SMALL SCALE HABITAT USE BY MALE AND FEMALE BROWN BEARS (*URSUS ARCTOS*) IN THE MATING AND THE HYPERPHAGY SEASONS

SMÅSKALA HABITATBRUK HOS HANNBJØRNER OG BINNER (*URSUS ARCTOS*) I BRUNSTSESONGEN OG BÆRSESONGEN

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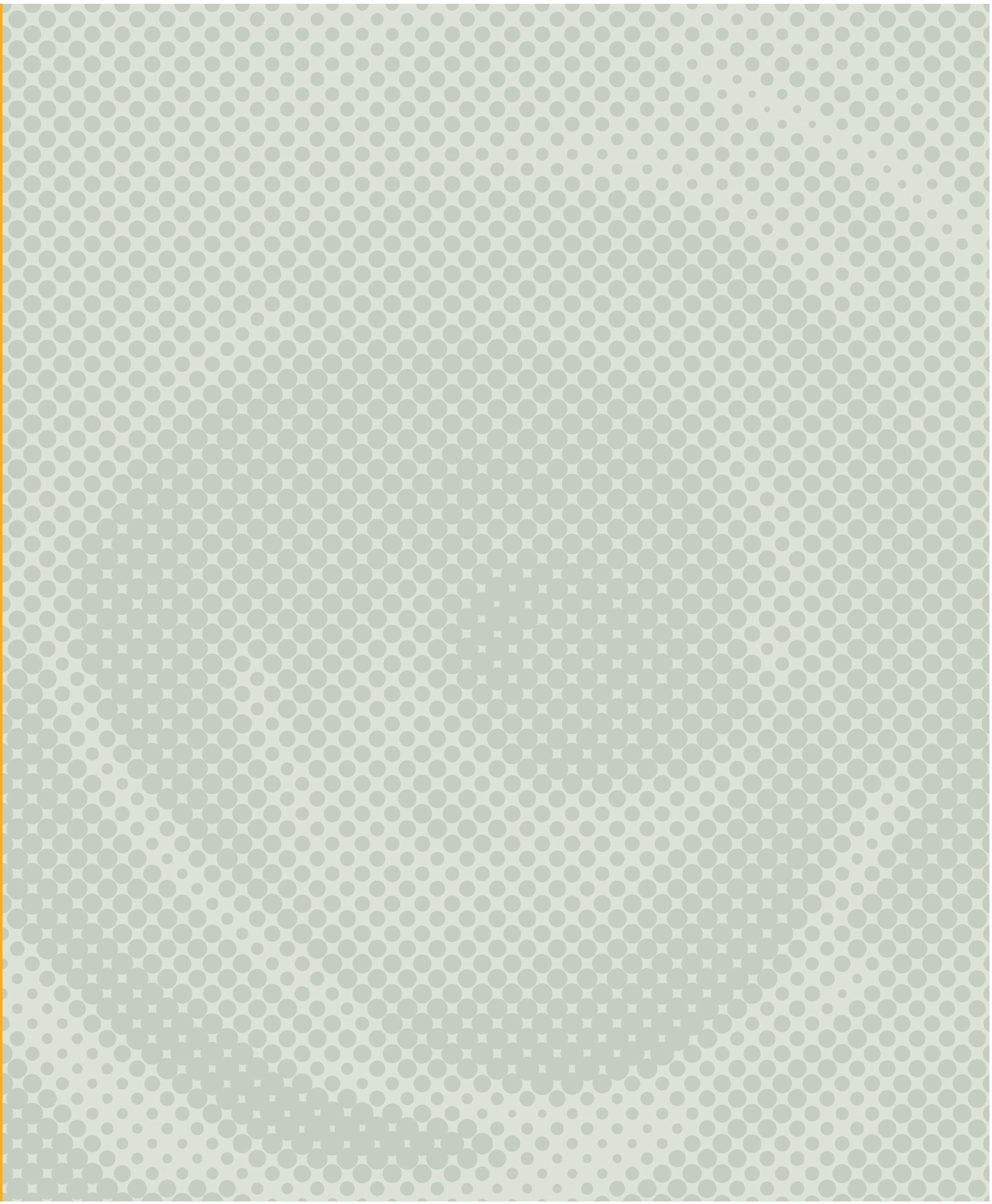

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ABSTRACT

Sexual differences in small scale habitat use between adult male and lone adult female brown bears (*Ursus arctos*) have hardly been studied before. Previous studies on habitat use have not investigated habitat use in relation to the bears' primary behaviors (e.g. resting, foraging, traveling), and the main focus has been on habitat use in relation to foraging. Mainly VHF-technology has been used, with positions taken during daytime, thus previous studies may have been biased towards the study of habitat use during day time and important habitats and resources may have been neglected. I visited the GPS-locations of 12 male and 20 female brown bears in central Sweden equipped with either GPS Plus-3 or GPS Pro-4 radio-collars. My main goal was to (1) determine differences in habitat use related to resting, foraging and traveling behavior; (2) determine sexual differences in habitat use in relation to aforementioned behaviors; and (3) determine seasonal differences in habitat use for specific behaviors. In general, male and female brown bears tended to select forested habitats and tended to avoid open habitats without food opportunities. Both males and females selected denser vegetation for day resting compared to night resting, and selected the habitat categories which support most abundant food opportunities during foraging. In general, males selected denser habitats than females during foraging and traveling. I found strong sexual differences, in the overall habitat use and in habitats used for foraging and traveling. Sexual differences in resting sites only occurred between male day beds and female night beds during the hyperphagy season. In general, females showed a stronger distinction in use of the habitats for the different behaviors than males. Females selected significantly different habitats for all behaviors, with the exception of night beds in the hyperphagy season and for traveling, where they selected for relatively more open habitats. In contrast, males tended to choose the two habitats, young forest and middle-aged forest during foraging, traveling and day rest, but selected for a more open habitat during night rest. I found seasonal differences only in relation to females' habitat selection for resting sites. I found more signs of foraging per km bear track for females than males, indicating a difference in foraging strategies. No single habitat category characterized all of the bears' behaviors. My results suggest that analyzing data on habitat use across sex, and active and inactive behaviors, can lead to serious biases in the interpretation of results.

SAMMENDRAG

Kjønnsavhengige forskjeller i småskala habitatbruk mellom voksne hannbrunbjørner (*Ursus arctos*) og enslige voksne brunbjørnbinner har sjeldent vært studert. Tidligere studier har ikke sett på habitatbruk i forhold til alle bjørnens primære atferder (for eksempel bruk av dag og nattleier, furasjering, vandring), og hovedfokuset har vært på habitatbruk i forhold til hvor bjørnen furasjerer. Hovedsakelig har det blitt brukt VHF-teknologi der posisjonene har blitt registrert på dagtid, derfor kan tidligere studier være skjevfordelt mot habitatbruk på dagtid og viktige habitater og ressurser kan ha blitt oversett. Jeg oppsøkte GPS-lokasjonene til 12 hannbjørner og 20 binner i sentral Sverige utstyrt med enten GPS Plus-3 eller GPS Pro-4 radiohalsbånd. Mine hovedmål var å (1) beskrive forskjeller i habitatbruk i forhold til en hvilende, furasjerende og vandrende bjørn; (2) beskrive kjønnsmessige forskjeller i habitatbruk i forhold til de forannevnte atferdende; og (3) avgjøre om bjørnene viser sesongmessige forskjeller i habitatbruk i forhold til spesifikke atferder. Generelt valgte hanner og binner skogkledde habitater, og hadde også en tendens til å unngå åpne habitater med lite tilgang på føde eller ly. Både hanner og binner selekterte habitater med tettere vegetasjon for dagleier sammenlignet med nattleier, og valgte habitater med relativt høy mattilgang til å furasjere i. Generelt valgte hanner habitater med tettere vegetasjon enn binner for furasjering og vandring. Jeg fant store kjønnsavhengige forskjeller, både i den generelle habitatbruken og i habitatbruk angående furasjering og vandring. Kjønnsavhengige forskjeller angående habitatbruken for hvilende bjørner ble bare funnet mellom hannenes dagleier og binnenes nattleier i bærsesongen. Generelt viste binnene et sterkere skille mellom habitat de brukte til de ulike atferdene enn hannene. Binnene selekterte signifikant ulike habitat for alle atferdene, utenom mellom nattleier i bærsesongen og hvor de vandret, der de selekterte for relativt åpnere habitater. I motsetning til binnene, brukte hannene de samme to habitatene, ungskog og middelaldrende skog, for furasjering, vandring og dagleier, men valgte åpnere habitat for nattleier. Jeg fant sesongmessige forskjeller i habitatbruk kun for leier hos binnene. Jeg fant mer tegn etter furasjering per km etter binnenes spor enn etter hannene, noe som kan indikere ulike furasjeringsstrategier. Ikke en enkelt habitatkategori kunne beskrive alle bjørnens atferder. Mine resultater viser at det og ikke skille mellom kjønn, og aktive og inaktive atferder, under analyser av habitatdata, kan føre til store skjevheter i tolking av resultater.

1 INTRODUCTION

Space use and how an animal uses the available habitats within that space are important questions in wildlife ecology (Johnson 1980; Krebs 1985; Christ et al. 2008) and are influenced by the animals' requirements for certain resources and the need for suitable habitats. Some habitats are better suited to fulfill the various needs of an animal (Manly et al. 2002), like cover from danger, resting sites, and feeding and mating opportunities (Christ et al. 2008), and are therefore selected for (Manly et al. 2002). Habitat selection is a hierarchical process (Johnson 1980) and it is well known that ecological processes in general are scale dependent (Wiens 1989; Levin 1992) and mechanisms determining the search for resources by individuals therefore operate at several spatial and temporal scales (Johnson 1980; Levin 1992; Hobbs 2003). Hence, the outcome of ecological investigations will reflect the scale being studied (Hobbs 2003) and the scale itself will be a critical component of the conclusion (Rettie & Messier 2000), because variation in the spatial and temporal extent of availability affects the interpretation of habitat selection (Hobbs 2003; Ciarniello et al. 2007).

Habitat selection at spatial and temporal scales could be important in understanding the underlying mechanisms for sexual segregation (Gregory et al. 2009). Sexual segregation can arise when there are different strategies for optimizing fitness between the two sexes (Clutton-Brock & Parker 1992), caused by ranking critical resources differently (Dammhahn & Kappeler 2009). The spatial and temporal distribution of females is mainly decided by the distribution of risk and resources in the environment (Clutton-Brock & Harvey 1978; Dammhahn & Kappeler 2009), whereas male distribution is more dependent on the presence of estrous females and foraging opportunities (Clutton-Brock 1989; Sandell 1989). Examples from several studies on different species have put this on the agenda, e.g. in elk (*Cervus elaphus*) (Gregory et al. 2009), deer (*Cervidae*) (Barboza & Bowyer 2000), tropical deer (*Cervus eldi thamin*) (McShea et al. 2001), mountain sheep (*Ovis canadensis nelsoni*) (Vernon et al. 1997), river dolphins (Martin & da Silva 2004) and grizzly bears (*Ursus arctos horribilis* Ord.) (Wielgus & Bunnell 1994; Rode et al. 2006a).

The brown bear is an solitary omnivore and spends most of its time foraging and resting (MacHutchon 2001). The food supply and diet of the Scandinavian brown bear (*Ursus arctos*) is relatively stable from year to year (Johansen 1997; Dahle et al. 1998b), but the diet changes throughout the season (Johansen 1997; Dahle et al. 1998b; Swenson et al. 1999a) and the bear is capable of switching between the most abundant food resources (Swenson et al. 1999a). Seasonal changes in diet could cause seasonal changes in habitat use, as found in Scandinavia (Jansson 2005; Moe 2005; Signer 2005) and in many studies in North America (McLellan & Hovey 2001; Belant & Follmann 2002; McLoughlin et al. 2002). Habitat selection should reflect the different behaviors, e.g. bed sites should be found in more dense forested habitat, and not open areas, as found by Jansson (2005), Moe (2005) and Munro et al. (2006), whereas foraging should be found in habitats that offer a diversity of food resources, as habitat selection is highly influenced by food availability (McLoughlin et al. 2002).

The brown bear is sexually dimorphic, with adult males being 1.2-2.2 times larger than adult females (Swenson et al. 2007). Energetic constraints imposed by larger sized males force them to "utilize and potentially dominate only the highest quality food resources" (Rode et al. 2006a). Smaller bears like females and subadults, with lower energy demands can select poorer quality habitats, while simultaneously avoiding competing with adult males for the same resources (Rode et al. 2006a). Studies have shown that larger males depend more on proteins to obtain their body mass, whereas females can persist on a more vegetative diet (Welch et al. 1997; Jacoby et al. 1999; Hobson et al. 2000; Rode et al. 2001). Thus, nutritional constraints imposed by differing body sizes, in addition to the food abundance and distribution, have the potential to independently or interactively cause sexual segregation in habitat use (Jonkel & Cowan 1971; Rode et al. 2006a).

Few studies have investigated differences in habitat use between male brown bear and females without dependent young and most of them have been conducted in North America in landscapes that are very different than central Sweden. Where different habitat use has been detected, it was usually females with dependent young avoiding males due to the possibility of infanticide, and smaller subadults avoiding larger individuals. These differences in habitat use altered the foraging decisions made by such females and subadults because they avoid areas with the most energetic food resources (Mattson 2000; Ben-David et al. 2004; Rode et al. 2006a). Mattson et al. (1987) found that females with cubs of the year avoided not only adult males but also adult females, as did subadults. Fewer differences in habitat use have been found between adult males and lone adult females (Mattson 2000; Ben-David et al. 2004; Rode et al. 2006a). However, other studies have detected no differences in habitat use among the different age and sex categories (McLellan & Hovey 2001; McLoughlin et al. 2002).

In general, telemetry data allow the estimation of an animal's usage of space but, not the identification of its specific activity (e.g. sleeping, foraging or traveling) at any relocation site (Christ et al. 2008). Documentation of habitats used may be seriously biased if different behaviors are neglected during the active periods (Belant & Follmann 2002; Moe et al. 2007). Also failing to consider the different activities (e.g. digging for insects or roots) of an animal can lead to generalizations of interpretations. And our understanding of important differences among activities can be lost (Munro et al. 2006). Therefore it is important to know which habitats an animal uses for a specific behavior, and why they prefer some habitats over others.

In this thesis I have used the GPS positions of 12 male and 20 female (without dependent young) Scandinavian brown bears to (1) determine differences in habitat use related to resting, foraging and traveling behaviors; (2) determine sexual differences in habitat use in relation to aforementioned behavior; and (3) determine whether the bears show seasonal differences in habitat use for specific behaviors.

2 METHODS

2.1 Study area

The study was performed in the counties of Dalarna and Gävleborg in south-central Sweden (~61 °N, 15°E). The area consists of 13,000 km^2 of intensively managed boreal forest in a rolling landscape. Elevations range from about 200 m in the southeastern part to about 1,000 m in the western part, but only a minority of the area is above timberline, which is at ~750 m. The mean temperatures in January and July are -7° C and 15° C, respectively. Snowcover lasts from late October until early May and the vegetation period is about 150-180 days (Moen 1998). Average precipitation is ~ 600-1000 mm annually (Lundqist 2002). The forest is dominated by Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), but deciduous trees like mountain birch (*Betula pubsecens*), silver birch (*Betula pendula*), European aspen (*Populus tremula*), and gray alder (*Alnus incana*) are common. Most of the forest is divided into singleaged stands in different stages of the production cycle. A harvest rotation of 90-100 years with a clearcut harvesting strategy has led to a clearcut coverage of approximately 8% of the forested area, and 42% of the forest stand is less than 35 years old (Swenson et al. 1999a). The landscape contains a dense network of gravel roads (Nellemann et al. 2007). Common juniper (*Juniperus comunis*), common and silver birch, willows (*Salix spp.*) and mountain ash (*Sorbus aucuparia*) dominate the understory (Swenson et al. 1999a). Bilberry (*Vaccinium myrtillus*), cowberry (*Vaccinium vitis-idaea*) and crowberry (*Empetrum hermaphroditum*) are the most important field shrubs and are important food sources for the bears before entering hibernation (Dahle et al. 1998b). In addition to berries, bear diet consists of moose calves (*Alces alces*), ants (*Camponotus herculeanus* and *Formica spp.*), forbs, and carrion (Dahle et al. 1998b; Swenson et al. 1999a). Bears obtain 44-46% and 14-30% of their total energy from berries and ungulates respectively, and the remaining energy from insects (14-22%, mostly ants) forbs and graminoids (12-18%) (Dahle et al. 1998b). Bears are intensively hunted in the entire area, and the average population density is ~30 individuals/1000 km^2 (Solberg et al. 2006).

I defined the mating season as lasting from May 15 to July 15 (Zedrosser et al. 2009), and the hyperphagy season, when bears are foraging intensively in berries from July 16 until the last observations of bears for this study (October 9 2007 and July 31 2008).

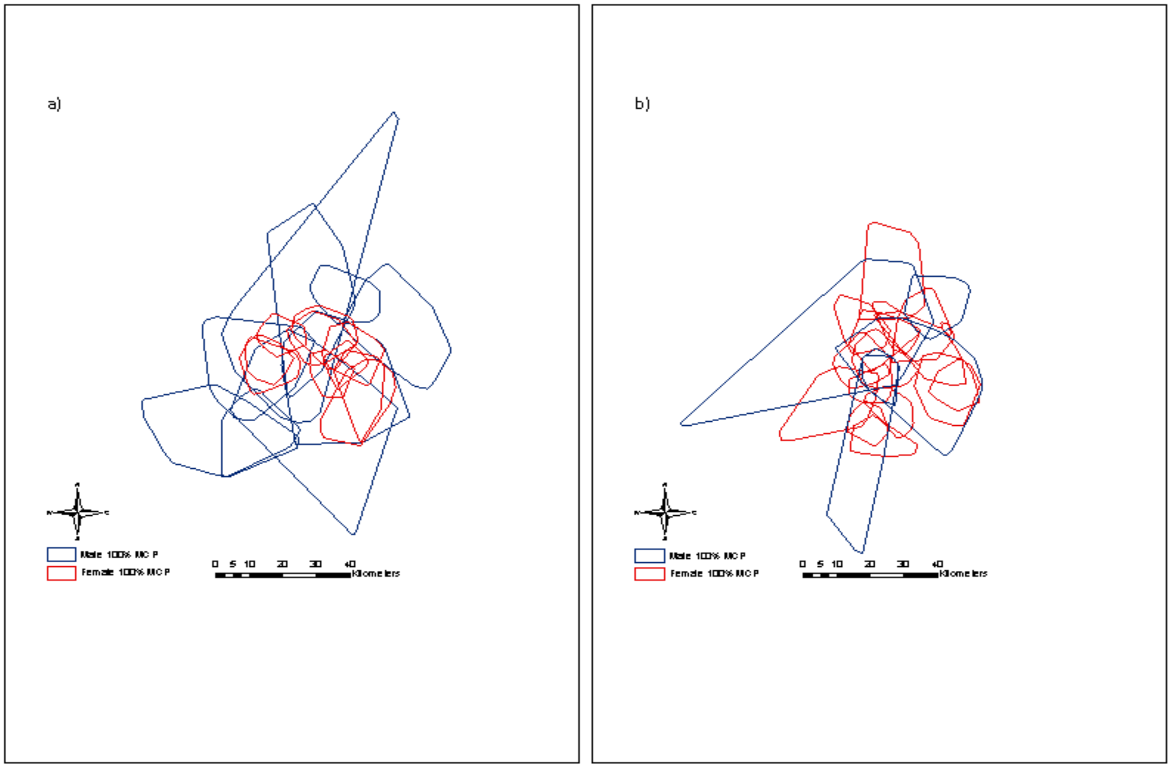

Figure 1: Annual 100% MCP home ranges of the 12 male and 20 female brown bears in central Sweden in **a)** 2007, and **b)** 2008.

2.2 Capture and GPS-telemetry

Brown bears were immobilized with a dart gun from a helicopter in April, shortly after den emergence. For a further description of capture methods refer to Arnemo et al. (2006) and Zedrosser et al. (2007). Adult (>3 years (Zedrosser et al. 2007; Zedrosser et al. 2009)) bears were fitted with either GPS Plus-3 or GPS Pro-4 radio-collars (VECTRONIC Aerospace GmbH, Berlin, Germany) with activity loggers and GSM (Global System of Mobile communication) modems. Females with dependent offspring were not used in this study. The coordinates and the time of a position was obtained by the NAVSTAR global positioning system (Rodgers et al. 1996). Data packages of seven locations were automatically transmitted as a text message to a ground station and downloaded to a 1:50 000 map in the ArcGIS (Geographic Information System) 9.0 software (Environmental Research Institute, Redlands, California Inc 2004). In 2007 the location schedule was set to record a position every 30 minutes, but twice a week, the GPS collar of a randomly selected individual was set to recording a position every one minute during the time interval 02:00-05:00 GMT (04:00-07:00 local time). In 2008 the relocation schedule was set to recording a position every 10 minutes, and every day the GPS-collar of a randomly selected individual was set to recording a position every one minute for the time interval 18:00-20:00 GMT (20:00-22:00 local time). The time periods for the minute positions were chosen to obtain accurate movement patterns during the bears' active periods (Moe et al. 2007). In general, the relocation schedules chosen were trade-offs between obtaining as many positions as possible and battery life.

2.3 Definitions of the behaviors resting, foraging and traveling

The behavior of a bear was defined as resting when a bed site was found based on GPS-locations. To find bed sites we visited clusters of GPS-locations where a bear had spent ≥ 1.5 hours within a radius ≤ 30 m. Clusters were visited ≥ 48 hours after the bear used the area and after confirmation that no marked bear was there to avoid disturbance (Ordiz et al. in prep). If a bed site was found within the cluster, it was only defined as an actual resting site if it contained bear hairs (Ordiz et al. in prep). Moe et al. (2007) found that Scandinavian brown bears have two resting periods, the longest during daytime and the other during the night. I therefore distinguished between night- and day resting sites. All of the bed sites were examined in 2007.

To obtain habitat descriptions of locations where a bear was foraging, the track between either 1 minute or 30 minute GPS relocations of a bear were followed with the use of tracking dogs (Vang 2009; Vang et al. 2009). Almost all tracks ended in resting sites in 2007. In 2008 random portions of tracks which, based on GPS-locations (see above), that did not contain resting sites were chosen. The tracks were randomly distributed in the terrain, dependent on the bears' movements and positions, and were 10-24 hours old in an attempt to avoid disturbance, but still obtain relatively fresh bear signs. The bears' GPS positions were downloaded into a handheld GPS unit (Garmin GPSMAP 60 csx (Olathe, Kansas, USA)) and used by the dog trackers during the tracking exercise. By programming the handheld GPS unit to take positions every ten minutes on the track log, the bears' GPS positions were followed and the movements of the tracking team were documented. Every GPS position in the track log of the tracking teams' movements was registered as either tracking success or not success. The localization errors for both the bears' GPS collar and the handheld GPS unit were accounted for by the tracking leader during the tracking exercise. This was done by defining tracking as successful when the tracking teams GPS position was < 15 m from the bears' GPS positions. The distance of 15 m was chosen because it summarizes the localization error of the bears' GPS collar (7.98 m, 99% of the time (DeCesare et al. 2005)) and the handheld GPS unit (buffer zone with a radius of 6.5 m (Garmin 2007)). Tracking on 1 minute positions is more detailed than tracking on 30 minute positions. The tracking was therefore stopped by the tracking leader when the tracking team (dog and its handler) was 1.5 times the distance between two successive locations without arriving within the buffer zone (8 m) of the second bear location Vang et al. (2009). Also, determining if the dog was tracking a bear or not with the 30 minute positions was subjective and made using a combination of the dogs' behavior, presence of fresh bear sign, and sign of other animals. In 2008 two training methods were used during the tracking exercise. However, successful tracking distance was defined in the same way.

Signs of foraging behavior were recorded along the track. I defined foraging behavior when I found freshly opened anthills, tree stumps, turned stones, ground scratches, vegetation that was foraged upon, or other signs of foraging activity along a bear's trail. I defined a sign as fresh when the tracking dog marked it, it visually appeared to be fresh (e.g., soil was not dry yet), and vegetation covered by soil or wood appeared to be fresh and green. Any other signs of foraging found during later revisits of the sites for habitat evaluation were not used.

A bear's behavior was defined as traveling if no sign of foraging was found for a ≥100 m straight line of successful tracking. For example, if a bear had walked 120 m without obvious sign of foraging, its behavior was defined as traveling, and a habitat evaluation was made in the middle, i.e. 60 m from the last foraging sign. This was done by making a half-way point on the bear trail and using the "go to" function on the handheld GPS unit to locate the center of the traveling trail to the nearest meter. For traveling distances of >200 m between foraging signs, a habitat evaluation was made every 100 m.

The main goal of the dog tracking exercises were to investigate whether dogs can be used for the tracking of individual bears, and to test the ability and accuracy of tracking teams (dog and its' dog handler) (Vang 2009). By using this method, I was able to quite accurately walk in the footprints of the bears and thereby being confident in my conclusions on what the bear had been doing there.

2.4 Habitat evaluation

We carried out a habitat analysis within a radius of 30 m around a resting site, foraging sign or a traveling plot. Habitat features at the plot were classified into 13 different habitat categories according to their proportions within the 30 m radius, using the definitions of the Swedish forest inventory system (Karlsson and Westman (1998a): riparian zone, bog, tree-rich bog, impediment, swamp/swamp forest, water, road, two categories of clearcuts (K1 - bare area not yet planted or the outcome of plants is unsure and K2 - tree planting was successful (no need to fill in gaps with new trees)), two categories of young forest (R1 - from stage K1 until the average tree was < 1.3 m tall and R2 - average tree is ≥1.3 m but < 10 cm in diameter at breast height), middle-aged forest, and forest awaiting final cutting).

To compare habitats around behavioral signs and the traveling plots with general habitat availability in the study area, habitats at 80 randomly selected locations within the study area were sampled following the same method as the behavioral sign locations. Because the habitat evaluations were carried out by different field personnel, the evaluation methods were calibrated at the beginning of and throughout both field seasons.

2.5 Data analysis

To be able to pool the 1 minute positions with the 30 minute positions, I tested if there were significant differences between the number of signs found per 1000 m for both categories. I used Mann Whitney U-test for this analysis. I used chi-square (χ^2) statistics to test for homogeneity between the seasons, the sexes, and the different behaviors, and goodness of fit test to test the relationship between observed and expected habitat use.

Where the χ^2 tests showed that the bears used habitats nonrandomly, I applied nominal logistic regression to analyze habitat preference for the different behaviors. I used a binomial response variable (present/absent) to compare habitats used by bears with random habitat locations. I used the minimum Akaike's Information Criterion Estimate (MAICE) (Akaike 1987) for model selection. The model with the lowest AIC-value was considered to be the best fitting, but all models within $\Delta AIC \leq 2$ were considered for interpretation of the results. To make an indication of selection or avoidance of a certain habitat category, I used a selection index, calculated as the ratio of the proportion used to the proportion available for a habitat category. Values > 1 and <1 indicate selection and avoidance, respectively, and a value = 1 indicates no selection (Manly et al. 2002).

I have no data on the overall food availability in the different habitats. The analyses of where the bear found food and foraged therefore compare all of the available (random) habitats with habitats where the different foraging signs were found. For this analysis I used χ^2 tables in a worksheet. The selection index was calculated from the expected values from the χ^2 test. To test for significance I applied nominal logistic regression analysis, and used a binomial response variable (sign present/sign absent) with the random habitat locations.

To test if males and females foraged at the same rate while traveling, I used 1 minute GPS location intervals where the gaps between locations had been completely filled in by the tracking team, i.e. total successful tracking distance. I only used positions from 2008 data for this analysis and both the mating season and the hyperphagy seasons were pooled. I used the Mann Whitney-U test to test for differences between the foraging signs found per 1000 meter between the two sexes.

To determine whether there was an association between sex and activity in mating season and hyperphagy season I performed a χ^2 test for association using cross tabulation and χ^2, using sex and activity as the associated variables. Activity here refers to the behaviors foraging and traveling. I performed two tests, one for the mating season and one for the hyperphagy season. To determine whether there was an association between season and activity for each sex, I also performed a χ^2 test for association using cross tabulation and χ^2, but here I used season and activity as the associated variables. I performed two separated tests, one for males and one for females.

All χ^2 tests and the Mann Whitney U test were carried out in Minitab 14.0 (Minitab Inc., Pennsylvania, USA). All nominal logistic regression analyze were performed in JMP 8.0.1 (SAS Institute Inc. 2009, Cary, NC, USA).

Due to the small sample size (< 5 observations), some habitat categories that I considered to have the same biological importance for the bears were collapsed into larger categories (Neu et al. 1974; Manly et al. 2002; Nakagawa 2004). To avoid severe violation of the assumption of independence and heterogeneity (overdispersion), it is important that the merged habitats are not very biologically different (Mysterud & Ims 1998). I chose six habitat categories that I used in further analysis: bog, tree-rich bog/swamp forest, clearcut, young forest, middle-aged forest and mature forest (Table 1). Where zero observations of a habitat category were recorded, they were excluded in the chi-square analysis. Due to small sample size for male resting sites, I pooled day and night resting sites from both seasons into one test and tested for differences between day and night resting sites.

3 RESULTS

3.1 General habitat selection

There was no significant difference between number of bear signs found along trails with 1 minute positions and 30 minute positions (Mann Whitney U-test: *U*: 4649.0, $N_{1\ \mathrm{minute}} = 81$, $N_{30\ \mathrm{minute}} = 38$, $p = 0.23$). Therefore I pooled 1 minute and 30 minute positions for further analysis. I used the locations of 12 males (N locations = 261) and 20 females (N locations = 622) aged from 3-19 years (9 adult and 3 subadult males; 17 adult and 3 subadult females) for this study (Table 2). The mean number of locations per individual was 27.6 ± 20.8 (mean ± SD). I found significant differences between males and females in overall habitat selection ($\chi^2 = 27.504$; df = 5; p = 0.000). Male bears did not show seasonal differences in habitat use between the mating and the hyperphagia season ($N_{\mathrm{mating\ season}} = 188$, $N_{\mathrm{hyperphagy\ season}} = 73$; $\chi^2 = 2.768$; df = 4; p = 0.60). Use of the available habitats differed from what would be expected in the case of random use (χ^2 = 75.9819; df = 5; p = 0.000) (Table 3). The best model based on the AIC criteria, Model 1 (Table 4) showed that males significantly selected young and middle-aged forest stands (Fig. 2). However, the second best model, Model 2 (Table 4) showed that males significantly avoided the habitats bog, tree-rich bog/swamp forest and mature forest (Fig. 2). Also female bears showed no significant seasonal difference in overall habitat use between the mating and the hyperphagy season ($N_{\text{mating season}}$ = 231, $N_{\text{hyperphagy season}}$ = 391; χ^2 = 1.730; df = 4; p = 0.79). Use of the available habitats differed from what would be expected in the case of random use (χ^2 = 141.050; df = 5; p = 0.000) (Table 3). The best model, Model 1, showed that female brown bears significantly avoided bog and tree-rich bog/swamp forest, and the second-best model added middle-aged forest; however, selection for middle-aged forest was not significant (Table 5 & Fig. 2).

Male brown bears traveled more and foraged less than female brown bears during the mating season (χ^2 = 29.473; df = 1; p = 0.000). During the hyperphagy season there were no differences between the sexes in foraging or traveling behavior (χ^2 = 1.670; df = 1; p = 0.196). The comparison of the activities travel and foraging between the mating and hyperphagy season revealed that male bears showed more roaming behavior during the mating season (e.g. they moved more than they ate) than they did during the hyperphagy season (χ^2 = 17.185; df =1; p = 0.000). Female bears showed no difference in the activities traveling and foraging in relation to season (χ^2 = 0.692; df = 1; p = 0.405).

3.2 Habitat selection for bed sites

I found significant differences in male and female habitat use for night beds (N_{male} = 40, N_{female} = 108; χ^2 =20.740; df = 4; p = 0.000). Both males and females selected clearcuts, but females in the hyperphagy season also selected middle-aged forest and mature forest during night rest. No other significant differences in habitat use in relation to resting behavior were found between the two sexes (Fig. 3 a, b).

A total of 64 beds used by male brown bear were found, with an average of 12.8 ± 10.4 beds per individual. Forty locations contained day beds and 24 night beds (Table 6). Male brown bears showed a significant difference in habitat use between day and night beds (χ^2 = 8.041; df = 3; p = 0.031). Use of the available habitats during day rest differed from what would be expected in the case of random use (χ^2 = 14.296; df = 5; p = 0.014). For day beds males significantly preferred young and middle-aged forest (Table 7 & Fig. 3a). The use of habitats for day beds did not differ significantly from neither foraging (χ^2 = 1.360; df = 3; p = 0.72) nor traveling (χ^2 = 1.478; df = 3; p = 0.69). Use of the available habitats during night rest differed from what would be expected in the case of random use (χ^2 = 12.717; df = 5; p = 0.026). Clearcut was significantly selected for during night rest (Table 7a & Fig. 3a). The second best model, Model 2 (Table 7b) added middle-aged forest, but this habitat was not significantly selected for. The use of habitats for night rest differed significantly from the use of both foraging habitats (χ^2 = 18.009; df = 4; p = 0.001) and traveling habitats (χ^2 = 10.651; df = 3; p = 0.014).

In total 331 bed sites used by female brown bear were found, with an average of 19.5 ± 13.5 per individual. During the mating season 54 day beds and 68 night beds were found, and 101 day beds and 108 night beds were found during the hyperphagy season (Table 8a, b). There were seasonal differences in habitat selection for the resting sites (day: χ^2 = 12.936; df = 4; p = 0.012, night: χ^2 = 10.817; df = 4; p = 0.029). There was no significant difference in habitat selection between day and night bed sites for female bears during mating season (χ^2 = 4.299; df = 4; p = 0.367). Therefore I pooled the habitats for these behaviors in the further analysis. Use of the available habitats during resting in mating season differed from what would be expected in the case of random use (χ^2 = 22.825; df = 5; $p < 0.001$) (Table 8a). The best model based on the AIC criteria, Model 1 (Table 9), showed that females significantly selected young forest, middle-aged forest and mature forest for bed sites (Fig. 3b). The habitat category clearcut was also a part of the model, but was not significant. The next best model, Model 2, showed a selection for the habitat categories middle-aged forest and mature forest. Young forest was also a part of Model 2 but was not significant (Table 9). The third best model, Model 3 (Table 9), showed a selection for middle-aged forest and a tendency for selection of mature forest. The use of resting sites during mating season was significant different than the use of both foraging habitats (χ^2 = 35.968; df = 4; p = 0.000) and traveling habitats (χ^2 = 9.505; df = 4; p = 0.050).

Female bears used significantly different habitats for day- and nightbed sites during the hyperphagy season (χ^2 = 39.991; df = 4; p = 0.000). Use of the available habitats both during day rest and night rest differed from what would be expected in the case of random use (day: χ^2 = 21.2817; df = 5; $p < 0.001$, night: χ^2 = 68.4094; df = 5; $p < 0.001$) (Table 8b). The best model based on the AIC criteria, Model 1 (Table 10), showed that females significantly selected young forest and middle-aged forest for daybeds, whereas tree-rich bog/swamp forest was significantly avoided (Fig. 3b). Mature forest was also part of Model 1, but was not significant. The next best model, Model 2 (Table 10), also showed selection for middle-aged forest and young forest, but showed only a tendency for avoidance of tree-rich bog/swamp forest. The use of day beds during the hyperphagy season differed significantly from the use of foraging habitats (χ^2 = 26.815; df = 4; p = 0.000) and traveling habitats (χ^2 = 30.021; df = 4; p = 0.000). The best model based on the AIC criteria, Model 1 (Table 11), showed that for night beds females significantly selected middle-aged forest, mature forest and clearcut (Fig. 3b). Young forest was a part of Model 1, but was not significant. The next best model, Model 2 (Table 11) also showed a selection for mature forest, middle-aged forest and clearcut. The use of night beds during the hyperphagy season differed significantly from the use of foraging habitats (χ^2 = 66.669; df = 4; p = 0.000), but not from the use of traveling habitats (χ^2 = 6.911; df = 4; p = 0.141).

3.3 Habitat selection for foraging

Male and female brown bears showed a significant difference in habitat use for foraging (χ^2 = 16.620; df = 4; p = 0.002). Males used the same foraging habitats during the mating and the hyperphagy season (χ^2 = 3.926; df = 3; p = 0.270), as did females (χ^2 = 7.665; df = 4; p = 0.105).

A total of 113 male foraging locations were visited, with an average of 11.3 ± 10.6 locations per individual. Use of the available habitats during foraging differed from what would be expected in the case of random use (χ^2 = 46.847; df = 5; p = 0.000) (Table 12). Males significantly selected young forest and middle-aged forest when foraging (Table 13 & Fig. 4). The use of foraging habitats differed significantly from the use of night beds (see habitat selection for bed sites) and showed a strong tendency for different use of traveling habitats (χ^2 = 9.162; df = 4; p = 0.057).

A total of 233 female foraging locations were visited, with an average of 13.7 ± 8.7 locations per individual. Use of the available habitats during foraging differed from what would be expected in the case of random use (χ^2 = 159.408; df = 5; p = 0.000) (Table 12). Female bears significantly selected young forest and clearcuts and significantly avoided middle-aged forest and had a tendency to avoid mature forest (Table 14 & Fig. 4). The use of foraging habitats differed significantly from the use of all of the resting sites (see habitat selection for bed sites) and also differed in use from the traveling habitats (χ^2 = 32.492; df = 4; p = 0.000).

Male bears significantly selected young and middle-aged forest for foraging in tree stumps (Table 15); they had opened 196 tree stumps, and 59% and 38% were opened in young forest and middle-aged forest, respectively. They also opened 28 anthills, turned 19 stones and I also recorded 42 ground scratches, but no significant habitat selection was found for either of these foraging signs (Table 15). Of all the foraging signs found, 50% and 40% were found in young forest and middle-aged forest, respectively.

Female bears had opened 487 tree stumps in 233 foraging locations. They significantly selected young forest (67.2% of the stumps were found here) for foraging in tree stumps, and they significantly avoided tree-rich bog/swamp forest and showed a tendency to avoid mature forest when opening tree stumps (Table 16). A total of 83 opened anthills were recorded, young forest was used significantly more during this activity and 40% of the anthills were opened in this habitat. In addition I found 52 turned stones and 150 ground scratches. The females did not show selection for any of the habitats when turning stones, but they avoided clearcuts, young forest and middle-aged forest when turning stones. The females selected young forest when searching for insects in the ground and 62% of the ground scratches were found in this habitat (Table 16). Of all the foraging signs, > 60% were found in young forest and 20% were found in middle-aged forest.

Total bear track was 60.83 km and 38.65 km for males and females, respectively. And total successful bear track was 39.58 km and 20 km for males and females, respectively. Females opened significantly more anthills and tree stumps than males per km track, (anthills: U = 1905.0; N (♂) = 53; N (♀) = 26; p = 0.025; tree stumps: U = 1837.5, N (♂) = 53; N (♀) = 26; p =0.003) (anthills: ♀ = 2.05/km, ♂ = 0.88/km, tree stumps: ♀ = 8.44/km, ♂ = 2.35/km). Females also showed a tendency of turning more stones along the trail than males per km track (U = 1948.9; N (♂) = 53; N (♀) = 26; p = 0.074) (turned stones: ♀ = 1.85/km. ♂ = 0.53/km).

3.4 Habitat selection for traveling

Male (N = 84, on average 9.3 ± 6.7 locations per individual) and female brown bears (N = 58, on average 3.4 ± 2.9 locations per individual) showed significant differences in habitats used for traveling (χ^2 = 19.334; df = 5; p = 0.002) (Table 17). I found no seasonal differences for female traveling habitats (χ^2 = 4.185; df = 3; p = 0.242). The sample size for males during hyperphagy season (N = 4) was so small that testing for seasonal differences was not possible. The male brown bears' use of the available habitats during traveling differed from what would be expected in the case of random use ($\chi^2 = 28.377$; df = 5; p = 0.000) (Table 17). Males significantly selected young forest and middle-aged forest for traveling (Table 18 & Fig. 5). The use of traveling habitats differed significantly from those used for night beds and showed a tendency for different use of foraging habitats (see habitat selection for bed sites and habitat selection for foraging).

Female brown bear use of the available habitats during traveling differed from what would be expected in the case of random use ($\chi^2 = 35.464$; df = 5; p = 0.000) and females significantly selected mature forest and significantly avoided tree-rich bog/swamp forest for traveling (Table 19, Fig. 5). The use of traveling habitats differed significantly from the use of night beds in hyperphagy season and the use of foraging habitats (see habitat selection for bed sites and habitat selection for foraging).

4 DISCUSSION

Both male and female Scandinavian brown bears chose and avoided particular habitats for resting, foraging and traveling. I found strong differences between the sexes in habitat use for foraging and traveling, but sexual differences in resting sites only occurred between male day beds and female night beds during the hyperphagy season. In general, females showed a stronger distinction between the habitats used for the different behaviors than males. Females selected significantly different habitats for all of the behaviors except between the night beds in the hyperphagy season and for traveling, where they selected for relatively more open habitats. In contrast, males tended to choose the two same habitats, young forest and middle-aged forest, for foraging, traveling, and day rest, but selected for a more open habitat use during night rest. Because the brown bears' main activities are resting and foraging (MacHutchon 2001), the choices of when and where to rest and forage are among the most important decisions a brown bear can take.

My results show the importance of distinguishing among the active behaviors foraging and traveling and the inactive behavior resting. For example, females only showed avoidance of certain habitats in the overall habitat use (Fig. 2), but showed strong selection for certain habitats when each behavior was examined separately. Similarly, males showed no significant selection or avoidance of clearcuts in the overall habitat selection (Fig. 2), but significantly selected clearcuts during night rest (Fig. 3b). Males had a more roaming behavior than females during the mating season but not in the hyperphagy season, and in contrast to females, showed a difference in amount of time spent foraging and traveling between the mating and the hyperphagy season. Also I found less sign of foraging per km along the tracks of males compared to females, indicating different foraging strategies between the sexes. In contrast to results of previous studies on habitat choice in the Scandinavian brown bear (Jansson 2005; Signer 2005; Moe et al. 2007), the bears did not show seasonal patterns in habitat use, except for seasonal differences in the use of resting sites by females.

4.1 Overall habitat selection

Both male and female bears significantly avoided bog and tree-rich bog/swamp forest in the overall habitat use. In addition, the males also significantly avoided mature forest (Fig. 2). These habitats offered only few opportunities for foraging in addition to being open habitats that in general offer little cover. Only the males selected for the forest categories young forest and middle-aged forest, which are the habitat types that offer the most feeding opportunities in the study area (Fig. 2). In comparison, females did not select for any type of habitats in the overall habitat use, suggesting that avoidance of open areas is more important than selecting for habitats with foraging opportunities. Middle-aged forest was included in the second-best model for female overall habitat use, Model 2 (Table 5), but was not significantly selected for.

4.2 Habitat selection for bed sites

Previous studies of bed site habitat selection in bears have mainly focused on the choices that females make or did not distinguish between males and females. This is the first study which compares this habitat use between male and lone female brown bears. Earlier studies mainly used VHF-technology, and animal positions were primarily taken during daytime, thus previous studies might be biased towards the study of day resting habitat use.

As mentioned in the method section, I didn’t have enough data to test for seasonal differences in habitat use for resting sites by males. However, males showed a different habitat use for day beds compared to night beds when both seasons were pooled. Females showed seasonal differences in the habitats used for resting, but only showed different habitat use between day and night resting sites in the hyperphagy season.

Mysterud (1983) characterized the typical bear day bed as "inside a patch of dark and shady medium-aged spruce thicket or timber stand". Both males and females (in the hyperphagy season) selected for young forest and middle-aged forest for day rest. Females also avoided tree-rich bog swamp forest (Fig. 3a, b). Mature forest was included in Model 1 (Table 10) of female day rest habitat use, but was not significantly avoided (Fig. 3b). My results suggest that for bed site selection bears tend to avoid open habitats, and select for more closed forested habitats with more opportunities for cover and close to food. This is also consistent with previous studies on resting sites chosen by bears (Jansson 2005; Munro et al. 2006; Moe et al. 2007), which also found that the bears rested mostly in forested habitats. Jansson (2005) argued that for female bears in Scandinavia, habitat selection for resting was more important than the selection of foraging habitats. However, my results indicate that both opportunities for cover *and* foraging might be important. The avoidance of tree-rich bog/swamp forest by females is inconsistent with the findings of Moe (2005), who found a selection for this habitat category by female brown bears in the same study area. Also, Munro et al. (2006) found that grizzly bears in west-central Alberta, Canada, selected for wet forest during rest which could be comparable to tree-rich bog/swamp forest in our study area. However, Munro et al. (2006) did not differentiate between day or night beds. During daylight hours there is more human activity in our study area than during dark hours, and therefore a greater need to avoid exposure by the bears, hence higher safety needs and a greater need for denser vegetation cover. Selection for forested habitats makes bears less vulnerable to exposure and human encounters in addition to more shade, as the exposure to sunlight is higher in open areas (Blanchard 1983; McLellan 1990; Wielgus & Vernier 2003; Apps et al. 2004; Nielsen et al. 2004a). The bears in Mysteruds' (1983) study in Norway showed similar patterns as in this study; they selected young forest, but also selected mature forest, however, they selected against middle-aged forest, and the cover of the beds ranged from extremely dense to average, few of the beds had relatively open cover.

Bears might also show a more cautious behavior during autumn due to increased human activity in the forest (e.g. berry pickers and hunters). Some species have shown avoidance in their behavior related to their main predator, for example Boydston et al. (2003) explained the increased use of dense vegetation by spotted hyenas (*Crocuta crocuta*) in Kenya with the increased human activity in the area. In the Appenine Mountains, Italy, female roe deer (*Capreolus capreolus*) with fawns changed their habitat use to denser habitats in times when their offspring were most vulnerable to wolf predation (Bongi et al. 2008). Moen (2009) studied how brown bears reacted to human approaches on foot. She found that the bears moved away more often when approached during the hyperphagy season than during the mating season. Ordiz et al. (unpublished data) found that bears selected day beds with more horizontal and vertical cover in the hyperphagy season compared with the mating season. In addition, during daytime the bears rested further away from human settlements in the hyperphagy season (Ordiz et al. unpublished data). Although I did not analyze the horizontal or vertical cover in the habitats, in addition to selecting young forest and middle-aged forest, the females selected mature forest for resting sites in the mating season (Fig. 3b). This is consistent with what Mysterud (1983) found. Mature forest is very spacious and open habitats, suggesting that cautious behavior are less pronounced during day rest in the mating season. However, the selection of young forest for resting sites in the mating must be interpreted with caution because the selection index for young forest was 1.003, thus indicating no selection or avoidance of this habitat (i.e. availability was the same as use). Unfortunately, I did not have enough data to test for seasonal patterns in the males' habitat selection of resting sites.

As perceived risks for the bear (e.g. the risk of human encounters and/or the risk of getting shot by hunters) are higher during daytime than during nighttime, the bears should have less need for cover during the dark hours. My results support this, as both males and females selected night beds in more open habitats than during day rest. Both sexes selected for clearcuts during night rest, in addition the female's selected middle-aged forest and mature forest (Fig. 3a, b). Young forest was a part of Model 1 for the females, but was not significant and was not a part of Model 2 (Table 11). Model 2 (Table 7a) added middle-aged forest to the males' selection of night resting sites, but this was not significant. The selection of clearcuts was quite surprising, as these habitats are very open and spacious with little or no opportunities for cover. This selection was most pronounced for males with a very high selection index (Table 6). Male brown bears were not recorded to use clearcuts during day rest, but used clearcuts 16.7% of the time during night rest (Table 6). These findings contrast to some degree with the findings of Moe (2005), who found an avoidance of clearcuts by female brown bears in central Sweden during the hyperphagy season, but a selection for clearcuts during night rest in the mating season. Ordiz et al. (unpublished data) found that both vertical and horizontal cover were higher during day rest than during night rest for female brown bears in central Sweden. Also Jansson (2005) discovered that the female brown bears used more open habitat categories during night rest compared to day rest in central Sweden. As mentioned earlier, females did not distinguish between day and night resting sites in the mating season, which in fact means that the females selected relatively denser habitats for night resting sites in the mating season than for night rest in the hyperphagy season.

4.3 Habitat selection for foraging

The males in my study selected for young forest and middle-aged forest while foraging (Table 13 & Fig. 4). The females also selected for young forest, but in contrast to males, they significantly avoided middle-aged forest. Females also selected for the more open habitat category clearcut and had a strong tendency for avoiding mature forest (Table 14 & Fig. 4). McLoughlin et al. (2002) argued that food is an important factor for explaining habitat use in barren-ground grizzly bears in the central Canadian arctic. Bears in central Sweden obtain 44-46% and 14-30% of their total energy from berries and ungulates respectively, and the remaining energy from insects (14-22%, mostly ants (carpenter ants and mound building red forest ants)) forbs and graminoids (12-18%) (Dahle et al. 1998b). Most of the foraging sign I found along the trail were opened tree stumps, excavated anthills, turned stones and ground scratches. All of these foraging sign was easy detectable evidence of the bear's searching for insects. My data might be biased towards certain feeding activities, because all foraging signs are not similarly detectable (see the discussions' paragraph 4.1). However, relative detectability should not vary between the sexes. The main goal of this thesis was to find sexual differences in the utilization of the different habitat categories in the study area, and not to document absolute use of the different food resources. In addition habitat analyses around a carcass or kill might rather reflect the prey species habitat use, and not necessarily the predators' habitat use.

Barck (2005) studied factors affecting foraging of brown bears on carpenter ants. The most important factor was density of stumps in the plot. Rolstad et al. (1998) found that most dead wood was present in forest stands up to 40 years old in south central Scandinavia. Puntilla (1991) found that carpenter ants were most abundant in mature forest, however, the carpenter ants are able to colonize dead wood and stumps rapidly after clearcutting (Sanders 1970). The strong selection for young forest by both male and female brown bears, and the selection for middle aged forest by males during foraging correspond well with the fact that the carpenter ant biomass available to bears in this area is highest in clearcuts from 5-35 years (Swenson et al. 1999a) and is consistent with findings in Alberta, Canada (Nielsen et al. 2004a). Both males and females selected young forest when opening tree stumps (Table 15 & 16), and 59% and 67.2% of the tree stumps were opened in young forest by males and females, respectively. In addition, the females significantly used young forest when excavating anthills (40% of the anthills were excavated here) and searching for insects in the ground (54% of the ground scratches were found here) (Table 16). Of the male and female foraging signs, 50% and 62% respectively were found in young forest. Forty percent of the foraging signs by male bears were found in middle-aged forest, and males significantly selected this habitat when opening tree stumps (Table 15). In contrast, only 20% of the female foraging signs were found in middle-aged forest and females seemed to avoid opening tree stumps in middle-aged forest (Table 16). The second most important factor for the bears' choice of where to forage for carpenter ants is the cover of blueberries in the plot (Barck 2005). The highest abundance of ripe berries (blueberries, lingonberries and crowberries) is found in forest stands older than 10 and younger than 60 years (Rønning 2001), and the periods when bears forage on blueberries and carpenter ants overlap (Johansen 1997). This may explain the selection of young forest by both sexes and middle-aged forest by males. The females' high use of middle-aged forest (25% of their active time) without selecting it may be explained by the high availability of this habitat (Table 12). Craighead et al. (1995) and Nielsen et al. (2004b) who studied grizzly bears in Yellowstone National Park, USA, found that occurrence of critical bear food were more common in clearcuts than in surrounding forest. This was also found in a study of black bears (*Ursus americanus*) in Quebec, Canada (Brodeur et al. 2008). Other studies of bear habitat use in heavily managed forests also show a selection for different clearcut categories (Wielgus & Vernier 2003; Nielsen et al. 2004a; Brodeur et al. 2008) and avoidance of middle-aged forest and mature forest (Brodeur et al. 2008). This may be an adaption to an environment lacking natural openings and different succession stages created by e.g. natural wildfires. Grizzly bears in Waterton Lakes, Alberta Canada, used fire succession communities where fruit production was high (Hamer et al. 1991). None of these studies have made a distinction between adult male and lone adult female bears. However, another possible explanation could be that females prefer more dense vegetation when foraging on ants and berries. Jansson (2005) argued that the need for shelter was more important than food resources for female brown bears in central Sweden. However, this does not explain the selection of the very open habitat clearcut by females. Moe (2005) found that during mating season female brown bears selected clearcuts (but avoided clearcuts in the hyperphagy season) and young forest, while avoiding tall and poor coniferous forest (similar to mature forest). That is consistent with my findings. The females used clearcuts either late in the evening or at dusk, this are periods with low human activity and may explain the use of clearcuts as preferred foraging habitats.

Different habitat use between adult males and lone adult females should reflect differences in diet in relation to bodysize related energy requirements and therefore possibly different foraging strategies. Also intraspecific predation by adult male bears on lone adult females has rarely been recorded (Mattson et al. 1992; Swenson et al. 2001b). Wielgus and Bunnel (1994) argued that differences in habitat use may be caused by sexual differences in dietary preferences, and that these differences should decrease as similarity in the diet increased. No research has been carried out on sexual differences in dietary preferences in our study area. However, Nilsen (2002) found no intraspecific competition for the berries between adult males and lone adult females in the area. Berries are the most important food resource in the hyperphagy season and are high in carbohydrate content. Most studies have not discovered any significant differences between habitat use by adult males and lone adult females. Mattson (2000) studied grizzly bears in Yellowstone National Park, USA, and found little differences in habitat use between adult males and lone adult females, but he found that males of all age classes were segregated from females of all age classes during spring and estrous by being located more often at lower elevations, thus, showing a difference in landscape use. These differences were probably explained by different diet preferences. Rode et al. (2006a) found no relationship between the percentage of lone females (or subadults) and adult males visiting the same food resources, and Ben-David et al. (2004) found that females without cubs did not avoid adult males. McLoughlin et al. (2002) detected no differences in habitat selection between adult males and lone females, either at the level of the home range or within the home ranges in grizzly bears in the Canadian Arctic. However, greater differences between the sexes have been recorded in relation to human settlements. Nellemann et al. (2007) argued that area use by bears in relation to human settlements seemed to be a function of variation in sensitivity influenced by sex, age and social organization. Chruszcz et al. (2003) argued that the distribution of grizzly bear in relation to roads was influenced by sex. Other studies of grizzly bear populations support these findings (Mattson et al. 1987; McLellan & Shackleton 1988; Wielgus et al. 2002).

My results show that differences in habitat use could be a result of different foraging strategies between the sexes. Male brown bear might need to utilize more energetic food resources than females (Welch et al. 1997; Jacoby et al. 1999; Hobson et al. 2000; Rode et al. 2001). In order to find such high energy resources (e.g. ungulates, neonates, carcasses) they need to travel over larger distances than females. Johansen (1997) found that male brown bear traveled twice the distance per day as females did, which is also reflected in the larger home ranges of males in comparison to lone adult females (Lindzey & Meslow 1977; McLoughlin et al. 2002; Dahle & Swenson 2003). My results also indicated a more roaming behavior of males, especially in the mating season. Males seemed to travel more than females and eat less. By traveling over greater distances the males might travel through less preferred, but highly available habitats, hence showing a selection for habitats with high availability even though they are not particularly selecting them.

Males kill more moose than females (Swenson et al. 2001a), and Mattson (2000) found that male grizzly bears exploited ungulate carcasses more than females did. In contrast, Johansen (1997) did not find any differences in number of hunting attempts on adult moose per km bear track between male and female brown bears (none of the hunting attempts were successful). No aggregated high energy food resources are available in this area in contrast to e.g. grizzly bears in North America with easy access to salmon streams. In grizzly bear populations where meat is a small part of the diet, males normally have higher meat consumption than females (Mowat & Heard 2006). The meat fraction of the bears' diet in this study area are relatively small (14-30%), however, they also get protein from insects (14-22%) making the protein content of their diet ~ 50%. Johansen (1997)found that female brown bears excavated more anthills and opened more wood per km than males. This is also consistent with my findings. Females could be more energetically rewarded than males by utilizing more of these food resources. Similar findings were detected in grizzly bears in Yellowstone National Park, USA, where smaller bears utilized more often roots with low energy content than larger bears did (Mattson 2000).

4.4 Habitat selection for traveling

The small sample size for males (N = 4) in the hyperphagy season was due to that the dog tracking teams used more females than males in the hyperphagy season. And the males spent more time foraging, the foraging signs after the bears were closer to each other, hence less traveling habitats were obtained. The use of traveling habitats therefore reflects the use in the mating season, rather than in both seasons.

Little research has been carried out on which specific habitat types a bear uses for traveling. Earlier studies on habitat use were often based on VHF-technology, and distinguishing between the active behaviors foraging and traveling was difficult. With the new GPS-technology in situ observations are possible and foraging activity can be differentiated from traveling. One should expect the bears to travel through habitat types that are easily traversable and may contain little foraging opportunities. This was the case for female bears, which used mature forest during traveling, but avoided tree-rich bog/swamp forest (Fig. 5). A similar habitat use of both males and females for traveling could be expected. However, males consistently selected the same two habitat categories as they did for foraging and day resting, namely young forest and middle-aged forest (Fig. 5). Signers' (2005) findings regarding female brown bear use of traveling habitats are to some extent consistent with my findings for female habitat use; i.e. females selected open terrain (bog, impediment and clearcut) and other habitat (e.g. roads) for traveling, while young forest was the least used habitat category. All of these habitat types are spacious and have only few foraging opportunities.

To my knowledge, this is the first study to report sexual segregation in the use of traveling habitats. This difference may be explained by greater roaming behavior of males, as explained previously (see also habitat selection for foraging). Hunting can act as a selective force if hunting pressure is large enough. And by hunting daring animals, the whole population can become more wary (Swenson 1999b). Previous studies have pointed out that males are more wary in the presence of humans than females, probably because of trophy hunting for larger males (Egbert et al. 1976; Aumiller & Matt 1994; Rode et al. 2006a). If the males in our study area are more wary, the use of denser forested habitats by males could indicate that they rate cover as more important than an easier travel route. However, in central Sweden, there is no hunting selection for sex (Bischof et al. 2008). Consistent with Bischof et als' (2008) findings, Moen (2009) found no sexual differences in the way brown bears in central Sweden reacted to human encounters on foot and suggested that there are no "sexual differences in wariness and behavior towards human encounters". The approaches that Moen (2009) conducted was during daytime when most of the bears was in their daybed, hence reflecting daytime behavior. However, my GPS locations are from active bears in the time period 04:00-07:00 and 20:00-22:00, when there is less human activity in the area, thus suggesting that different habitat use for traveling between the sexes are not influenced by human disturbance.

4.5 Seasonal differences

Whereas seasonal differences in the use of foraging habitats could reflect the temporal and spatial variation in food resources, seasonal differences in the use of resting sites may reflect differences in e.g. disturbance related to human activity. Signer (2005) studied habitat selection of female brown bear in central Sweden, and detected only weak seasonal differences in habitat use in relation to foraging, resting and moving. Jansson (2005) and Moe (2005) studied the same female brown bears as Signer (see above) in central Sweden, they detected seasonal patterns in the use of foraging habitats, however, no strong seasonal differences were detected for resting sites (Moe 2005). The findings of Jansson (2005) and Moe (2005) contradicts to some extent my findings, as I detected no seasonal differences except for resting sites for females. In contrast to the findings of Signer (2005), Jansson (2005) and Moe (2005), I did not distinguish between the individual bear's home ranges, but instead I used the whole study area and analyzed the bears on a population level. This could explain the difference, that this study is population based, while they have looked at a few female individual bears. Because habitat availability measured at the full range of the population level guarantees that the spectrum of variance across the landscape is represented (Boyce et al. 2003), I am therefore confident that my results reflect male and female brown bear habitat use in central Sweden. I also used broader habitat definitions than other studies. Some studies have detected different seasonal patterns in habitat use of male and female bears in North America (McLellan & Hovey 2001; McLoughlin et al. 2002; Nielsen et al. 2004a; Nielsen et al. 2004b; Berland et al. 2008), while some have not. Brodeur et al. (2008) detected no seasonal effect on habitat use between spring, early- and late summer and fall within the home ranges of female black bears in Quebec, Canada.

The bears in my study area showed great home range overlap (Fig. 1). Large overlaps in home ranges could suggest low quality habitats as discussed by McLoughlin et al. (2000), however, Signer (2005) found that female brown bear established their home ranges randomly in this study area, which indicates that the whole area consists of evenly distributed suitable bear habitat. Lack of seasonal habitat selection patterns could also indicate a substantial seasonal overlap in home ranges in this population, as suggested by Lindzey and Mezlow (1977). Also seasonally important foods are distributed in the same habitat types; hence there is no need to change habitat use through the seasons.

4.6 Possible weaknesses

There was a large variance in observations among the number of habitats per bear and behavior. This was because my data collection of the foraging and traveling plots, were based on the findings from the dog tracking exercises (See section 2.3). This meant that I had no control over which bears were chosen; hence some individuals were tracked more than others. Also the quality of the bear track and the quality of the dog tracking team varied (Vang 2009), and this also affected the amount of data I was able to obtain per individual bear.

The assumption of independent observations can be violated if an individual's choice made in the previous observation affects the choice made at the current location (Cooper & Millspaugh 2001). Moe et. al (2007) found a median patch size of 22500 m^2 with an average maximum exit distance of 85 m in our study area. I calculated the average distance between foraging signs to see if the signs after foraging were closer than 85 m to avoid analyzing the same foraging habitat twice. Average distance between foraging signs in my study was 206.4 m and therefore exceeded the distance between the average maximum exit distances from one habitat to the next. This should be enough to avoid the problem of autocorrelation in my data on foraging habitats (Neu et al. 1974; Aebischer et al. 1993; Arthur et al. 1996). Also, violation of independence was avoided by differentiating between sex, behavior and by choosing random individuals for tracking. Defining behavior as just active or inactive may not account for an animal's use of different resources related to e.g. diel (24 hour period) behavior or feeding versus moving (Cooper & Millspaugh 2001). I therefore distinguished between active (foraging and traveling) and inactive (day rest and night rest).

The activities of the bears were not equally detectable. Foraging activities like excavation of anthills and tree stumps, digging for insects in the ground and turning of stones, are easily detected by the dog tracking team. In contrast, grazing on forbs and grasses could be confused with grazing by ungulates and/or easily overlooked. Also sign after foraging on berries was difficult to detect, however, looking at the bears' GPS locations gave an idea about if it had been eating berries or not (e.g. the habitat patch had large amounts of ripe berries, we did not detect any other sign of foraging, but the bear had spent some time there without being inactive, thus indicating foraging on berries). Based on this, there is a chance that some of the foraging habitats therefore have been misinterpreted as traveling habitats.

4.7 CONCLUSIONS

Studying habitat use is complex because several factors (e.g. biotic, abiotic, physiological, and anthropogenic) are important in an animal's decision on where to carry out its daily activities. This thesis focused on differences in habitat use of male and lone female brown bears, and did not directly measure any other factors determining the habitat use, i.e. distance to nearest road or human settlement. This thesis therefore mainly describes the general patterns in the populations' use of available habitats.

There were sex related differences in habitat use for the activities foraging and traveling. Males selected young forest and middle-aged forest for both activities. Females selected young forest and clearcuts for foraging, but in contrast to the males they avoided middle-aged forest for foraging. Females selected mature forest and avoided tree-rich bog/swamp forest for traveling. Females separate foraging and traveling habitat use, while males don't.

There were fewer differences between the sexes in their choice of resting habitats, as cover seemed to be most important for both sexes during daytime and during periods with high human activities. For night resting sites more open habitats were selected by both sexes. For day rest, males again selected for young and middle-aged forest, while females selected for young and middle-aged forest in the mating season and for day rest in the hyperphagy season. In addition, females used mature forest for resting during the mating season and avoided tree-rich bog/swamp forest for day resting in the hyperphagy season. Males and females (in the hyperphagy season) selected clearcuts for night resting, in addition females also selected for middle-aged and mature forest.

Young forest and middle-aged forest seemed to be the two most important habitats for both male and female brown bears. These habitats offer high food abundance as well as cover from conspecifics as well as humans and exposure from sunlight. Thus, suggesting that food availability and cover are the most important variables influencing bears' decisions of habitat use. However, bears did not select for young forest and middle-aged forest in all of their behaviors. My results shows that no single habitat category characterized *all* of the bears' behaviors, thus the bears used different habitats for specific activities. Some habitats were selected for in certain activities while avoided in other activities. My results suggest that analyzing data on habitat use across sex, and active and inactive behaviors, can lead to serious biases in the interpretation of results.

5 ACKNOWLEDGEMENTS

I would compare the process of writing this thesis with a normal pregnancy. At times you don't know if this was the right thing to do, you doubt yourself, feel confused and uncertain, nevertheless there is excitement. As time goes by, thoughts grow and progress into ideas. The thesis begins to form, the skeleton has evolved. In the end, everything happens so fast, everything is falling in its' right place. And just as you begin to get used to it and love the situation, you go to press, and you realize there is no turning back. Out comes your baby!

This thesis was a part of the Scandinavian Brown Bear Research Project which is funded by the Norwegian Directorate for Nature Management, The Swedish Environmental Protection Agency, the Swedish Association for Hunting and Wildlife Management, World Wildlife Fund – Sweden, the Norwegian Research Council and the research program "Adaptive management of fish and wildlife populations". Many, many thanks to my supervisors Andreas Zedrosser and Jon E. Swenson for useful comments along the way, and for proofreading! Bear crew 2007 and 2008; field supervisor Sven Brunberg, Andres Ordiz, Magnus Hansson, Ingela Jansson, Heddeke Stolker, Sam Steyaert, Joni Lidberg, Gro K. Moen and Silje Vang. Especially thanks to Edward Moss my patient field assistant! Also, thoughts go to the dog trackers. Bear crew, thank you for some good times in the Swedish forests and the occasional car wash. Thanks to Vidar Selås for useful statistical help. Thank you Alf Erik Røyrvik for really useful comments on the manuscript! Special thanks to Andreas R. Seim, without you this would never have happened! To my sweet parents for taking care of me this autumn. To the wolf crew summer 2009, Canada, who gave me motivation by just being you. To the random persons making my day, thank you. To my fellow students, cheers! And last, but not least, the magnificent bears that have given us so much information without even knowing it!

Table 1: Habitat categories and their descriptions used to classify brown bear behavior in Sweden 2007-2008. The habitat categories follow the classification system of the Swedish forestry inventory (Karlsson & Westman 1991).

Habitat category	**Habitat description**
Bog	Wet peat ground with low productivity. Lacking trees or just very few trees. There is no in- or outflow of ground water.
Tree-rich bog/swamp forest	Tree-rich bog is like a bog, but richer in trees. Swamp forest is on waterlogged ground with in- and outflow of groundwater that makes it more productive. A swamp forest often has herbs that demand high productivity.
Clearcut	Varies from bare area not yet planted or the outcome is unsure, to successful tree planting (no need to fill in the gaps with new trees). Generally very open habitat.
Young forest	From very young forest to average tree is ≥ 1.3m, but < 10 cm in diameter at breast height. (Primary, non commercial, thinning). From relative open to very dense habitat. Supports many feeding opportunities.
Middle-aged forest	Secondary (commercial thinning). Average tree is ≥ 10 cm in diameter at breast height. Approximately 25-70 years. Relative open forest which supports many feeding opportunities.
Mature forest	Forest at the age when ca 10 years remain before the final harvest and older (≈ 80-90 years and above). Generally rather spacious, with limited undergrowth.

Table 2: The number of adult male (>3 years), adult female (≥4 years), and subadult (1-3 years) male and female brown bears with GPS transmitters used to evaluate behavior in relation to habitat use in central Sweden during 2007 and 2008, and the number of individuals used in both field seasons (2007+2008).

	Males			**Females**		
Year	**Adult**	**Subadult**	**Total**	**Adult**	**Subadult**	**Total**
2007	3	2	5	15	2	17
2008	8	1	9	9	1	10
2007+2008	2	0	2	7	0	7

Table 3: Proportion of habitats available and used in the study area, number of observations (N) and selection indices (S.I.) for overall habitat use of male and female brown bears in central Sweden in 2007-2008. S.I. with values > 1 and < 1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance.

	% Available	**Use males**			**Use females**		
Habitat		**%**	**N**	**S.I.**	**%**	**N**	**S.I.**
Bog	6.3	1.1	3	0.184	0.2	1	0.026
Tree-rich bog/swamp forest	23.8	10.0	26	0.419	10.3	64	0.433
Clearcut	3.8	2.3	6	0.613	4.8	30	1.286
Young forest	21.3	34	90	1.623	33.6	209	1.581
Middle-aged forest	32.5	46	119	1.403	34.2	213	1.054
Mature forest	12.5	6.5	17	0.521	16.9	105	1.350

Table 4: Results of the two best nominal logistic regression models on overall habitat selection of male brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best models. All models within ΔAIC≤2 are shown.

Model	**Variable**	**Parameter estimates**	**χ^2**	**df**	**P**	**ΔAIC**
Model 1						0
	Intercept	-1.594	-	-	< 0.001	
	Young forest	0.663	16.225	1	< 0.001	
	Middle-aged forest	0.590	15.366	1	< 0.001	
Model 2						1.609
	Intercept	0.604	-	-	0.179	
	Bog	-1.026	7.613	1	0.006	
	Tree-rich bog/swamp forest	-0.614	12.131	1	< 0.001	
	Mature forest	-0.506	5.075	1	0.024	

Table 5: Results of the two best nominal logistic regression models on overall habitat selection for female brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model. All models within ΔAIC≤2 are shown.

Model	**Variable**	**Parameter estimates**	χ^2	**df**	**P**	**ΔAIC**
Model 1						0
	Intercept	0.197	-	-	0.726	
	Bog	-1.953	18.338	1	< 0.001	
	Tree-rich bog/swamp forest	-0.541	11.750	1	< 0.001	
Model 2						0.59
	Intercept	0.365	-	-	0.529	
	Bog	-2.024	19.293	1	< 0.001	
	Tree-rich bog/swamp forest	-0.612	13.156	1	< 0.001	
	Middle-aged forest	-0.168	1.410	1	0.235	

Table 6: Proportion of habitats available and used in the study area, number of observations (N) and selection indices (S.I.) for day and night resting sites habitat use (mating and hyperphagy season are pooled together) of male brown bears in central Sweden in 2007-2008. S.I. with values > 1 and < 1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance.

	% Available	**Day resting use**			**Night resting use**		
Habitat		**%**	**N**	**S.I.**	**%**	**N**	**S.I.**
Bog	6.3	0	No observations		0	No observations	
Tree-rich bog/swamp forest	23.8	12.5	5	0.526	16.7	4	0.702
Clearcut	3.8	0	No observations		16.7	4	4.444
Young forest	21.3	30	12	1.412	12.5	3	0.588
Middle-aged forest	32.5	52.5	21	1.615	41.7	10	1.282
Mature forest	12.5	5	2	0.400	12.5	3	1.000

Table 7: Results of the best nominal logistic regression model on **a)** day rest habitat selection, and the two best nominal logistic regression models on **b)** night rest habitat selection of male brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model. All models within ΔAIC≤2 are shown.

Model	**Variable**	**Parameter estimates**	**χ^2**	**df**	**P**	**ΔAIC**
a) Day resting sites						
Model 1						0
	Intercept	0.281	-	-	0.240	
	Middle-aged forest	0.726	9.157	1	0.003	
	Young forest	0.658	5.814	1	0.016	
b) Night resting sites						
Model 1						0
	Intercept	0.530	-	-	0.187	
	Clearcut	0.818	4.083	1	0.043	
Model 2						0.221
	Intercept	0.334	-	-	0.432	
	Clearcut	0.958	5.160	1	0.023	
	Middle-aged forest	0.337	1.749	1	0.186	

Table 8: Proportion of habitats available and used in the study area, number of observations (N) and selection indices (S.I.) for **a)** resting sites during mating season (there was no significant difference between day and night resting sites), and **b)** day and night resting sites during hyperphagy season, of female brown bears in central Sweden 2007-2008. S.I. with values > 1 and < 1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance.

a)	**% Available**	**Use resting sites mating**		
Habitat		**%**	**N**	**S.I.**
Bog	6.3	0	No observations	
Tree-rich bog/swamp forest	23.8	12.3	15	0.518
Clearcut	3.8	9	6	1.311
Young forest	21.3	21.3	26	1.003
Middle-aged forest	32.5	42.6	52	1.311
Mature forest	12.5	18.9	25	1.508

b)	**% Available**	**Use day rest**			**Use night rest**		
Habitat		**%**	**N**	**S.I.**	**%**	**N**	**S.I.**
Bog	6.3	0	No observations		0	No observations	
Tree-rich bog/swamp forest	23.8	18.8	19	0.792	7.4	8	0.312
Clearcut	3.8	1.0	1	0.264	9.3	10	2.469
Young forest	21.3	29.7	30	1.398	12.0	13	0.556
Middle-aged forest	32.5	44.6	45	1.371	38.0	41	1.168
Mature forest	12.5	5.9	6	0.475	33.3	36	2.667

Table 9: Results of the three best nominal logistic regression models on resting site habitat selection during mating season of female brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model. All models within ΔAIC≤2 are shown.

Model	Variable	Parameter estimates	χ^2	df	P	ΔAIC
Model 1						0
	Intercept	-1.792	-	-	0.001	
	Middle-aged forest	0.582	8.452	1	0.004	
	Mature forest	0.651	7.136	1	0.008	
	Young forest	0.447	3.993	1	0.046	
	Clearcut	0.582	2.363	1	0.124	
Model 2						0.363
	Intercept	-1.101	-	-	< 0.001	
	Middle-aged forest	0.472	6.399	1	0.011	
	Mature forest	0.542	5.409	1	0.020	
	Young forest	0.338	2.551	1	0.110	
Model 3						0.914
	Intercept	-0.763	-	-	< 0.001	
	Middle-aged forest	0.958	3.937	1	0.047	
	Mature forest	0.337	3.291	1	0.070	

Table 10: Results of the two best nominal logistic regression models on day rest habitat selection of female brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model.

Model	Variable	Parameter estimates	χ^2	df	P	ΔAIC
Model 1						0
	Intercept	-2.382	-	-	0.034	
	Middle-aged forest	1.314	9.538	1	0.002	
	Young forest	1.323	9.197	1	0.002	
	Tree-rich bog/swamp forest	1.040	5.151	1	0.023	
	Mature forest	0.784	2.199	1	0.138	
Model 2						0.199
	Intercept	-1.031	-	-	0.002	
	Middle-aged forest	0.747	9.489	1	0.002	
	Young forest	0.756	8.597	1	0.003	
	Tree-rich bog/swamp forest	0.472	3.079	1	0.079	

Table 11: Results of the two best nominal logistic regression models on night rest habitat selection of female brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model.

Model	**Variable**	**Parameter estimates**	**χ^2**	**df**	**P**	**ΔAIC**
Model 1						0
	Intercept	-2.435	-	-	< 0.001	
	Mature forest	1.190	22.686	1	< 0.001	
	Middle-aged forest	0.777	11.749	1	< 0.001	
	Clearcut	1.151	10.536	1	0.001	
	Young forest	0.415	2.338	1	0.126	
Model 2						0.338
	Intercept	-1.805	-	-	< 0.001	
	Mature forest	0.975	21.835	1	< 0.001	
	Middle-aged forest	0.562	9.761	1	0.002	
	Clearcut	0.937	8.280	1	0.004	

Table 12: Proportion of habitats available and used, number of observations (N) and selection indices (S.I.) for foraging habitat use for male and female brown bears in central Sweden 2007-2008. S.I. with values > 1 and < 1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance.

	% Available	**Use males**			**Use females**		
Habitat		**%**	**N**	**S.I.**	**%**	**N**	**S.I.**
Bog	6.3	0	No observations		0	No observations	
Tree-rich bog/swamp forest	23.8	10.6	12	0.447	8.6	20	0.361
Clearcut	3.8	1.8	2	0.472	4.3	10	1.144
Young forest	21.3	39.8	45	1.874	53.6	125	2.525
Middle-aged forest	32.5	44.2	50	1.361	24.9	58	0.766
Mature forest	12.5	4.0	4	0.238	8.6	20	0.687

Table 13: Results of the best nominal logistic regression models on foraging habitat selection of male brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model.

Model	**Variable**	**Parameter estimates**	χ^2	**df**	**P**	**ΔAIC**
Model 1						0
	Intercept	-0.814	-	-	< 0.001	
	Young forest	0.847	19.122	1	< 0.001	
	Middle-aged forest	0.687	14.220	1	< 0.001	

Table 14: Results of the best nominal logistic regression models on foraging habitat selection of female brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model.

Model	**Variable**	**Parameter estimates**	**χ^2**	**df**	**P**	**ΔAIC**
Model 1						0
	Intercept	-2.530	-	-	< 0.001	
	Young forest	1.090	31.432	1	< 0.001	
	Middle-aged forest	0.492	6.693	1	0.010	
	Clearcut	0.693	4.183	1	0.041	
	Mature forest	0.438	3.275	1	0.070	

Table 15: Total foraging signs found (N) and selection indices (S.I.) for habitats used for foraging by male brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant S.I.'s ($p < 0.05$) are marked *. Significant results from the nominal logistic regression analysis are shown at the bottom row.

	Tree stumps		**Anthills**		**Turned stones**		**Ground scratch**	
Habitat	**N**	**S.I.**	**N**	**S.I.**	**N**	**S.I.**	**N**	**S.I.**
Tree-rich bog/swamp forest	5	0.12	3	0.38	No observation		9	0.85
Clearcut	1	0.37	2	2.38	No observation		1	0.60
Young forest	115	2.17*	5	0.84	10	1.93	13	1.37
Middle-aged forest	74	1.29**	16	1.51	9	1.26	17	1.17
Mature forest	1	0.11	2	0.71	No observation		2	0.36
	* $\chi^2 = 28.332$, df = 1, $p < 0.001$							
	** $\chi^2 = 18.743$, df = 1, $p < 0.001$							

Table 16: Total foraging signs found (N) and selection indices (S.I.) for habitats used for foraging by female brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant S.I.'s ($p < 0.05$) are marked *, (***) means a tendency. Significant results from the nominal logistic regression analysis are shown at the bottom row.

	Tree stumps		**Anthills**		**Turned stones**		**Ground scratch**	
Habitat	**N**	**S.I.**	**N**	**S.I.**	**N**	**S.I.**	**N**	**S.I.**
Tree-rich bog/swamp forest	11	0.14*	16	0.69	1	1.90	18	0.51
Clearcut	27	1.31	5	1.98	5	0.77*	6	1.08
Young forest	327	2.82**	33	1.82*	39	0.15**	82	2.32*
Middle-aged forest	100	0.62	19	0.69	5	0.38***	32	0.62
Mature forest	22	0.44 (***)	10	0.71	2	0.95	12	0.65
	*χ^2=12.236, df=1, p<0.001 **χ^2=16.732, df=1, p<0.001 (***)χ^2=3.189, df=1, p=0.074		*χ^2=5.533,df=1, p=0.012		*χ^2=8.756, df=1, p=0.003 **χ^2=28.369, df=1, p<0.001 ***χ^2=7.377, df=1, p=0.007		*χ^2=18.617,df=1, p<0.001	

Table 17: Proportion of habitats available and used in the study area, number of habitats (N) and selection indices (S.I.) for traveling habitat use of male and female brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant S.I.'s ($p < 0.05$) are marked *.

	% Available	**Use males**			**Use females**		
Habitat		**%**	**N**	**S.I.**	**%**	**N**	**S.I.**
Bog	6.3	3.6	3	0.571	1.7	1	0.276
Tree-rich bog/swamp forest	23.8	6.0	5	0.251	3.4	2	0.145
Clearcut	3.8	0	No observations		5.2	3	1.379
Young forest	21.3	35.7	30	1.681	25.9	15	1.217
Middle-aged forest	32.5	45.2	38	1.392	29.3	17	0.902
Mature forest	12.5	9.5	8	0.762	34.5	20	2.759

Table 18: Results of the best nominal logistic regression model on traveling habitat selection of male brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model.

Model	**Variable**	**Parameter estimates**	**χ^2**	**df**	**P**	**ΔAIC**
Model 1						0
	Intercept	-0.474	-	-	0.017	
	Young forest	0.703	11.556	1	< 0.001	
	Middle-aged forest	0.609	10.124	1	0.002	

Table 19: Results of the best nominal logistic regression model on traveling habitat selection of male brown bears in central Sweden 2007-2008. A minimum information theoretical criterion (AIC) estimate (MAICE) was used to determine the best fit model.

Model	Variable	Parameter estimates	χ^2	df	P	ΔAIC
Model 1						0
	Intercept	0.780	-	-	0.063	
	Tree-rich bog/swamp forest	-0.951	8.877	1	0.003	
	Mature forest	0.521	5.783	1	0.016	

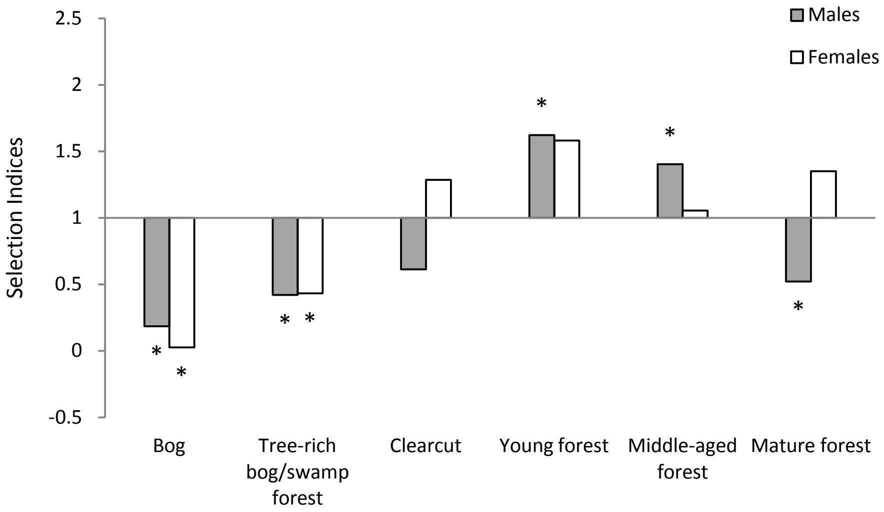

Figure 2: Selection indices (S.I.) of overall habitat use of male and female brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant selected and avoided habitats from the nominal logistic regression models (Table 4 & Table 5) are marked *.

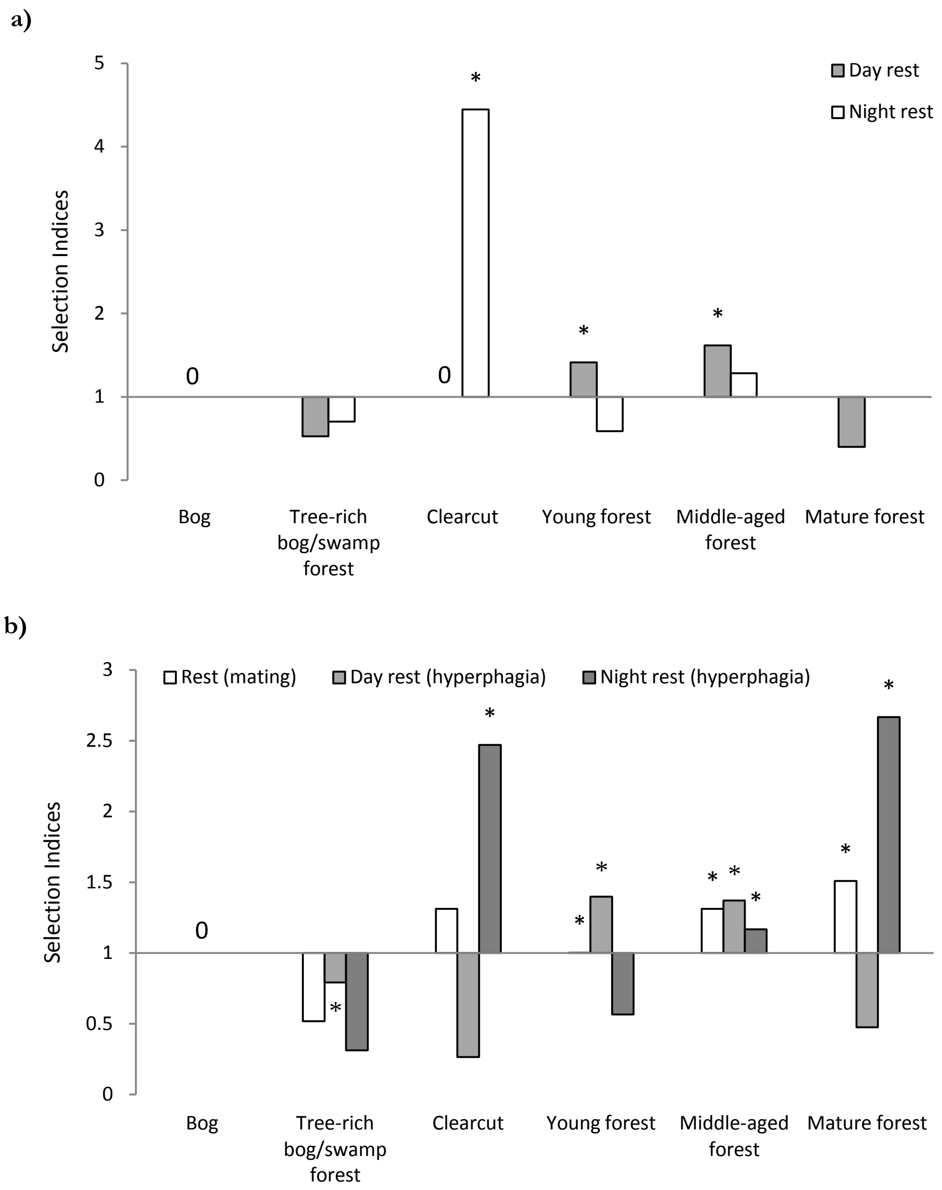

Figure 3: Selection indices (S.I.) of habitats used for resting sites of **a)** male and **b)** female brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant selected and avoided habitats from the nominal logistic regression models (Table 7, 8, 10 & 11) are marked *. Zero observations marked with 0.

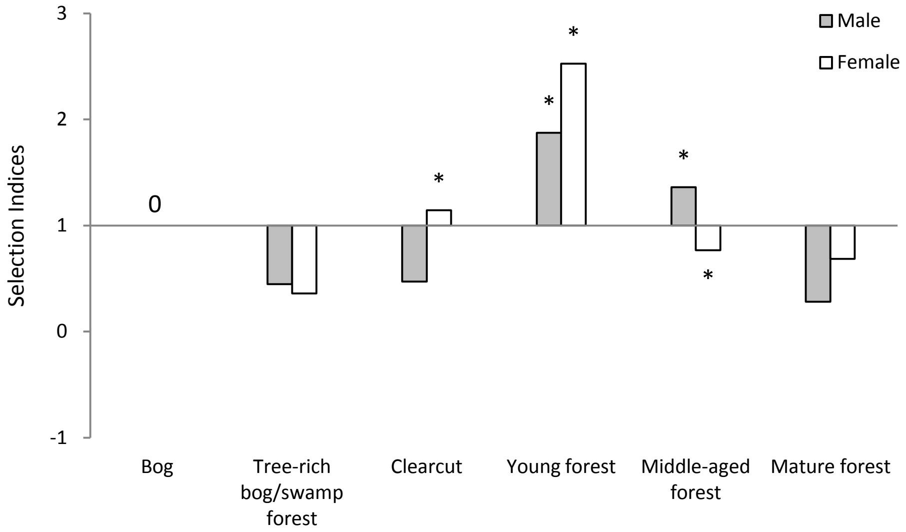

Figure 4: Selection indices (S.I.) of habitats used for foraging of male and female brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant selected and avoided habitats from the nominal logistic regression models (Table 13 & Table 14) are marked *. Zero observations marked with 0.

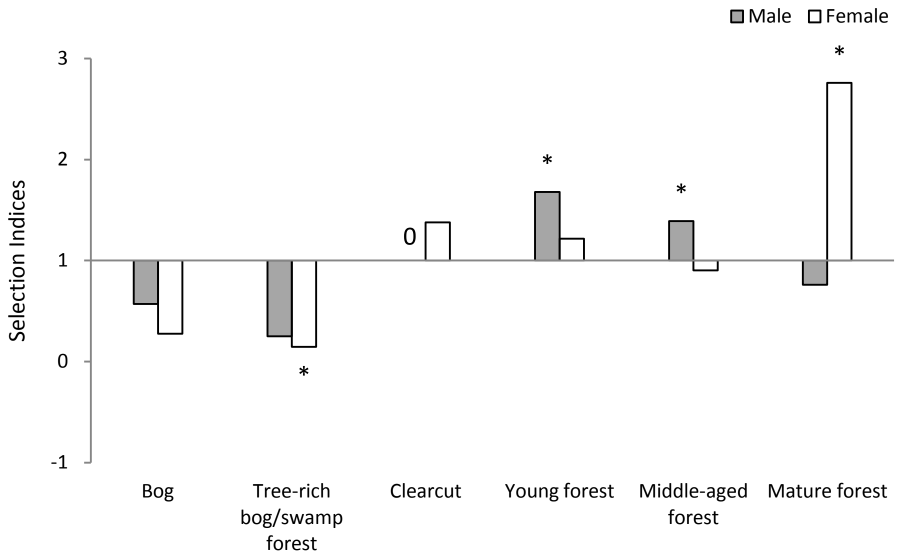

Figure 5: Selection indices (S.I.) of habitats used for traveling of male and female brown bears in central Sweden 2007-2008. S.I. with values >1 and <1 indicates selection and avoidance respectively, a S.I. = 1 indicates no selection or avoidance. Significant selected and avoided habitats from the nominal logistic regression models (Table 18 & Table 19) are marked *. Zero observations marked with 0.

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