus tremula*) covering the remaining area. Important ground vegetation includes bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*), crowberry (*Empetrum hermaphroditum*), some forbs, and heather (*Calluna vulgaris*). Most areas are also covered with lichens or mosses. The winter population of moose (*Alces alces*) was estimated to about 920 individuals per 1,000 km^2 (Swenson et al. 2005), and the estimated brown bear (*Ursus arctos*) population density was approximately 30 bears per 1,000 km^2 (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).

Figure 1: The distribution of the brown bear (*Ursus arctos*) in Scandinavia; the three core areas of breeding. This study was conducted in the southernmost core area (after Swenson et al. 2005).

MATERIAL AND METHODS

Data collection and GPS-radiotelemetry

I studied six sexually mature female brown bears, ranging from three to ten years of age. They were all equipped with GPS-Plus-3 collars including activity loggers and GSM modems (VECTRONIC Aerospace GmbH, Berlin, Germany). The bears' coordinates and activity status (N=19,209) 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 behavior and diet (McLellan & Hovey 2001; McLoughlin et al. 2002), the study period was divided in the mating (20 May – 6 July; field observations did not start until 4 June) (Dahle & Swenson 2003*a*) and berry seasons (16 July – 24 August), with a break in between when berries started ripening. Using handheld GPS-receivers (*MAGELLAN SporTrak Pro* [Thales, Santa Clara, California] and *MAGELLAN GPS 315* [Thales], both with the updated software *Magellan Backup LT*), I investigated a random selection of 1,051 sites and registered all bear sign within a radius of 30 m. I mainly used three-day-old coordinates as a compromise between using as fresh sign as possible and not disturbing the bears.

Presently, there are three main problems with the use of GPS radiotelemetry (D'Eon et al. 2002). First, radiocollars sometimes malfunction. In fact, this was a problem for one of the transmitters, 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, I chose to include the available data from this bear in my analyses. The second problem is location error, which D'Eon et al. (2002) found to be approximately 31m 95% of the time. Swenson et al. (2005) reported it to be even less than this (±10m), which also was my personal experience from the fieldwork. Thus the use of a radius of 30 m at the observation site should have covered most true locations. The third problem is the fix-rate bias. This appears as a lack of contact between the GPS collars and the satellites, resulting in loss of data. There are several factors that can disturb this connection, e.g. animal behavior, 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 is a serious problem, as it can lead to erroneous conclusions (D'Eon 2003). For example, loss of data in dense forests will lead to an underestimation of this habitat. There are, unfortunately, few appropriate ways of avoiding this problem, but it should be remembered when analyzing habitat selection patterns. A practical result of the first and third problems was that I often received less than the expected 48 positions per day. To avoid the bias this could cause, I did not use coordinates from bears with less than 35 positions during a day.

Habitat description

Home range habitats were defined using digital land cover maps from the Swedish CORINE Land Cover Data (Engberg 2002). These maps were made from satellite images and field inventories from 1999 and 2002. The minimum recorded habitat patch size was one hectare, and the patch unit (pixel) of the map was 25x25 m.

Home ranges were defined separately for each season, and a 100% Minimum Convex Polygon was created for each bear. For more information on the procedure, see Jansson (2005). I defined available habitat as the overall habitat proportions within these home ranges, and combined some of the SMD habitat classes (Svenska Marktäcke Data; 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 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).

Table 1: Habitat categories of the home ranges of six female brown bears in Dalarna, Sweden 2004. SMD (Svenska Marktäcke Data) habitat classes are from the Swedish CORINE Land Cover Data (Engberg 2003).

Habitat class	Habitat description	SMD classes
Fcc	Forest: clearcut (without trees or shrub/tree height <2m)	54
Fyf	Forest: young forest (tree height 2-5m, canopy cover >30%)	55
Fcs	Forest: coniferous short (tree height 5-15m, canopy cover >30%)	44
Fct	Forest: coniferous tall (tree height >15m, canopy cover >30%)	45
Fcp	Forest: coniferous poor (as Fcs and Fct but on lichen dominated ground)	43
Fmf	Forest: mixed forest (tree height >5m, canopy cover >30% of which coniferous trees constitute <75%)	40,48
Bfc	Bog: forest-covered (as Fcs, Fct, and Fmf but on boggy ground)	41,46,49
Bnf	Bog: no forest cover (shrubs/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

Behavior classifications

Primary behavior was defined by the findings in each observed site and recorded as one of five categories: foraging (considerable sign of foraging), resting (resting site with bear hair present), foraging/resting (both foraging and resting sign), unsure (sign of bear activity, but primary behavior was difficult to decide) and no sign (no sign of bear activity).

Different foraging behaviors were also determined. Bears in this region feed on moose, ants (mainly *Camponotus herculeanus*. and *Formica* spp.), wasps (*Vespidae*), bumblebees (*Apidae*), berries (mainly bilberries, cowberries and crowberries), and other plants (Johansen 1997; Dahle et al. 1998; Swenson et al. 1999). It was easy to recognize sign of foraging on moose (carcasses) and Hymenoptera (diggings in anthills, broken tree stumps, turned stones and diggings for nests in the ground), but it was difficult to find sign of foraging on plants, and especially berries. Plants and berries were therefore likely underrepresented in the foraging category. According to Johansen (1997), graminoids and forbs constituted only 5% of the bears' assimilated energy in this region, and thus the underestimation of these foods was probably not problematic. Berries, however, constituted approximately 50% of the bears' assimilated energy (Johansen 1997), and to compensate for this loss of data, I ranked the abundance of ripe berries in each site and analyzed these data separately. Ripe berries were present in 397 sites, and the abundances were categorized as no berries, medium amount of berries (the highest amount in the mating season), and abundant berries (the highest amount in the berry season). The study was conducted in a year with low berry production, and hence I used fewer categories than would be used in years of good berry production. Sign of foraging were recorded as “fresh” if I thought the food item had been eaten at the time of the GPS fix, otherwise they were recorded as “old”. In the analysis of tree stumps I pooled the fresh and old findings, and for anthills I also included the untouched anthills.

Five of the bears had activity loggers that recorded an activity index between 0 and 510 every five minutes (the sixth individual had a different activity logger and the observations from this bear were excluded when analyzing data based on activity levels). The activity index was an indication of the bear’s head movement in two directions during these five minutes. The mean activity of a bear at a site was the mean of the six recordings during the 30-minute interval surrounding the time of the GPS fix. I defined all periods where the bears showed a mean activity of less than 50 as passive periods and above 50 as active periods. Gervasi et al. (manus) found that it is possible to differentiate between active and passive (sleeping, or awake but resting) periods from a threshold level of 45-65. According to this, my use of 50 as a threshold level should be ecologically sound.

Statistics

Compositional analysis has been widely used to analyze habitat selection in animals, because it avoids the problems of unit-sum constraints (that avoidance of one habitat leads to a selection of the alternatives), autocorrelation among observations (as the individual is the sampling unit), and differential use of habitats among different groups of animals (Aebischer et al. 1993; Manly et al. 2002). But in my study there were only six individuals available, and such a low sample size would seriously limit the power of this test (Aebischer et al. 1993; Heyden & Meslow 1999). Also, three of the six bears were related (a mother and her two daughters), and could therefore be autocorrelated (Manly et al. 2002). Because of these problems, I chose to use χ^2 goodness-of-fit tests, with the individual observation as the sample unit and not the individual bear. To examine whether these observations were autocorrelated, I also analyzed the movement of the bears to find their ability to exit any habitat patch within the scope of two preceding observations. This was done by calculating the distance between subsequent GPS positions corrected for irregularities in time (should be 30 min). These distances were underestimations of the actual distances walked by the bears, as they were measured as a straight-line distance. Where there were missing data in the preceding or present positions, I excluded the observation from the analysis. This was to avoid a possible bias towards lower distances as a result of the bears walking back and forth during the longer time intervals.

The movement was analyzed using Mann-Whitney tests in MiniTab 13.0 (Minitab Inc., Pennsylvania, USA), and I also used this program for the χ^2 tests. Where these χ^2 tests showed that the bears used their home range habitats nonrandomly ($P \leq 0.05$), I used a modified version of the methods of Neu et al. (1974) to determine which habitats were selected or avoided. I used the method described by Krebs (1999: 480-481), which differed from Neu et al. (1974) by using a selection index, with confidence intervals surrounding this index instead of the actual proportion of habitats used. The selection index was the proportion of habitat used divided by the proportion available. Thus, no selection resulted in a selection index of 1. I defined selection indices significantly lower than 1 as habitat avoidance and selection indices significantly higher than 1 as 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, I performed a Bonferroni adjustment when calculating the 95% confidence intervals (α-level $0.05/n$). I considered two categories to be significantly different from each other when their confidence intervals did not overlap. This was a very conservative assumption (Krebs 1999), and together with the Bonferroni adjustment, this decreased the power of my tests (Nakagawa 2004). To avoid missing important use patterns as a result of this lowered power, I have reported not only significant results ($\alpha \leq 0.05$), but also obvious (but nonsignificant) trends.

RESULTS

All reported results are significant ($\alpha \leq 0.05$) unless otherwise stated. Nonsignificant patterns are referred to as trends. There were no observations of primary behaviors in "Other" habitats, and this category was therefore excluded from these results.

Rates of movement

When calculating straight-line movement (m/30 min), I used all sites where the bears had been active (mean activity ≥50) (Fig. 2). Pooling the seasons, the median movement was 361 m/30 min (N=9,088), and the overall maximum distance walked in 30 minutes was 2,551 m. Most of the time, the bears walked less than 500 m. A Mann-Whitney test revealed no difference between the mating and berry seasons, the medians being 361 and 360 m/30 min, respectively (W = 20,643,114; N[mating] = 5,015; N[berry] = 3,152; P = 0.119). However, including the passive periods, the medians were 143 and 258 m/30 min for the mating and berry seasons, respectively (W = 69,142,668; N[mating] = 9,673; N[berry] = 5,320; P = 0.000).

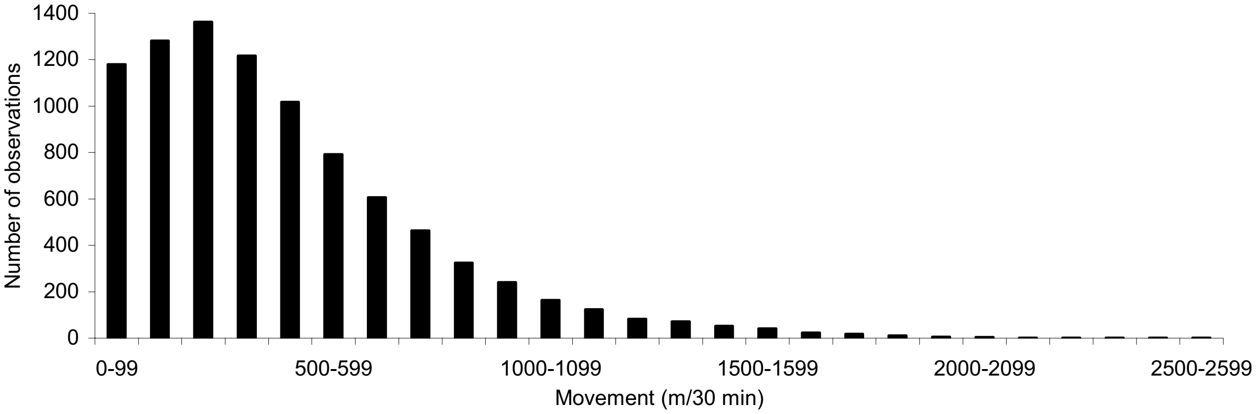

Figure 2: Movement measured as distance in meters between positions taken each 30 min (mean activity ≥50; N=9,088) from five female brown bears in Dalarna, Sweden 2004.

Overall habitat selection

During the mating season, the bears used the available habitats nonrandomly (χ^2 =1281.7; df = 8; p = 0.000) (Table 2). The pooled data show that the bears selected clearcuts (Fcc), young forests (Fyf), short coniferous forests (Fcs), mixed forests (Fmf), and forest-covered bogs (Bfc). They avoided tall coniferous forests (Fct), poor coniferous forests (Fcp), nonforested bogs (Bnf), and other habitats (Other).

Table 2: Combined available and used habitats (in %), number of observations, selection indices (S.I.) and 95% confidence intervals with Bonferroni correction (C.I.) of the habitat selection for six female brown bears in Dalarna, Sweden 2004. Significant positive/negative selection indices (P<0.05) are marked +/-. Selection index (±CI) <1 indicates avoidance, selection index (±CI) >1 indicates selection.

	Mating season						Berry season					
	Available	Bear use					Available	Bear use				
Habitat[a]	%	%	*N*	S.I.	C.I.		%	%	*N*	S.I.	C.I.	
Fcc	12.0	19.6	2130	1.637 +	1.556	1.718	13.5	9.2	603	0.677 -	0.610	0.743
Fyf	14.0	21.3	2313	1.515 +	1.443	1.586	13.4	21.2	1397	1.589 +	1.493	1.685
Fcs	13.6	15.7	1703	1.155 +	1.090	1.221	18.0	23.0	1513	1.274 +	1.200	1.347
Fct	28.2	25.3	2752	0.897 -	0.859	0.934	28.9	29.0	1910	1.004	0.955	1.053
Fcp	7.8	5.3	571	0.670 -	0.600	0.739	6.0	4.3	285	0.723 -	0.617	0.830
Fmf	3.1	3.9	422	1.249 +	1.097	1.401	2.7	6.4	423	2.419 +	2.129	2.709
Bfc	2.1	3.4	368	1.597 +	1.388	1.805	1.8	2.1	141	1.168	0.920	1.416
Bnf	14.6	5.0	541	0.341 -	0.305	0.378	12.3	4.6	303	0.375 -	0.322	0.429
Other	4.6	0.7	78	0.156 -	0.111	0.201	3.5	0.2	11	0.048 -	0.011	0.085

[a] See Table 1 for explanation of abbreviations

Also during the berry season, the bears showed a nonrandom use of habitats (χ^2 = 972.8; df = 8; p = 0.000) (Table 2). They selected young forests (Fyf), short coniferous forests (Fcs), and mixed forests (Fmf), and avoided clearcuts (Fcc), poor coniferous forests (Fcp), nonforested bogs (Bnf), and other habitats (Other). They showed no selection for tall coniferous forests (Fct) and nonforested bogs (Bfc). Although not selected for, the most used habitat during both seasons was tall coniferous forests (Fct), and the bears spent more than 80% of their time in the four habitats clearcuts (Fcc), young forests (Fyf), short (Fcs), and tall coniferous forests (Fct). The degree of selection for each habitat during the mating and the berry season is summarized graphically in Fig. 3.

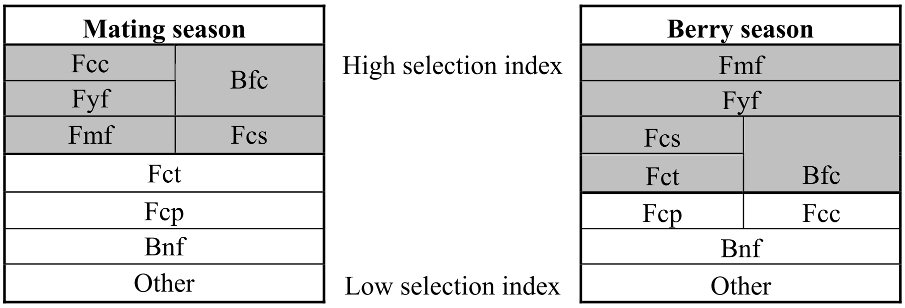

Figure 3: Habitat selection by six female brown bears in Dalarna, Sweden, during the mating and berry seasons of 2004. Habitats with positive selection indices are gray; negative are white. The habitats with the highest selection indices are on top, with significantly decreasing selection towards the bottom. There is no significant difference between habitats placed next to each other. See Table 1 for explanation of abbreviations.

The bears' home ranges were different in habitat composition during the mating compared to the berry season, resulting in significant seasonal differences in available habitats ($\chi^2 = 170.6$; df = 8; p = 0.000) (Table 2). There were also seasonal differences in the habitats used by the bears ($\chi^2 = 534.4$; df = 8; p = 0.000), and some of these differences were quite pronounced. The bears shifted from selecting to avoiding clearcuts (Fcc). Tall coniferous forests (Fct) were avoided during the mating season, but not during the berry season. Mixed forests (Fmf) were selected for in both seasons, but the selection was significantly higher during the berry season. "Other" habitats were avoided during both seasons and even more so during the berry season. I examined the seasonal changes in the different habitats within this category (Other), and found that they were all highly avoided during both seasons (data not shown). The only exception was "watercourses", which was selected during the mating season.

Habitat selection in relation to primary behavior

The use of habitats for the primary behaviors differed significantly from random in both seasons (Mating: $\chi^2 = 107.4$; df = 18; p = 0.000. Berry: $\chi^2 = 40.1$; df = 18; p = 0.002) (Table 3). In these tests I excluded the category "foraging/resting" because the number of observations was too low to be tested (<5 % of the observations). Focusing on foraging, I found that during the mating season the bears selected clearcuts (Fcc) and young forest (Fyf) while foraging, and they avoided short (Fcs), tall (Fct), and poor coniferous forests (Fcp), and nonforested bogs (Bnf). During the berry season they selected young forests (Fyf), but avoided nonforested bogs (Bnf) and tended to avoid tall coniferous forests (Fct). From the mating to the berry season, foraging bears showed less selection of clearcuts (Fcc) and less avoidance of short (Fcs) and tall coniferous forests (Fct).

I found a less pronounced selection for habitats used for resting during either seasons, but they avoided clearcuts (Fcc) and nonforested bogs (Bnf) (Table 3). There were no seasonal differences.

Table 3: Selection indices (S.I) of habitats used for foraging and resting by six female brown bears in Dalarna, Sweden 2004 (using Krebs' method with Bonferroni correction of 95% C.I.). Selection index (±CI) <1 indicates avoidance, selection index (±CI) >1 indicates selection.

	Foraging						Resting					
	Mating season			Berry season			Mating season			Berry season		
Habitat[a]	N	S.I.	+/- C.I.	N	S.I.	+/- C.I.	N	S.I.	+/- C.I.	N	S.I.	+/- C.I.
Fcc	47	3.970 +	1.068	10	0.711	0.544	2	0.293 -	0.519	4	0.389 -	0.482
Fyf	38	2.734 +	0.886	39	2.809 +	0.905	10	1.250	0.914	15	1.478	0.871
Fcs	3	0.224 -	0.324	23	1.226	0.574	10	1.295	0.946	16	1.167	0.660
Fct	3	0.107 -	0.155	20	0.666	0.341	23	1.430	0.586	29	1.321	0.491
Fcp	1	0.129 -	0.326	4	0.643	0.802	2	0.448	0.792	3	0.660	0.950
Fmf	2	0.650	1.159	6	2.173	2.192	8	4.519	3.772	5	2.478	2.727
Bfc	2	0.953	1.699	0	*No observations*		1	0.828	2.089	2	1.436	2.550
Bnf	3	0.208 -	0.301	2	0.157 -	0.280	1	0.120 -	0.304	2	0.215 -	0.381

[a] see Table 1 for explanation of abbreviations

+/- significant at $p<0.05$

Habitat selection in relation to foraging behavior

I found nine fresh moose calf carcasses, all killed by bears and all killed during the mating season. I also found some older parts of moose calves and adults, but it was difficult to determine the cause of death of these animals. I located 72 nests of wasps and bumblebees at 56 sites. The bears only used this food source during the berry season, but I had too few observations to relate their use to habitat.

Anthills were found in 518 of the observed sites (total sum of anthills; 1,050), and in 89 of these sites the bears had dug for ants during the last three days (total sum of opened anthills; 106). In the mating season, the bears selected sites with anthills in clearcuts (Fcc) and young forests (Fyf), and they avoided sites with anthills in tall (Fct) and poor coniferous forests (Fcp), and nonforested bogs (Bnf) (Table 4). During the berry season they selectively opened available anthills in sites in young (Fyf) and mixed forests (Fmf), and avoided opening them in clearcuts (Fcc), poor coniferous forests (Fcp), and nonforested bogs (Bnf). There was no significant selection for habitats containing freshly opened anthills during either season, but the sample size of each habitat was very small (<5 observations in six of the nine habitats).

The bears had also opened 2,554 tree stumps at 201 sites. I have no data on presence of tree stumps in the different habitats, so this analysis compares all available habitats with habitats where bears had opened tree stumps. During the mating season the bears selected sites in clearcuts (Fcc) and young forests (Fyf) to open tree stumps, and avoided them in tall (Fct) and poor coniferous forests (Fcp), forest-covered (Bfc), and nonforested bogs (Bnf) (Table 4). During the berry season they selected sites in young (Fyf) and mixed forests (Fmf) to open tree stumps and avoided them in tall (Fct) and poor coniferous forests (Fcp), forest-covered bogs (Bfc) and nonforested bogs (Bnf).

Table 4: Selection indices (S.I.) for habitats in relation to use of anthills present and tree stumps opened by six female brown bears of Dalarna, Sweden 2004 (using Krebs' method with Bonferroni correction of 95% C.I.). Selection index (±CI) <1 indicates avoidance, selection index (±CI) >1 indicates selection.

	Anthills				Tree Stumps			
	Mating season		Berry season		Mating season		Berry season	
Habitat[a]	S.I.	± C.I.	S.I.	± C.I.	S.I.	± C.I.	S.I.	± C.I.
Fcc	1.858+	0.629	0.554-	0.277	2.869+	0.654	0.705	0.341
Fyf	2.194+	0.595	2.083+	0.478	2.682+	0.568	2.830+	0.571
Fcs	1.118	0.479	1.195	0.325	0.710	0.358	1.248	0.364
Fct	0.555-	0.233	0.822	0.210	0.326-	0.169	0.555-	0.200
Fcp	0.451-	0.426	0.522-	0.414	0.427-	0.378	0.383-	0.393
Fmf	1.789	1.334	2.472+	1.327	1.212	1.009	4.025+	1.830
Bfc	1.192	1.340	1.023	1.053	0.197-	0.502	0.208-	0.529-
Bnf	0.312-	0.259	0.637-	0.311	0.115-	0.145	0.062-	0.112

[a] see Table 1 for explanation of abbreviations

+/- significant at $p<0.05$

The use of sites was nonrandom in respect to berry abundance during the berry season ($\chi^2 = 76.1$; df = 14; p = 0.000; four cells with expected counts <5) (Fig. 4), but there were not enough observations to adequately test this for the mating season ($\chi^2 = 33.2$; df = 7; five cells with expected counts <5, one cell with expected count <1). However, the trend during the mating season was that the bears used fewer sites with abundant berries in tall coniferous forests (Fct) than their overall use of this habitat, and they used more sites with abundant berries in clearcuts (Fcc). Compared to their overall habitat use during the berry season, they visited fewer sites without berries and more sites with abundant berries in tall coniferous forests (Fct), and they also used fewer sites with abundant berries in young forests (Fyf), short coniferous forests (Fcs), and nonforested bogs (Bnf) (Fig. 4). There was a tendency towards a selection of sites with medium amounts of berries in young (Fyf) and mixed forests (Fmf) during the berry season.

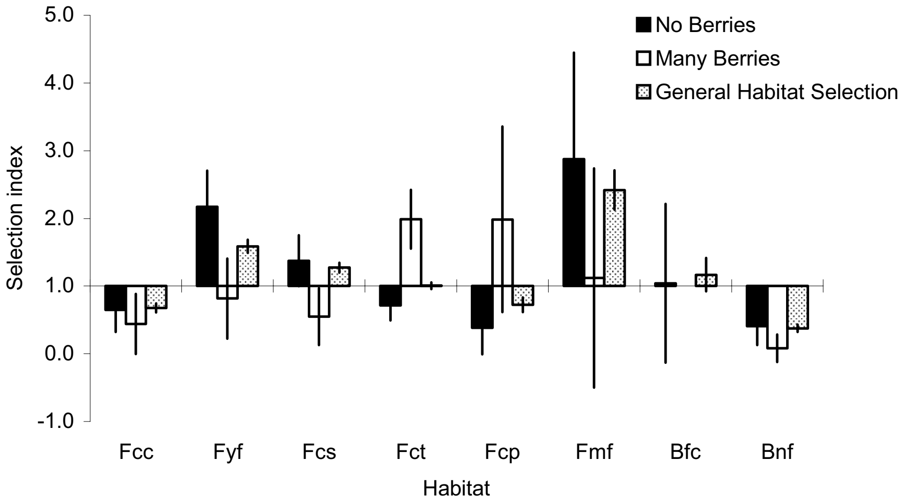

Figure 4: Selection indices (± 95% confidence interval) of habitats with different berry abundances compared with the overall habitat selection (see Table 2) in sites visited by six female brown bears during the berry season in Dalarna, Sweden 2004 (N = 627). See Table 1 for explanation of abbreviations.

To examine whether the 1,051 observed sites were in fact random positions with respect to the bears' use of habitat, I compared the habitats of these sites with the overall habitat use by the bears. Tall coniferous forests (Fct) were significantly underrepresented (no overlap of confidence intervals) in the observed sites, resulting in a conservative estimate of use of this habitat for the different primary behaviors.

Diel habitat selection in relation to activity periods

The activity periods were based on the mean activity levels of each half hour interval. I divided the day into four separate activity periods, defined by the mean activity of the bears during the two seasons (Fig. 5):

Night Rest (NR) 00:30-02:59 mating season, 00:00-03:29 berry season.

Early-Day Activity (EDA) 03:00-08:29 mating season, 03:30-08:59 berry season.

Day Rest (DR) 08:30-17:59 mating season, 09:00-17:29 berry season.

Late-Day Activity (LDA) 18:00-00:29 mating season, 17:30-23:59 berry season.

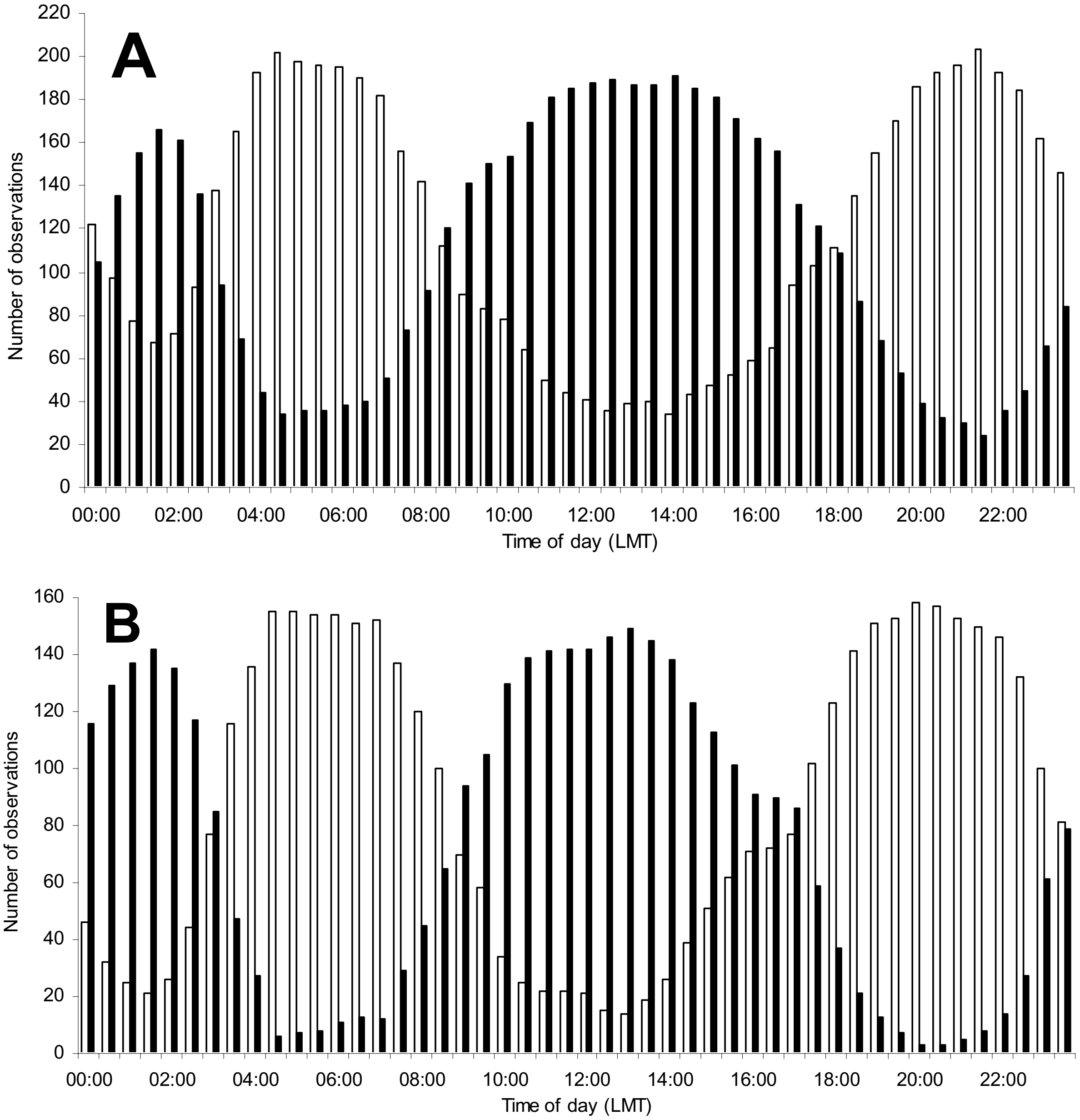

Figure 5: Mean activity for each half-hour period (local mean time) during a diel cycle for five female brown bears in Dalarna, Sweden during the mating (A) and berry (B) seasons of 2004. White bars are active periods (mean activity ≥50; $N_A = 5,692$; $N_B = 4,246$), black bars are passive periods (mean activity <50; $N_A = 5,285$; $N_B = 3,543$).

There was a significant difference in use of habitats during the different activity periods for both seasons (Mating: $\chi^2 = 508.9$; df= 24; p = 0.000. Berry: $\chi^2 = 174.9$; df= 24; p = 0.000) (Table 5, Fig. 6). In the mating season the bears selected clearcuts (Fcc), young forests (Fyf), short coniferous forests (Fcs), and forest-covered bogs (Bfc) during the early-day activity (EDA) and avoided tall (Fct) and poor coniferous forests (Fcp), nonforested bogs (Bnf), and "Other" habitats (Fig. 6 A). They selected clearcuts (Fcc), young forests (Fyf), short (Fcs) and tall coniferous forests (Fct), mixed forests (Fmf), and forest-covered bogs

(Bfc) during the day rest (DR) and avoided poor coniferous forests (Fcp), nonforested bogs (Bnf), and “Other” habitats. The bears selected clearcuts (Fcc) and young forests (Fyf) for late-day activity (LDA) and avoided tall (Fct) and poor coniferous forests (Fcp), nonforested bogs (Bnf), and “Other” habitats. For night rest (NR) they showed a selection of clearcuts (Fcc) and young forests (Fyf), and an avoidance of tall coniferous forests (Fct), nonforested bogs (Bnf), and “Other” habitats.

In the berry season there was a selection of young (Fyf), short coniferous (Fcs), and mixed forests (Fmf) during early-day activity (EDA) and an avoidance of clearcuts (Fcc), poor coniferous forests (Fcp), nonforested bogs (Bnf), and “Other” habitats (Fig. 6 B). The bears selected young forests (Fyf), short (Fcs) and tall coniferous (Fct), and mixed forests (Fmf) during day rest (DR) and an avoided clearcuts (Fcc), poor coniferous forests (Fcp), and nonforested bogs (Bnf). There were no observations in “Other” habitats. During late-day activity (LDA), the bears selected young (Fyf), short coniferous (Fcs), and mixed forests (Fmf) and avoided clearcuts (Fcc), tall (Fct) and poor coniferous forests (Fcp), nonforested bogs (Bnf), and “Other” habitats. During night rest (NR) they selected short coniferous (Fcs) and mixed forests (Fmf), and avoided clearcuts (Fcc), nonforested bogs (Bnf), and “Other” habitats.

Table 5: Habitats visited (in %) during different activity periods (defined in footnote) by six female brown bears of Dalarna, Sweden during the mating and the berry seasons of 2004.

	Mating season				Berry season			
Habitat[a]	EDA	DR	LDA	NR	EDA	DR	LDA	NR
Fcc	22.84	13.48	23.24	20.90	11.01	4.07	11.47	10.10
Fyf	22.38	16.82	25.93	19.80	20.31	22.41	22.37	16.83
Fcs	15.29	18.55	12.76	15.27	22.30	23.79	22.19	24.96
Fct	20.36	32.66	21.46	24.40	29.00	32.71	26.01	29.03
Fcp	6.00	4.39	5.00	6.83	4.76	3.58	4.58	4.35
Fmf	3.12	5.82	2.94	2.13	5.59	8.54	5.78	5.19
Bfc	3.26	4.74	2.25	2.47	1.83	2.81	1.56	3.09
Bnf	5.43	3.20	5.79	7.25	5.09	2.09	5.74	6.17
Other	1.31	0.35	0.63	0.94	0.11	0.00	0.31	0.28
N observations	2,819	3,693	3,197	1,172	1,807	1,816	2,249	713

[a] see Table 1 for explanation of abbreviations

EDA = early-day activity; DR = day rest; LDA = late-day activity; NR = night rest

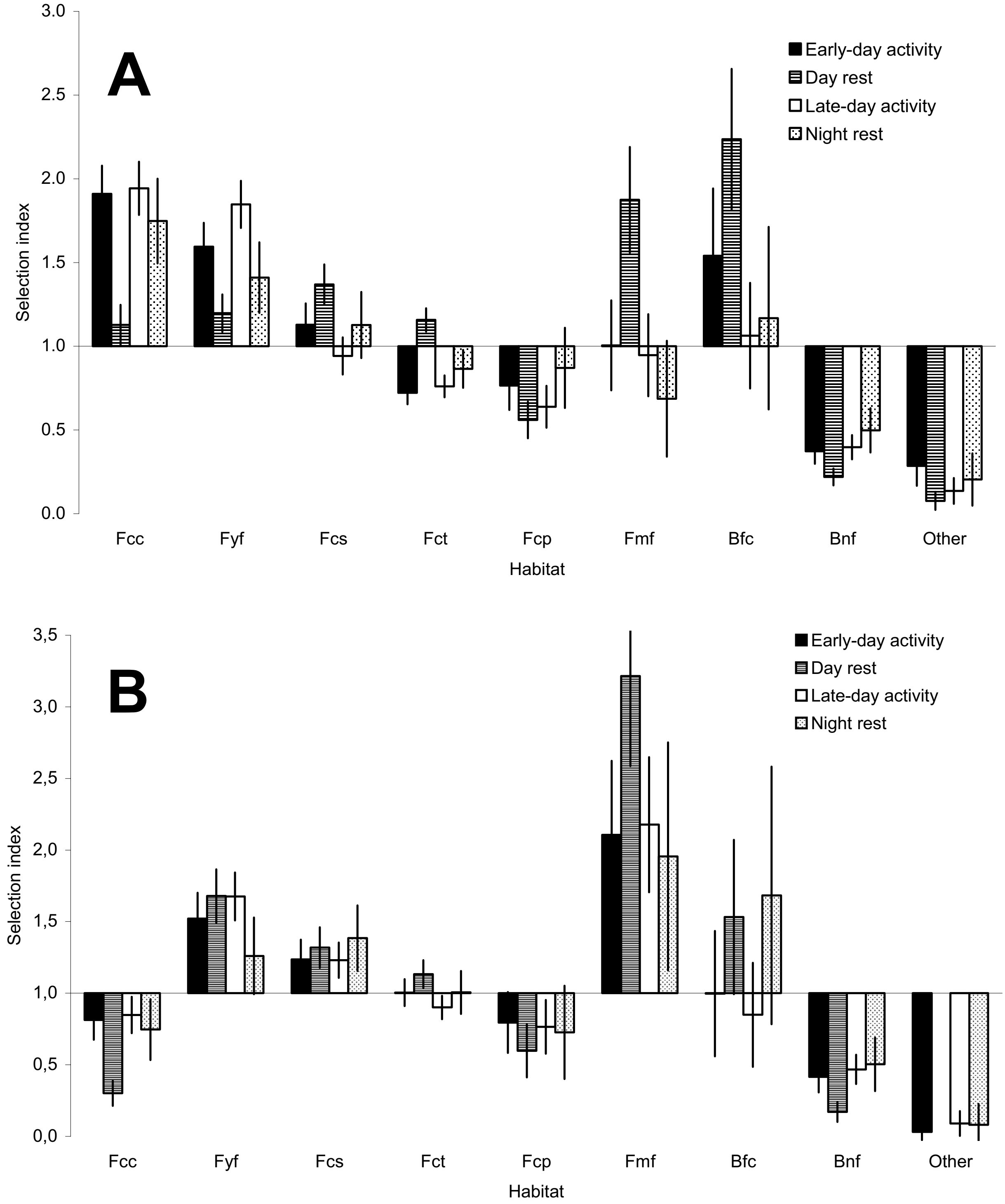

Figure 6: Selection indices (± 95% confidence interval) of habitats used during different activity periods by six female brown bears in Dalarna, Sweden during the A) mating season (N=10,881), and B) berry season (N=6,585) (there were no observations in “Other” habitats during “day rest” in the berry season). See Table 1 for explanation of abbreviations.

I also examined whether the primary behaviors differed among the activity periods, and I found significant differences for both seasons (Mating: $\chi^2 = 69.4$; df = 12; p = 0.000; four cells with expected counts <5. Berry: $\chi^2 = 143.1$; df = 12; p = 0.000) (Fig. 7). During the early-day active period (EDA) of the mating season, there was less resting than would have been expected if random (Fig. 7 A). During the day rest (DR) there was less foraging and “unsure”, and more resting. During the late-day activity (LDA) there was less resting and more foraging than expected. During the early-day activity (EDA) of the berry season there was less resting and more “no sign” than expected (Fig 7 B). During the day rest (DR) there was less foraging and “unsure”, and more resting and foraging/resting. During the late-day activity (LDA) there was less resting and foraging/resting, and during the night rest (NR) there was less “no sign” than expected. Based on these activity data, I also found that foraging/resting more closely resembled the pattern of resting than the pattern of foraging, and that the pattern of foraging more closely resembled the pattern of “unsure” and “no sign” than the pattern of resting or foraging/resting. It was also obvious that day rest (DR) was the most important period for resting; confirming the pattern of Fig. 5, and that night rest (NR) more closely resembled the pattern of the active periods than the pattern of the day rest (DR).

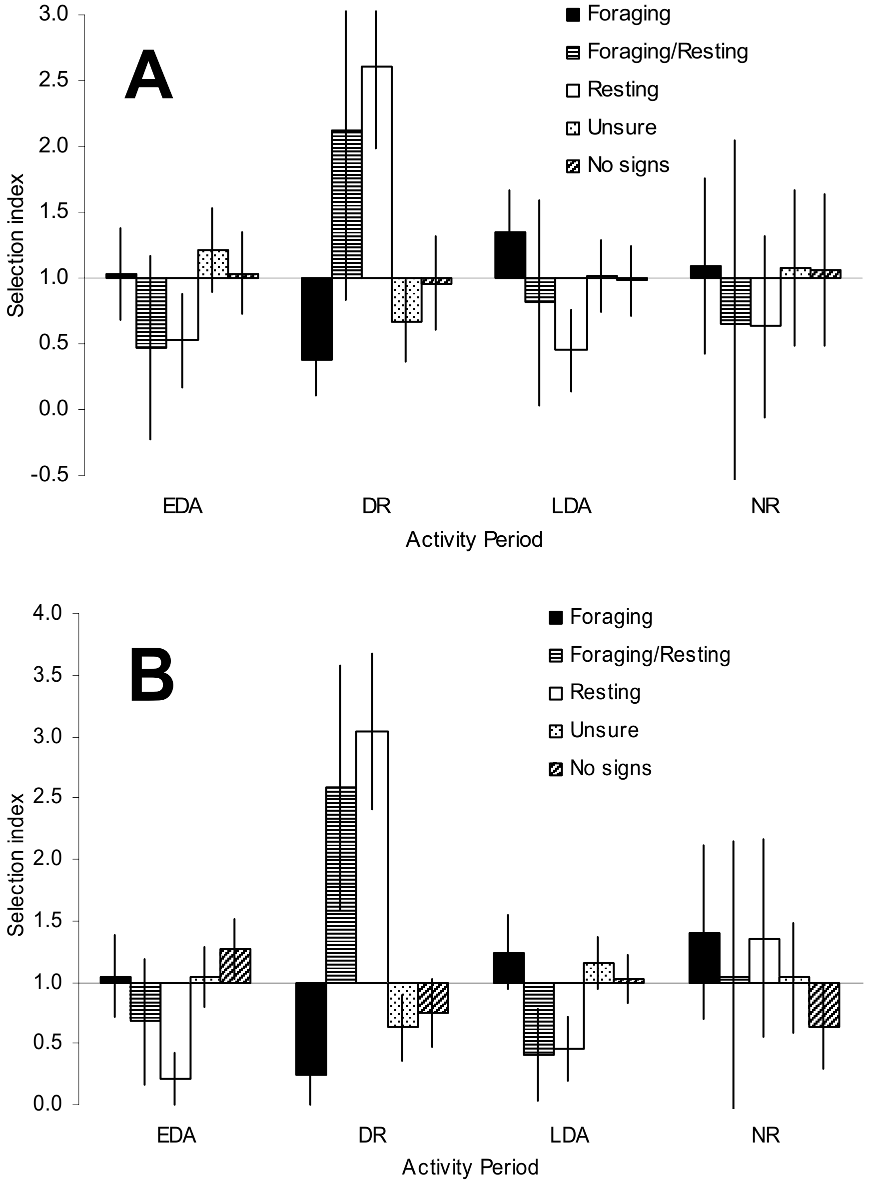

Figure 7: Selection indices (± 95% confidence interval) of primary behaviors (from field observations) during the activity periods of the day for six female brown bears in Dalarna, Sweden during the mating (A) and berry (B) seasons of 2004 (see text for further details) (N = 1,051). EDA = Early-day Activity, DR = Day Rest, LDA = Late-Day Activity, NR = Night Rest.

DISCUSSION

As hypothesized, I found that Scandinavian female brown bears used their home range habitats nonrandomly during both the mating and the berry season. As bears mainly use their time to forage and rest (MacHutchon 2001), these should be the two most important behaviors for selection of habitats by bears. I found that the habitat selection varied greatly throughout the day, and that this was related to differences in habitat selection of foraging compared to resting bears. For example, habitats avoided in the overall habitat selection were selected during the “day rest” period. This shows the importance of understanding diel behavioral patterns when studying habitat selection, as has also been argued by others (Beyer & Haufler 1994; Mysterud et al. 1999; Belant & Follmann 2002; Apps et al. 2004; Nielsen et al. 2004*a*).

Results of habitat selection studies, where traditional VHF radiotransmitters have been used, might not be comparable with those based on the newer GPS radiotransmitters, as the former mainly used day positions whereas the latter are based on positions from all 24 hours. Understanding how animals select habitats differently according to their needs for food and shelter is crucial for the management of any species with diel behavioral changes.

Rates of movement

Using all observations, I found that the speed of the bears almost doubled in the berry season compared to the mating season. This probably indicated that the bears spent less time resting in the berry season, as would be assumed from their need to accumulate high amounts of fat reserves before winter dormancy (Craighead et al. 1995; Farley & Robbins 1995; Barboza et al. 1998). However, using only passive periods resulted in no difference in movement between the two seasons, indicating that, when first active, the bears did not move faster during any of the seasons. These two different results show the importance of using only observations where the animals have been active when analyzing movement.

I calculated the overall average rate of movement to determine whether the bears were actually able to exit any habitat within the 30 min available between each GPS fix. This was to ensure that autocorrelation would not be a problem (Neu et al. 1974; Aebischer et al. 1993; Arthur et al. 1996). Considering that the bears walked a median distance of almost 400 m during this time interval (Fig. 2), they would have no problem exiting any habitat in this patchy study area (median patch size of 22,500 m^2 gives an average maximum exit distance of 85 m). And given that the maximum straight-line distance recorded was 2.5 km, they should certainly be able to walk both out of and into most habitats in the area.

Methodology

Pooling the two seasons, the average success rate for GPS fixes was 76% (Jansson 2005). Jansson (2005) found that the success rate was dependent on the activity of the bear, with 78% of the failed fixes occurring when the bears were passive. Bowman et al. (2000) also found the success rate to be behavior dependent in white-tailed deer (*Odocoileus virginianus*). The difference in fix rate between behaviors is probably due to one or both of two factors. First is the position of the antenna inside the collar. Resting bears might be lying on the side or in the shade of a rock or other object. This might prevent the transmitter from having a clear line of contact with the satellites. 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 percent of canopy cover and mature stands limit the transmitter's ability to obtain contact with the satellites. These two factors of behavioral bias might have led to an undersampling of resting sites.

It was not equally easy to find sign of animal use in all habitats. In open habitats it was generally easier to find sign of animal use, but where there were only lichens and mosses it was difficult to identify the sign as bear sign and/or as a sign of a particular behavior. In denser areas with more forbs, it was usually more difficult to find the sign of animal use, but when first found, they were easier to identify as bear sign. Thus for an analysis of resting habitats, it is wise to combine the use of field surveys with data on the bears' activity (to obtain both on-the-spot habitat description and find which habitats are undersampled when only using field sign as an indicator of resting).

Primary behavior in relation to activity periods

The field observations of primary behavior confirmed the main patterns found from the activity data (Fig. 7); the bears preferred to rest and foraged little during the day-rest period, and they rested little during the early and late active periods. The night rest, however, was not a typical resting period, and it could not be separated statistically from the early and late active periods for any other behavior than resting during the early-day active period of the berry season. The lack of difference between the night rest and active periods might be due to the relatively short interval of the night rest, only two hours (Fig. 5). Most bears probably spent a few hours resting during the night, but the exact period might differ among nights and/or individuals.

There appeared to be a selection for sites showing both foraging and resting during the day-rest period. In these sites the bears probably foraged before or after they rested, and hence not within the day-rest period, as could be argued from Fig. 7. The avoidance of foraging sites during the day rest also indicated this. For the three other periods, there were no differences in use of foraging sites, except for more foraging during the late active period of the mating season. There were no differences between sites with unsure or no sign during the mating season. However, there were fewer than expected sites with unsure sign during the day rest of both seasons. This was probably due to the fact that most sites during this period were used for resting, suggesting that day beds were easily recognized. During the berry season there were also more sites with no sign during the early active period and fewer sites with no sign during the night rest. This might be a result of the bears eating berries during the crepuscular hours, as foraging on berries was difficult to observe.

Based on these findings, I believe that one could use the day-rest periods in Fig. 6 as actual bear resting periods. There was also significantly more foraging than resting during most of the active periods, and the bears foraged significantly more in these periods than during the day rest. Also, MacHutchon (2001) argued that brown bears forage most of the time when they are not resting.

Habitat selection for resting sites

The bears tended to avoid open, treeless habitats while resting (nonforested bogs and clearcuts) (Table 3, Fig. 6), as was also found by Katajisto (2001). This might be due to the higher temperatures of these open areas, or of the increased probability of encountering humans (Wielgus & Vernier 2003; Apps et al. 2004; Nielsen et al. 2004*a*). The avoidance of poor coniferous forests might also be due to the relative openness of this habitat, with only lichens covering the ground and generally sparse trees. Instead, the bears seemed to select forested habitats. And although their highest selection was for mixed forests and forest-covered bogs, they spent most of their time resting in young, short and especially tall coniferous forests (Table 5). This corresponded well with the findings of Mysterud (1983), who reported that in Norway, almost 50% of the beds were in forests of 80-160 years, and nearly 20% were in forests of 30-80 years. Also Katajisto (2001) found that almost 50% of the beds of female brown bears were in mature forests. Jansson (2005) looked at resting habitat selection of the six brown bears I have studied, but she did not find a selection of mature forests. However, she did not use a totally random sample when deciding which sites to visit. To avoid autocorrelation by exploring the same site twice, she excluded observations within 100 meters of a previously visited site the same day. This probably led to a bias against resting sites; more so during the day rest, as this time interval was longer than the night-rest period. I used the same data as Jansson (2005) in my analyses, but I tested whether the observed sites differed from the overall habitat selection of the bears. I found that tall coniferous forests were underrepresented among the observed sites, and thus, most likely, resting sites in tall coniferous forests were undersampled. Had she taken this into account, Jansson (2005) may also have found a selection for resting in mature forests, and especially an increase in observations of day beds in this habitat.

Although mixed forests and forest-covered bogs were not very widely used, they were highly selected resting habitats (Table 5, Fig. 6). These habitats had a denser understory, which might have provided both cover and cooler climates (Nielsen et al. 2004*a*). Servheen (1983) found that also brown bears in Montana selected dense, wet areas for resting.

Based on the field survey, I found that there were great differences in the tree densities of different sites within the same habitats. The general trend, however, was that the visibility was greater in older forests, as regular thinning resulted in an open understory. However, I also found that the resting beds were often placed in a denser "island" within more open surroundings. Such details are not detectable in vegetation maps from satellite images. Although it is a time consuming procedure, it is important to combine the use of vegetation maps with on-the-spot habitat descriptions when studying finer-scale habitat-related behaviors (Adrados et al.2003).

Comparing habitat selection with use and availability, I found only minor differences between seasons in habitats chosen for resting. An exception from this was a large reduction in the use of clearcuts, from 13% during the mating season to only 4% during the berry season (Table 5). This has to be seen in relation to the overall decrease in use of this habitat, as the relative use of clearcuts for resting compared with foraging was almost the same for both seasons. Still, it was evident that resting bears avoided this habitat more during the berry season, although the reason is yet unknown.

Habitat selection for foraging sites

The bears appeared to select clearcuts and young forests when foraging during the mating season (Table 3, Fig. 6 A). Nearly 50% of the active observations were in these two habitats, almost twice as much as expected, based on availability (Table 2, 5). This corresponded well with my finding that the bears selected sites with anthills and to open tree stumps in these habitats (Table 4). Johansen (1997) found that 30% of the bears' assimilated energy during the mating season came from ants. Also in Alberta, Canada, ants (e.g. *Camponotus* spp. and *Formica* spp.) occurred more frequently in clearcuts than in forested areas, with a peak occurring in clearcuts 25-30 years old (Nielsen et al. 2004*b*). A similar result was found by Swenson et al. (1999) for *C. herculeanus* in central Sweden, with a high tree stump colonization rate following clearcutting, and a peak biomass in clearcuts of 5-35 years. With 26% of the study area consisting of clearcuts and young forests (Table 2), the protein- and lipid-rich ants seemed to be highly available to the bears.

Although the bears spent more than 20% of their active time in tall coniferous forests, this was a highly avoided habitat (Table 5, Fig. 6 A). The extended use of this habitat thus probably was due to the high availability of it (Table 2). Female brown bears have been found to extend their home ranges during the mating season and actively search for males to mate with (Dahle & Swenson 2003*b*). My results did not show a higher median movement during the mating season, but this does not necessarily mean that the bears did not extend their home ranges. It could however be that, when searching for a mate, the selection of habitats with abundant foods was less important (Jansson 2005), and hence the bears roamed through less preferred but abundant habitats.

With the exception of short coniferous forests, the bears spent less than 6% of their active time in each of the remaining habitats (Table 5). Poor coniferous forests, nonforested bogs and “other habitats” were highly avoided (Fig. 6), presumably because of a lack of food in these habitats. McLoughlin et al. (2002) reported a positive selection for lichen-dominated habitats during a study of brown bears in the Canadian Arctic. However, these lichen veneers were assumed to be associated with an important prey species, caribou (*Rangifer tarandus*). Thus the habitat probably was selected only because of the caribou’s preference for it. I found that “other habitats” were less avoided during the mating season than the berry season, due to a selection of watercourses. Riparian or wet habitats have repeatedly been reported to be rich in forbs (Servheen 1983; Waller & Mace 1997; McLellan & Hovey 2001; McLoughlin et al. 2002), and this is probably the reason for the bears’ selection of watercourses during the mating season. It might also explain the slight selection of forest-covered bogs.

I found a slight trend towards more berries in clearcuts and less berries in tall coniferous forests during the mating season. These berries were from the previous fall and cowberries were found in medium amounts on clearcuts during this season. Although Johansen (1997) reported berries to be of less importance to bears during both spring and summer, my observations of scats confirmed that they did use this food quite extensively during the mating season. The negative trend for usage of sites with berries in tall coniferous forests might be because fewer bilberries overwinter, and those that do are more dispersed than cowberries. This corresponded with the findings of Welch et al. (1997), who reported that bears depend on clusters of berries.

Moose calves assumed killed by the six bears were only discovered during the mating season. Brown bears usually only kill moose calves during the first weeks of the calves' lives (Johansen 1997), which corresponds with my findings. Still, moose is an important food source for central Scandinavian brown bears, constituting 24% of their total assimilated energy per year (Johansen 1997).

Young forests were selected for foraging also during the berry season, when it was a selected habitat for foraging on ants (Tables 3 and 4, Fig. 6 B). Clearcuts, however, were now avoided while foraging, as were sites with anthills and opened tree stumps in this habitat. During the berry season, *C. herculeanus* seemed to be selected above *Formica* spp., as the bears appeared to open tree stumps more than anthills in clearcuts and young forests. This selection was also reported by Swenson et al. (1999), and Johansen (1997) found that *C. herculeanus* contributed to more than twice the amount of assimilated energy as *Formica* spp. in the fall. However, ants appeared to be of less importance during the berry season. As Swenson et al. (1999) suggested, this was probably due to the great amount of easily obtainable, carbohydrate-rich berries in the area.

Mixed forests were also a selected habitat during the berry season, and the bears chose sites with both anthills and tree stumps here (Table 4, Fig. 6). Poor coniferous forests, nonforested bogs and “other habitats" were avoided also during the berry season.

It appeared as if tall coniferous forests were avoided, or at least not selected, during the berry season (Table 3, Fig. 6 B). However, the bears spent almost 30% of their active time in this habitat (Table 5). Berries are highly clumped in distribution (Nilsen 2002), and I found that the bears selected sites with abundant berries in tall coniferous forests (Fig. 4). Also Nilsen (2002) and Jigsved (2003) found that bears selected sites where berries were abundant. There were mainly bilberries in these tall coniferous forests, and according to Johansen (1997) bilberries contributed to almost 47% of the bears' assimilated energy in this area in the fall. Johansen (1997) also reported that another 26% of the bears' assimilated energy came from cowberries and crowberries. I found these berries in medium amounts during the berry season, and the bears selected sites with medium amounts of berries in young and mixed forests (Fig. 4).

Nests from wasps and bumblebees were only dug out during the berry season, but I did not have enough observations to correlate the use of these foods with habitat.

Overall habitat selection compared to the diel habitat selection

The bears showed a temporally dependent habitat selection, both on a seasonal and on a diel scale (Table 2, Fig. 3, 6). This emphasizes the importance of using the appropriate scale when studying habitat selection (Johnson 1980; Schooley 1994). The seasonal pattern was most obvious from the results of the bears' selection of clearcuts, as it shifted from a highly selected to a clearly avoided habitat through the year (Table 2). Clearcuts have usually been found to be avoided or not selected (Waller & Mace 1997; McLellan & Hovey 2001; Wielgus & Vernier 2003), but Wielgus & Vernier (2003) suggested that in many areas, this might reflect the bears' avoidance of the adjacent roads rather than their avoidance of the clearcuts themselves. Roads are associated with humans, and bears avoid both humans and human-influenced areas (Servheen 1983; Heyden & Meslow 1999; Mace et al. 1999; Kobler & Adamic 2000; Wielgus & Vernier 2003; Apps et al. 2004; Swenson et al. 2005; this study). I suggest that, despite the higher risk of encountering humans, bears used clearcuts in the mating season, because it was the habitat with the most abundant food during that time of year. When foods were more abundant in the forest during the berry season, the benefits of clearcuts decreased and hence they were avoided. Nielsen et al. (2004*a*) also found a seasonally dependent use of clearcuts by brown bears, with a selection of clearcuts during the summer. Their study area in Alberta, Canada, was quite similar to mine, with extensive boreal forests, high logging activity, and fire-suppression schemes. They suggested that the bears' use of clearcuts in these areas was due to the lack of natural openings and associated foods. Bears would thus be expected to avoid clearcuts in areas where there are natural openings, and this was the case in both the study of Wielgus & Vernier (2003) and in the study of McLellan & Hovey (2001).

Comparing my findings of the bears' overall habitat selection with the diel habitat selection revealed two important patterns. First, I found that bears rested and foraged at particular times of the day (Fig. 5, 7). Resting was mainly restricted to the working hours of humans, whereas foraging was restricted to the crepuscular and nocturnal hours. Servheen (1983) observed a similar trend for bears feeding on agricultural lands in Montana; they avoided using this open and human-associated habitat during the daylight hours, but foraged there during the night. The same was true for the bears of Nielsen et al. (2004*a*) in Alberta, which used clearcuts more often during the crepuscular/nocturnal hours than during the daylight hours. Traditionally, habitat studies of brown bears have been conducted without the use of GIS/GPS, and locating bears equipped with VHF-radiotransmitters has mainly been restricted to the daylight hours. My results reveal that this procedure might have induced serious biases to these studies, as they might have included only resting habitats.

Second, there were large differences between the habitats selected by foraging compared to resting bears. Based on the overall habitat selection, clearcuts appeared to be highly selected during the mating season (Table 2). However, the bears did not show a strong selection for this habitat when they were resting (Table 3, Fig. 6). And although an avoided habitat for both resting and foraging during the berry season, clearcuts were significantly more avoided when the bears were resting. From the overall habitat selection, it also appeared that the bears avoided or did not select tall coniferous forests. However, they significantly selected this habitat when resting. These findings show the serious biases that can result from drawing conclusions based on the bears' overall habitat selection. This is especially true 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 what habitats are important to bears, it is therefore crucial to differentiate between foraging and resting habitat selections.

My results thus show the importance of dividing the day into temporal categories based on the diel activity pattern of the particular animal studied. Horner & Powell (1990) studied habitat use in relation to activity for black bears (*U. americanus*) in North Carolina, and differentiated between moving, foraging and resting bears. In contrast to my 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 frequencies was not verified with observations in the field. Gervasi et al. (manus) 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 between active behaviors such as walking and foraging.

To my knowledge, Jansson's (2005) and my studies are the first to document differences in diel selection of resting and foraging habitats by brown bears. Individual studies of brown bear diet (Servheen 1983; McLellan & Hovey 1995; Johansen 1997; Dahle et al. 1998; Hilderbrand et al. 1999; Swenson et al. 1999; Persson et al. 2001; Groβe et al. 2003; Ben-David et al. 2004) and bed-site selection (Mysterud 1983; Servheen 1983; Katajisto 2001) have been conducted, but never combined in relation to diel habitat use. Based on my results, I strongly recommend using data from all 24 hours when studying habitat selection and dividing these data into relevant categories based on behavior.

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