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A pilot study of brown bear (*Ursus arctos*) habitat use in central Sweden at two temporal scales using GPS

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Abstract

The habitat selection of five brown bears (*Ursus arctos*) in central Sweden was studied from spring until late summer during 2005. All bears were sexually mature females equipped with GPS-receivers. The forest dominating landscape occupied by these bears is highly affected by forestry, dividing the forest into single age stands and large clear-cuts, intersected by lakes and mires. Habitat use within each bear's home range was compared at two temporal scales; seasonal and diel period. The study period was divided into the mating season and the berry season, corresponding to a shift in both dominant food types and behaviour. Further the 24 hour day was divided into four periods, relating to the bears predominating activity status; active or passive. Bears used the habitats within their home ranges non-randomly. Individual variation was large and there were few indications of a general selection for particular habitats, with the exception of mire which was selected against by all bears. Habitat use differed between the seasons for 4 of the 5 bears and among periods of the day. Bears were generally less selective of habitats during the mating season. During the 24 hour day, bears were most selective during the daytime resting period, particularly in the selection against more open habitat types; clear-cuts and mires. My data suggests that the bears' habitat selection was more driven by their need of shelter than food abundance, as the bear's omnivorous habits enables it to find food in most habitats of the boreal forest.

To verify precision and reliability of the GPS fixes a field inventory of GPS bear relocations were made. Fresh bear signs were detected in 64 - 74 % of 1057 visited sites, depending on season. The GPS-GSM set-up in this study generally functioned well, and the overall success for attempted fixes were 76 %, with a decreasing fix-success through the study period. However, there was a bias against successful GPS fixes when a bear was passive, which needs to be considered in analyses of habitat selection.

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1 Introduction

An area suitable for an animal should encompass the resources it requires such as food, water, reproductive opportunities, and escape cover. Certain habitat types and features better satisfy these needs, and a common assumption is that an animal will select for such resources (Manly et al. 2002). How an animal uses its surroundings is an integral part of its ecology, therefore biologists often aim to identify the important resources and habitats, and to document their availability. This knowledge is necessary, especially for management of exploited species. Habitat selection studies are commonly used to explore animals' use of an area and have received much attention (e.g. White and Garrott 1990, Manly et al. 2002). These studies usually compare the proportion of used resources or habitats to that available or un-used, and the animal is considered to be selective when its use is disproportional to availability.

Habitat selection can be analysed at the individual or population level. For wildlife management, the population level analyses are generally more valuable. Wildlife tracking studies uses relocations of animals to identify used habitats. The frequency of use is a common index to describe the importance of a habitat component to an animal (Powell 2000). If habitats differ in their qualities to provide for different activities such as resting and feeding, then animals' choice of habitats is likely to be behaviour dependent (Cooper and Millspaugh 2001). Hence, common behaviours and the habitats predominantly used for these, will dominate over rare behaviours in aggregated tracking data. Habitats selected for rare behaviours may be interpreted as relatively less important, but it may be of critical value for the individual animal (Powell 2000, Cooper and Millspaugh 2001).

Behaviours, and habitats tied to these, may be biased if data sampling is limited to certain periods of the day, particularly if the animals have a circadian activity pattern. If habitat selection exists, but varies depending on year, season, time of day and type of activity, this selection may not be noticed unless the data is separated into relevant categories (Palomares and Delibes 1992). A habitat selection analysis is also improved by dividing the data into relevant spatial scales, as animals may use different trade-offs in their selection on different spatial scales (Johnson 1980). This is often described as a hierarchical selection process, as the choice on the food patch level is conditional on the selection on the home range level (Johnson 1980). Nowadays, habitat selection studies are commonly divided into analyses at different spatial and temporal scales, such as landscape, home range and patch scale and into different years or seasons. However, one rarely in studies of larger mammals further divides the analyses into different types of behaviours or diel periods (i.e. periods of the 24 hour day) (Cooper and Millspaugh 2001, Palomares and Delibes 1992).

There is a vast documentation on habitat selection for a variety of animal species world wide. Many focus on species that requires special attention for their conservation, such as the brown bear (*Ursus arctos*). Though formerly widespread over much of the northern hemisphere, overharvesting and habitat degradation have lead to a decline and a fragmentation of most brown bear populations of today (Servheen et al.1999). In Europe however, many bear populations are increasing and have expanded their ranges during the last 50 years (Swenson et al. 2000). Bear management policies have a large impact on this long-lived and slowly reproducing specie (Swenson et al. 1995). Thus, a thorough knowledge of its ecology is crucial to conserve and manage the brown bear properly (Swenson el al. 2000). Habitat use studies of the brown and the grizzly (*Ursus arctos horribilis)* bear species have mainly been conducted in North America (e.g. Servheen 1983, Waller and Mace 1997, Craighead 1998, McLellan and Hovey 2001, Belant and Follmann 2002, Nielsen et al. 2002, Wielgus and Vernier 2003, Apps et al. 2004). Fewer studies have been conducted on brown bear in Europe (but see Kobler and Adamic 2000). Most studies show that bears make non-random use of the area, and selectivity has been shown to vary among seasons, years, individuals, sex and reproductive status and between day and night. The brown bear has a flexible food choice and its dominating diet varies both geographically and seasonally (Servheen et al. 1999, Swenson et al. 2000). As the variation is so large, habitat selection observed in one population cannot be used to draw reliable conclusions for bear populations elsewhere.

The brown bear occurred originally throughout Sweden, but excessive hunting during previous centuries almost lead to its extinction in the early 1900s (Lönnberg 1929; Swenson et al. 1995). Thereafter a change in policies has lead to a successful recovery (Lönnberg 1929; Swenson et al. 1995). Today there are around 2000 bears in Sweden (Kindberg et al. 2004), distributed over some large tracts of forest dominated or mountainous landscapes with low human presence. Previous investigations of brown bear habitat use in Scandinavia on a landscape scale suggests a preference of forests and an avoidance of open habitats with human influence (Katajisto, Moilanen and Swenson, unpublished manuscript, Swenson and Sandegren 2000). The bears' use of habitats within their home ranges has not yet been analysed; however studies of habitat selection for den-sites (Elfström 2004) and day-bed sites (Katajisto 2001) have been conducted.

Studies of Scandinavian brown bear have revealed a distinct change in diets and behaviour between spring-early summer and late summer-autumn. From the time when bears emerge from their winter dens in the spring (Friebe et al. 2001) and until the early summer, their major food types are ants and moose (Johansen 1997, Dahle et al. 1998, Swenson et al. 1999). The food during spring-time is more or less limited with a patchy distribution. Later on, during the late summer-autumn season the bears' diet in Sweden is dominated by berries (Johansen 1997, Dahle et al. 1998), a generally widespread and abundant food resource. At this stage bears have entered a condition of hyperphagia, and spend most of their time feeding large quantities of this abundant and widespread carbohydrate rich berry diet to gain enough energy and fat reserves for the coming denning period (Sandegren and Swenson 1997). The mating season occurs during spring-early summer, with a peak during first week of June (Dahle and Swenson 2003a). Female bears are commonly known to restrict their ranges to just cover their dietary needs (e.g. Bunnell and Tait 1981, Sandell 1989), but recently studies by Dahle and Swenson (2003b, c) have shown that oestrous females, like mature males, extend their ranges during the mating season. It is likely that oestrous females, contrary to previous assumptions, are actively involved in the mating activities by roaming the area in search of males to mate with (Dahle and Swenson 2003b, c). The Scandinavian brown bears' circadian activity rhythm during the vegetation period of the year (i.e. non-denning period) varies some between sexes and seasons. In general, they have an extended predominantly passive period during mid-day and a shorter passive period during the dark hours of the night (Sandegren and Swenson 1997, Myre 2000). When a bear is not resting it tends to spend most of its time feeding, particularly if they feed mainly on plant food (MacHutchon 2001).

Studies of movements of free-ranging wildlife and their use of the landscape are commonly done with radio telemetry, using very high frequency (VHF) transmitters attached to animals (Rodgers 2001). The relocation of radio-collared large wide-ranging animals is usually done from a vehicle or plane, which is expensive and time and manpower demanding. Thus most radio-tracking studies of these animals are limited to a few daytime relocations per week, or per month. However, during the last three decades there has been substantial development in wildlife telemetry with the advancing techniques of satellite systems, and later the NAVSTAR Global Positioning Systems (GPS) (Rodgers 2001). Attaching satellite and GPS receivers on animals allows frequent and, in the case of

GPS receivers, very precise animal tracking at regular intervals independent on time of day. Because of its many advantages the use of GPS receivers for wildlife research is increasing (Rodgers 2001). Its main disadvantage is the expensive initial investment in GPS receivers. Thus, researchers often opt to sample just a few individuals in a population from which they can obtain a very precise and large dataset, as the cost per each relocation is minimal. Studies of GPS performance have reported variations in fix success and validity that are affected especially by habitat variables such as canopy cover, and by animal behaviour (Rempel et al. 1995, Obbard et al. 1998, Schwartz and Arthur 1999, Moen et al. 2001, Rodgers 2001, D'Eon et al. 2002, D'Eon 2003). This could introduce bias for or against certain habitats and behaviours. Although there is still no established method to overcome this, it needs to be considered in habitat selection analyses using GPS data.

The objective of my study was to explore brown bear habitat use in central Sweden, using GPS, and to analyse if and how their use is influenced by the season and the period of day. Based on earlier habitat use studies on bears, I have formulated a major hypothesis: that bears' habitat selection varies between seasons and among individuals, and that time of day, related to their dominating activity - active or passive - influence the selection. I have used the following predictions to test this:

a) I predict bears to use the habitats differently between mating and berry season due to their shift in seasonal diet and behaviour.
b) I predict that bears use habitats non-randomly. My expectation is a selection for habitats with good supply of food types that dominate a bears' diet, which differs between the mating and the berry season. I expect to find less selectivity during mating season, as I predict that bears roam more during that season in search of food (when the major bear food is more patchily distributed), and perhaps also in search of mating partners.
c) Further I predict that bears' choice of habitats is influenced by the period of day, which can be related to their activity pattern, and that bears
i) would be more selective when resting, with preference for habitats with good shelter
ii) would be less selective when actively foraging, as the bear is an omnivore
iii) would be less discrete and use more open habitats night time, when human activities are the lowest

To test my predictions I have used GPS relocation and activity level data from six sexually mature female bears and indirect observation data from sites recently visited by them. Habitat selection was analysed at the home range spatial scale, comparing used habitat to that available within the home range, and at patch level scale by comparing the use within home ranges at two temporal scales; seasonal and diel periods. To relate use of habitat to food richness, I present a brief summary of the estimated ant and berry abundance at sites visited by bears. By involving so few individuals from one sub-group of a population, this study cannot draw conclusions for the whole population. Instead, as a pilot study, it may guide future studies on bears' habitat selection. The Scandinavian Bear Project is just starting to track bears by using GPS. This created a need to know the reliability (both of function and positioning accuracy) of the new technique, thus I provide a short summary of the performance GPS collars during this study.

2 Methods

During the summer of 2004 we collected data on location, activity levels and type of activity from six bears, fitted with GPS-GSM (Global System for Mobile communication) collars. For procedures on capture, marking and aging the bears, see Swenson et al. (2001). All bears were sexually mature females, 3-10 years old. In this area females reach sexual maturity at the age of three and successful mating at this age have been documented (Swenson et al. 2001). All were solitary, except one, who remained accompanied by her yearlings. This was unexpected, as nearly all yearlings separate from their mothers during the spring or early summer in this area (Dahle and Swenson 2003a). The other bears were assumed to have been in oestrous during the mating season. Data from one bear were excluded from the analyses due to substantial data losses and unreliable positioning from this bear.

2.1 Study period

Data on GPS relocations and activity levels were received from 20 May to 24 August 2004. Field observations took place from 4 June until 24 August, with a two week break in early-mid July. In total 1057 bear visited sites, indicated by GPS relocations, were investigated, hereafter termed plots. From the five bears considered in the habitat selection analyses the number of investigated plots was 948, ranging from 188 - 191 plots per bear. To divide the period into two seasons, I selected data to represent the mating season as a 35-day period around the peak of mating (20/5 - 23/6), and the berry season as a 34-day period starting the day we first noted berries in bearscats (21/7 - 24/8). These two seasons were separated by four weeks (intermediate period, 24/6 - 20/7). When dividing field observations into seasons, 219 (37 - 48 per bear) and 499 (95 - 105 per bear) plots were visited during mating and berry season, respectively.

To compare habitat use among different diel periods, the 24-hour day was divided into four periods according to the observed regular pattern of dominating active and passive bouts from the bears' activity data during the two seasons:

Night rest:	0000 - 0230 mating and berry season
Morning active:	0300 - 0830 mating season, and 0300 - 0900 berry season
Day rest:	0830 - 1730 mating season, and 0900 - 1630 berry season
Evening active:	1800 - 2330 mating season, and 1700 - 2330 berry season

To compare habitats chosen for day-beds and for night-beds observed in our field survey, a bed was defined as a day-bed if the bear used the site between 0700 - 2130, and a night-bed if the site was used between 2200 - 0630. This definition of day and night is more related to human activity, than hours of daylight.

2.2 Study area

I conducted the study in the southernmost reproductive core area of the Scandinavian brown bear in the county of Dalarna (61˚N, 15˚E) (Fig. 1). Forests dominate the area, intersected by lakes and mires. Scots pine (*Pinus sylvestris*) is the major tree species, and there are a number of lodgepole pine (*Pinus contorta*) plantations. Other common species are Norway spruce (*Picea abies*) and deciduous trees like birch (*Betula spp.*) and aspen (*Populus tremula*). Forestry is intensive in the region, with most forests divided into single-aged stands in different stages of the production cycle, intersected by clear-cuts. Clear-cuts cover ca 8 % of the forested area and ca 40 % of the forest is younger than 35 years (Swenson et al. 1999). The area has a dense net-work of roads, most of them small dirt-roads used in forestry. Land is either private or owned by larger forestry companies, which further divide the forest into smaller sections of different management classes. All this creates a very patchy landscape with forests in different stages of production, mires, lakes, rivers and roads. From the vegetation map (see below) the estimated mean patch size was 80 600 ± 4 410 m² (±S.E.) and the median patch size was 22 500 m². The human population is sparse and concentrated to a few small villages. One major road, E 45, crosses the area. The landscape is gently undulating and elevations range between 200 to 700 m.a.s.l., all below the tree-limit. Snow cover generally lasts from late October to April/May. In autumn bilberries (*Vaccinum myrtillus*), crowberries (*Empetrum hermaphroditum*) and lingonberries (*Vaccinum vitus-idaea*) are widespread and abundant in most years, providing an important food source for bears (Johansen 1997, Dahle et al. 1998). Density of bears in the study area is approximately 30 per 1000 km² (Bellemain et al. 2005). Other large predators, the lynx (*Lynx lynx*) and the wolf (*Canis lupus*) occur in low numbers (Liberg and Glöersen 2000, Aronsson and Wabakken 2004). Moose (*Alces alces*) are common, with a rather stable winter population of 0.4-0.5 per km² (Rune Delén, Orsa Besparingsskog, pers. communication, Oct. 2004).

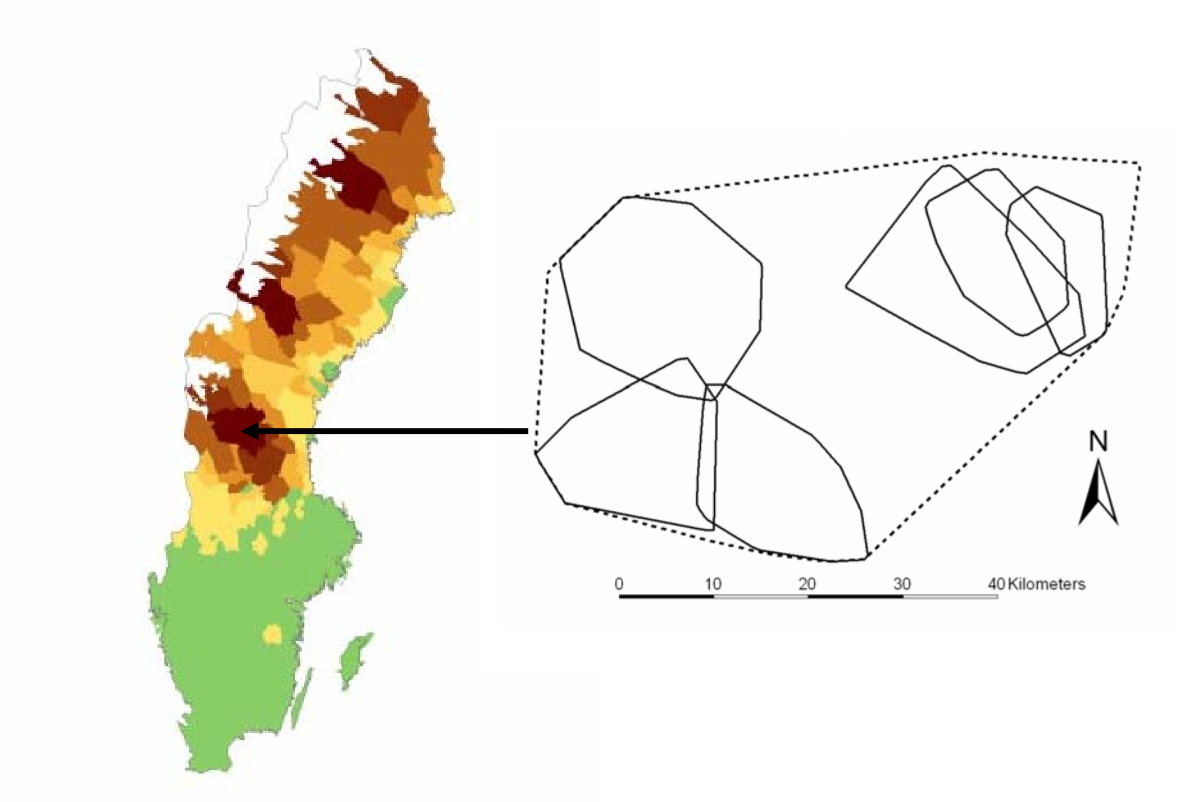

Fig. 1. Map of Sweden with the estimated distribution of brown bears in the northern two-thirds of the country. The darker areas illustrate areas of higher bear densities (Kindberg et al. 2004). Three areas have distinctly higher densities of bear, termed female reproductive core areas. The insert shows the study area with the home ranges during mating season of the six bears, and its location in the southernmost reproductive core area.

2.3 GPS and habitat data

Data were received from six bears using collars with GPS-receiver, GSM module, and activity sensor. The GPS receivers were programmed to take one position every half hour, resulting in 48 bear relocations per day and bear in optimal conditions. Activity levels were measured constantly and a mean from every five minute period was presented in the data. The activity data have been analysed (Gervasi, unpublished manuscript), providing individual boundary values to determinate if the bear was active or passive at each given time. Activity levels 30 % below and 30 % above the boundary value were regarded as passive and active, respectively. The activity level data could not be used to differentiate between activities such as feeding, walking and running (Gervasi, unpublished manuscript).

I used a digital land cover map to determine habitat availability and habitat use. This map was developed by the Swedish Landcover Data (SMD - Svenska Marktäcke Data, Engberg 2002) from satellite images with the support of data from field inventories. Most satellite images for our study area come from the summer of 1999, some sections from 2002. The National Land Survey of Sweden (Lantmäteriet) has generalized the original raster map to define habitats only if they exceeded a certain area. In the case of the habitats present in this study area, the minimum size to define a habitat patch was 1 hectare. To improve the power of the analysis I combined the 24 SMD habitat categories found in the area into 9 habitat classes, based on similarity in plant community composition and other attributes that I regarded as important to a bear. Some classes show less similarity, but were too small to be considered independently. (For SMD habitat classifications, see Ahlcrona, 2003).

The habitat classes are:

Human (Hu) – villages, houses or pastures (SMD classes 5, 6, 10, 30 and 32). Mean patch size 49 591 ± 3794 m² (± SE), median patch size 37 500 m².

Water (Wa) – Water, including watercourses, lakes and ponds (SMD classes 80, 81 and 82). Mean patch size 108 984 ± 18 931m² (± SE), median patch size 20 625 m².

Mix-Deciduous (MD) – Broadleaved and mixed forest (SMD classes 40, 41, 48 and 49). Mean patch size 26 148 ± 700 m² (± SE), median patch size 18 125 m².

Conifer-poor (CP) – Coniferous forest on less productive ground (SMD classes 43, 46 and 47). Mean patch size 35 930 ± 1 111 m² (± SE), median patch size 18 750 m².

Conifer-short (C<15) – Coniferous forest with tree height 5 - 15 metres (SMD class 44). Mean patch size 65 361 ± 2 847 m² (± SE), median patch size 23 750 m².

Conifer-tall (C>15) – Coniferous forest with tree height >15 metres (SMD class 45). Mean patch size 173 759 ± 28 206 m² (± SE), median patch size 27 500 m².

Clear-cut (CC) – Clear-cut, open or with re-growth < 2 metre (SMD class 54). Mean patch size 103 635 ± 4 400 m² (± SE), median patch size 33 125 m².

Young forest (YF) – Young forest, tree height 2 - 5 metre (SMD class 55). Mean patch size 86 578 ± 5 485 m² (± SE), median patch size 24 375 m².

Mire (Mi) – Mires (wet and other) and inland marshes (SMD classes 70, 71 and 72). Mean patch size 70 994 ± 9 394 m² (± SE), median patch size 23 125 m².

ArcGIS 9 (Environmental Systems Research Institute, Inc., California, USA) was used to extract the available and used habitats for the analysis. Available habitat was determined for each bear during each season as all habitats falling within their individual home ranges. I defined an animal's seasonal home range as the Minimum Convex Polygon that encompassed all locations from that animal during the specified time period (100 % MCP). Data on used habitat were extracted from imported bear location data. Arc View 3.2a (Environmental Systems Research Institute, Inc., California, USA), with the Home Range extension, was used to delineate and extract the MCP's.

2.4 Field observations

Using data that were approximately three days old (a compromise between using as recent positions as possible and avoiding disturbance of the bears), a random set of GPS-positions were drawn for each bear from a 24 hour period. We were five observers and to minimise biases from our subjective interpretations of bear-signs in the field, we rotated the bears we followed among us. The sites visited by bears were located to the nearest metre with a handheld GPS. Using this position as the centre, a plot of ca. 30 metre radius was searched systematically for all signs of bear activity. We measured the radius distance by steps and the distance to the centre was maintained visually during the search. The signs we found were beds, footprints or paths, scats, digs in anthills, tree stumps, and in ground, overturned stones, carcasses, and feeding signs on berries and herbs. We were conservative when judging the signs to obtain more reliable data. Bear signs were counted, and their freshness estimated visually (sometimes by smell) often using covered and affected vegetation as an indication. We made the assumption that a fresh sign was made by the bear we indirectly observed, during the time the GPS position was fixed. We calibrated our judgement of field signs thoroughly at the start of the study and a few times again during the field season. We made a conclusion for each plot as either a feeding or a resting site if fresh bear signs were found at a plot, and the size and/or numbers of the signs indicated a bear's main activity at the site. Plots where we did not detect any signs or the signs were too vague to be confirmed as bear signs, and plots where bear signs gave no good indication of the bears' main activity were classified separately as "no sign" and "un-sure", respectively.

Habitat features in the plot were classified into eight different habitat classes: Forest, Mire, Impediment, Swamp, Riparian, Water, Road and Other. The forest was further divide into sub-classes according to the stage in the production cycle, using the definitions by Karlsson and Westman (1991). We also noted if conifer trees or deciduous trees dominated in the forest classes. Sometimes a plot consisted of more than one habitat, and for analyses I have used the habitat that covered the largest proportional area of a plot. To enable an easier comparison between observed habitat categories and the classes defined by the vegetation map, I combined and reclassified some habitats, resulting in 6 habitat classes (Table 1). During the berry season the abundance of ripe berries in the plot was estimated visually into four indexed classes (none - few - medium - many). We only considered berries that bears commonly feed on; blueberries (*Vaccinium myrtillus*), lingonberries (*Vaccinium vitis-idaea*), crowberries (*Empetrum hermaphroditum*), and raspberries (*Rubusdaeus*).

Table 1: The habitat classes from the field observation plots in Dalarna, central Sweden (Clear-cut +/- re-growth refers to classes K1, K2 and R1 in Karlsson and Westman (1991); Pre-Commercial Thinning refers to class R2; and Mid-aged and Mature forest refers to G1 and S1 respectively)

Class	Description
Deciduous (Dec)	Deciduous-dominated habitats from the Mid-aged forest and the Pre-Commercial Thinning classes. Generally rather dense - very dense habitats.
Mature forest (Mat)	<10 years remaining until harvest (age ca 80 - 90 years for forest in study area). Generally rather spacious, with limited undergrowth.
Mid-aged forest (Mid)	Average tree stem > 10 cm diameter at breast height, age ca 25 - 70 years. Deciduous-dominated habitat excluded. Generally rather dense with tree sizes and ages mixing.
Clear-cut +/- re-growth (Cc)	Open or planted with the average tree < 1.3 metre tall. Generally very open habitat.
Pre-Commercial Thinning (PCT)	Average tree > 1.3 metre tall and tree stem < 10 cm diameter at breast height. Deciduous-dominated habitat excluded. Generally rather dense - very dense habitats.
Mire-Impediment (M-I)	Mire or Impediment (Impediment = low productive area with very sparse tree growth on peat-dominated ground). Generally very open habitat.

2.5 Data analysis

I used bear relocations estimated from GPS telemetry, from which I expected a general precision with an error less than 30 metres. To decrease autocorrelation for the overall seasonal habitat use, bear locations taken approximately every fifth hour were used. We observed that bears could travel > 2 km in 30 min. Thus I assumed that bears, if they wished, could easily traverse various habitats during a time span of 4 - 5 hours in this patchy landscape where the mean habitat patch was less than 200 m across (≤ 0.1 % of the habitat patches exceeded 2 km across). In addition, using bear relocations from every fifth hour resulted in an un-biased dataset regarding the time of day each fix was taken. A selected (every 5th-hour) fix that had failed was interpolated to the nearest (in time) successful fix. If the bear had been passive all times before or after the failed fix, the nearest successful fix during a passive bout was used as I assumed that the bear had stayed and rested at the given site. I suggest that this method of interpolating fixes within a passive bout lessened the bias against habitats for which a combination of habitat and behaviour negatively impacts the GPS fix attempts. When analysing diel period habitat use, a random set of 10 relocations per bear and day was used. When performing selectivity analyses for separate habitats during the diel periods, I deemed autocorrelation to be less of a problem as it compared habitat use on a finer scale, where available habitat was defined as all habitats used during all times of the day.

Before analysing habitat selection I separated the study period into two seasons, and tested the homogeneity in frequency of relocations in each habitat class between seasons with a χ^2-test of independence. The analyses were conducted for all bears combined and for each bear separately. Habitat selection during each season was analysed with a χ^2-test (Neu et al. 1974, White and Garrott 1990, Manly et al. 2002). The formal null hypotheses with the Neu et al. (1974) χ^2-test method are that (H_1) usage occurs in the proportion to availability considering all habitats simultaneously and that (H_2) usage occurs in proportion to availability, considering each habitat separately. Each bear was tested against its individual habitat availability (home range) using a $\log_e \chi^2$ calculation recommended by Manly et al (2002, p. 77), a more conservative version of χ^2-test. A test for all animals combined was conducted by adding the $\log_e \chi^2$values and the degrees of freedom from each bear, as described by White and Garrott (1990, p. 190). Habitat use during the different diel periods were tested for homogeneity using a χ^2- test of independence. To define whether an individual animal selected for or against a habitat in relation to habitat availability, a Bonferroni adjusted confidence interval was used with a corrected z-value (Neu et al. 1974, p. 544, White and Garrott 1990, p. 188). For the correction of the z value I used $\alpha = 0.10$, as suggested by Neu et al. (1974). Available habitat for the selection analysis of seasonal habitat use was defined as the habitat composition within each bear's home range. For the diel period habitat use, available habitats were defined by the composition of all the habitats used in the randomly selected data for diel period use (i.e. 10 positions per day and bear).

The analysis of selection for or against a certain habitat with the above method can only be made for each individual bear, thus for an indication of a general seasonal habitat use for all bears I tested how bears' mean preference indices (i.e. an average for all bears) diverged from a value of 1, and how it differed between seasons. The preference index is the ratio of the proportion used to the proportion available for a habitat, where values > 1 and < 1 indicate selection for and against a given habitat, respectively, and a value = 1 indicates no selection (Manly et al. 2002). I also tested the divergence of the mean preference indices against a value of 1 for habitat use during the different diel periods. A mean preference index for e.g. habitat i during diel period $A = 1$ indicates that habitat i is used more or less equally during period A compared to the total use of habitat i, and values > 1 and < 1 indicate a relatively higher and lower use, respectively, of habitat i during diel period A.

I used the non-parametric Wilcoxon (or Kruskal Wallis if more than two categories are compared) rank sum tests to compare means between categories, and Wilcoxon Signed Rank test to test means of the preference indexes against a hypothesised value of 1. The Wilcoxon and Kruskal Wallis tests are performed in JMP IN™ 5.1, SAS institute 1989. To define significance, $\alpha = 0.05$ was used, although because of a small sample size also higher α-values will be considered biologically relevant. The categories **Human** and **Water** were excluded from the χ^2-tests because of limited coverage (Table 2) (resulting in expected values <<5), and bear relocations in these habitats were few or none. Thus I regarded them as un-available to bears. Also I aimed to avoid an inflated type I error that an inclusion of a highly avoided habitat (such as **Human**) may lead to (Manly et al. 2002).

3 Results

In general, the GPS-GSM technology worked well, although the collar on one bear (W 0209) functioned poorly and her data were excluded from further analyses. More data on GPS performance are presented at the end of Results. The individual bear's age, size of home range and its proportional habitat availability for the two seasons are presented in Table 2.

Table 2: The ages of the individual brown bears, the size of their home ranges (100 % MCP), and the proportional availability of the different habitat classes within the mating and berry season home ranges. MD = Mix-Deciduous; CP = Poor-Conifer; C<15 = Conifer-short; C>15 = Conifer-tall; CC = Clear-cut; YF = Young Forest; Mi = Mire; Hu = Human; Wa = Water.

Bear	Age	Season	HR (km^2)	Available habitat (%)								
				MD	CP	C<15	C>15	CC	YF	Mi	Hu	Wa
W 0109	10	mating	306	1.3	11.2	11.2	39.2	11.9	4.2	12.8	0.4	7.7
		berry	135	1.1	10.2	11.1	41.6	11.5	4.0	12.9	0.5	7.1
W 0323	4	mating	309	2.8	1.3	23.6	25.2	6.3	17.0	20.3	0.2	3.2
		berry	162	3.9	1.2	26.1	24.4	5.8	19.1	18.6	0.1	0.8
W 0004	9	mating	197	2.5	6.0	18.3	20.4	16.1	17.9	18.1	0.2	0.6
		berry	181	3.4	7.2	20.0	21.3	16.4	17.6	13.0	0.3	0.9
W 0208	3	mating	129	1.6	11.9	17.0	29.7	21.1	8.0	6.2	0.7	3.9
		berry	104	1.8	12.7	18.7	26.7	21.8	8.6	4.7	0.8	4.1
W 0229	6	mating	227	2.9	5.6	18.1	30.0	12.4	18.5	11.5	0.2	0.8
		berry	131	2.9	4.0	18.9	34.1	11.6	19.5	8.1	0.3	0.6

3.1 Seasonal habitat use

The bears used habitats differently during the mating season and the berry season (Table 3). Moreover, testing individual bears showed that four out of the five bears used habitats differently between seasons.

Table 3: Results from a χ^2 Goodness of Fit Test for the use of habitats (7 categories, see text) by brown bears in central Sweden during the mating and the berry seasons. (Critical values for χ^2 distribution at $\alpha=0.05$ with df = 6 is 12.6)

Bear	Mating (n)	Berry (n)	χ^2-value	df
W 0109	166	163	12.7**	6
W 0323	168	163	4.1	6
W 0004	168	163	16.4**	6
W 0208	168	163	26.6***	6
W 0229	168	163	15.4**	6
All Bears	836	812	43.7***	6

** significant at $p \leq 0.01$; *** significant at $p \leq 0.001$

When all bears were pooled, the results showed that bears used habitats within their home ranges non-randomly during both mating and berry season (Table 4). Judging from the χ^2-values and the number of habitats that were significantly selected for or against in each season (10 and 13 habitats during mating and berry season respectively), the degree of selection was higher during berry season. When looking at individual bear's habitat use, four out of five bears showed non-random habitat use during each season (Table 4). Four of the five bears selected against Mire (Mi) during each season, and the bears that did not (W 0109 and W 0208) were the same individuals that showed random habitat use during the mating and the berry season, respectively. During both seasons there were large variations in habitat selectivity among the individual bears. Many habitat classes were not significantly selected either for or against, and for some habitats the direction of selection was the opposite for different bears.

Table 4: Results from the ln χ^2-test of habitat selection by brown bears in central Sweden during the mating and berry seasons. n = number of relocations for each bear. + = selection for, and − = selection against a given habitat, as defined by a Bonferroni adjusted confidence interval. (Critical value for χ^2-distribution at $\alpha = 0.05$ with df = 6 is 12.6, and with df = 30 is 43.8). MD = Mix-Deciduous; CP = Conifer-poor; C<15 = Conifer-short; C>15 = Conifer-tall; CC = Clear-cut; YF = Young Forest; Mi = Mire.

Bear (n)	Season	ln χ^2 value	df	Habitat						
				MD	CP	C<15	C>15	CC	YF	Mi
All Bears	mating	86.3***	30							
W 0109 (n=164)	mating	1.5	6							
W 0323 (n=168)	mating	29.9***	6						+	−
W 0004 (n=168)	mating	21.1**	6	+						−
W 0208 (n=168)	mating	16.3**	6		+		−			−
W 0229 (n=168)	mating	17.5**	6		−		+			−
All Bears	berry	97.2***	30							
W 0109 (163)	berry	13.5*	6				+			−
W 0323 (163)	berry	23.5***	6	+						−
W 0004 (163)	berry	28.9***	6	+	−					−
W 0208 (162)	berry	6.7	6			+				
W 0229 (161)	berry	24.7***	6		−		+	−	+	−

* significant at $p \le 0.05$; ** significant at $p \le 0.01$; *** significant at $p \le 0.001$

The tests of mean preference indices indicated how bears in general selected for or against different habitats. Preference indices diversion from a hypothesised value of 1 were not significant at the pre-defined $\alpha = 0.05$ level (Table 5), though there were strong tendencies for Young forest (YF) and Conifer-short (C<15) to be selected for during mating and berry season, respectively, and Mire (Mi) and Clear-cut (CC) to be selected against during both seasons and during the berry season, respectively (Fig 2). Mixed-Deciduous (MD) had the highest mean preference value, though it did not significantly diverge from a value of 1. The most abundant and most used habitat, Conifer-tall (C>15), had a mean preference value very close to 1, i.e. it was used according to its proportional availability.

Table 5: Results (p-values) from Wilcoxon Signed Rank test of the mean preference indices (from all brown bears) against a hypothised value of 1, and a Wilcoxon Rank Sum test of the mean preference indices between the mating and the berry season. MD = Mix-Deciduous; CP = Conifer-poor; C<15 = Conifer-short; C>15 = Conifer-tall; CC = Clear-cut; YF = Young Forest; Mi = Mire.

Season	Test	p-value						
		MD	CP	C<15	C>15	CC	YF	Mi
mating	mean to value 1	0.31	0.81	0.44	1	0.63	0.06	0.06
berry	mean to value 1	0.13	0.13	0.06	1	0.06	0.19	0.06
both	Between seasons	0.40	0.40	0.04*	0.83	0.09	0.53	0.33

* significant at $p \le 0.05$

Between seasons, the bears' preference for Conifer-short (C<15) was significantly higher during the berry season, and during the same season they showed a strong tendency for a lower preference for Clear-cut (CC) (Table 5, Fig 2). Results from the remaining habitats were insignificant, though there was a large difference in mean preference indices for Mixed-Deciduous (MD) between seasons, a habitat that appeared more favoured during the berry season.

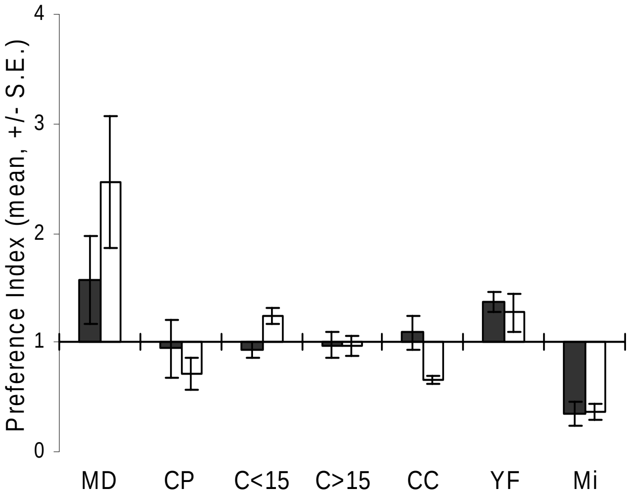

Fig. 2. The preference indices (= prop. used/prop. available) for each habitat category shown as a mean from all bears. A preference index =1 indicates random use, <1 indicates selection against, and >1 indicates selection for a given habitat. Black columns and white columns show values from the mating and the berry season respectively. MD = Mix-Deciduous; CP = Conifer-poor; C<15 = Conifer-short; C>15 = Conifer-tall; CC = Clear-cut; YF = Young Forest; Mi = Mire.

Thus, the bears' selectivity of habitats in general, and between seasons, confirmed my predictions; that habitat use differed between seasons and that habitats were used non-randomly, particularly during the berry season. There were large variations among the individual bears, and few habitats stood out as particularly important or avoided.

3.2 Diel period habitat use

As there was a significant difference between habitat uses during the mating and the berry season, seasons were kept separate in the following analysis. The results from the test of all bears showed that habitat use differed between the diel periods, during both seasons (Table 6). The test of individual bears identified a difference in habitat use during different diel periods for three out of the five bears during the mating season, and for all bears during the berry season (Table 6).

Table 6: Results from the χ^2 Goodness of Fit Test for the use of the 7 habitat categories (see text) by brown bears in central Sweden during the different diel periods. n = number of relocations during each diel period. (Critical values for χ^2-distribution at $\alpha=0.05$ with df = 18 is 28.87)

Bear	Season	Night rest (n)	Morning active (n)	Day rest (n)	Evening active (n)	χ^2-value	df
All Bears	mating	215	405	691	430	78.75***	18
W 0109	mating	37	75	141	88	22.48	18
W 0323	mating	47	84	141	78	63.39***	18
W 0004	mating	48	80	132	90	43.06**	18
W 0208	mating	42	82	133	93	21.86	18
W 0229	mating	41	84	144	81	51.74***	18
All Bears	berry	185	461	502	551	85.58***	18
W 0109	berry	37	95	95	113	34.55**	18
W 0323	berry	47	84	101	108	34.42**	18
W 0004	berry	38	104	86	112	63.72***	18
W 0208	berry	35	77	116	111	42.99***	18
W 0229	berry	28	101	104	107	42.67***	18

* significant at $p \leq 0.05$; ** significant at $p \leq 0.01$; *** significant at $p \leq 0.001$

The selectivity for or against habitats varied much among individuals, though there were no occasions where bears made opposite selection for a habitat during the same diel period (Table 7). Most significant selection occurred during the day rest period in both seasons. Some habitats, e.g. Conifer-tall (C>15), were selected both for and against depending on diel period.

Table 7: Habitat selectivity of individual brown bears in central Sweden during the four different diel periods, defined by a Bonferroni adjusted confidence interval. + = selection for, and − = selection against a given habitat. Bears are identified with the letters a - e; W 0109 = a, W 0323 = b, W 0004 = c, W 0208 = d, and W 0229 = e. MD = Mix-Deciduous; CP = Conifer-poor; C<15 = Conifer-short; C>15 = Conifer-tall; CC = Clear-cut; YF = Young Forest; Mi = Mire.

Diel period	Season	Habitat						
		MD	CP	C<15	C>15	CC	YF	Mi
Night rest	mating				b−			
Morning active	mating				e−			
Day rest	mating	b−			b,e+	b,c−	b,e−	b−
Evening active	mating				b,c−	c+		
Night rest	berry	c−						
Morning active	berry	b−		d−			c−	
Day rest	berry				c−	a,c,d−	c+	b,c,d−
Evening active	berry							

A test of the mean preference index to a hypothesised value of 1 for each *habitat - diel period combination* identified bears' diel period habitat use in general. If an individual bear had no relocation data from a certain habitat-diel period combination, her data were excluded from the preference index mean estimate for that combination category. During the mating season (Fig. 3a) there were strong tendencies towards a mean preference index <1 for Clear-cut (CC) during *day rest*, and >1 for Young forest (YF) during *evening active* (Wilcoxon Sign Rank for both combinations; p = 0.06 and n = 5 bears). Also there were weak tendencies towards a mean preference index <1 for Young forest (YF) during *night rest*; <1for Conifer-tall (C>15) during *morning active*; >1for Conifer-short (C<15) during *day rest*; <1 for Conifer short (C<15) and >1 for Clear-cut (CC) during *evening active* (Wilcoxon Sign Rank for all five combinations; p = 0.13 and n = 5 bears). The remaining habitat-diel period combinations showed less or no tendencies of mean preference indices $\neq 1$ (Wilcoxon Sign Rank; $p \geq 0.19$).

During the berry season (Fig. 3b) there were strong tendencies towards a mean preference index >1 for Clear-cut (CC) and >1 for Mire (Mi) during *morning active*, and >1 for Mix deciduous (MD) during *day rest* (Wilcoxon Sign Rank for all three combinations; p = 0.06 and n = 5 bears). Also there were weak tendencies towards >1 for Conifer-poor (CP) and <1 for Young forest (YF) during the *night rest*, and <1 for Clear-cut (CC) during *day rest*. (Wilcoxon Sign Rank for all three combinations; p = 0.13 and n = 4 bears). The remaining habitat-diel period combinations showed less or no tendencies of a mean preference index ≠ 1 (Wilcoxon Sign Rank; p ≥ 0.19).

The four diel periods relate to the bears' predominant behaviours; resting and active. As predicted, bears' selection of habitats during the four diel periods differed, indicating that bears used different habitats for different behaviours, though there were large variations among the individual bears.

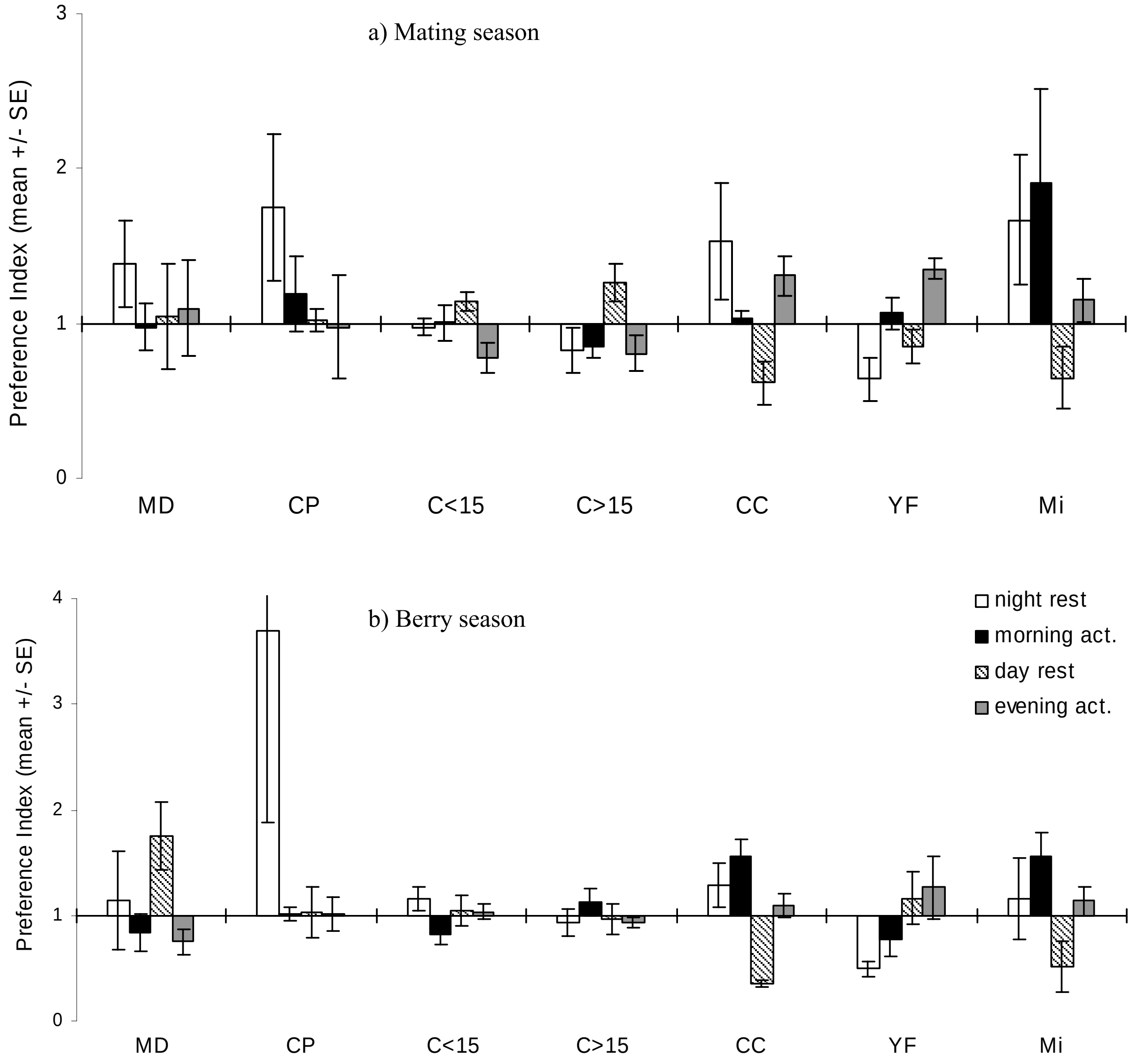

Fig. 3. The mean preference indices (±SE) from all five brown bears combined for each habitat during each of the four diel periods during the a) mating season and b) berry season. MD = Mix-Deciduous; CP = Conifer-poor; C<15 = Conifer-short; C>15 = Conifer-tall; CC = Clear-cut; YF = Young Forest; Mi = Mire.

3.3 Bed site habitat use

We experienced great difficulties in detecting and confirming certain signs in the field, especially signs from bears' berry feeding. Therefore I judged our indirect observations of feeding as too biased against certain feeding activities to be further analysed and only habitat used by bears when resting were tested. In total 158 plots with confirmed beds were found (ranging between 22 - 46 plots per bear). Due to a limited sample size, the whole field season and all bears were pooled into one test. The habitats bears used for resting were significantly different from the habitat available in all observed plots visited by bears ($\chi^2 = 26.58$, df = 5, $p \leq 0.001$). For resting sites, bears significantly selected for Deciduous dominated forest, against Clear-cuts, and against Mire-Impediment (significance defined by the Bonferroni adjusted confidence intervals).

The resting plots were divided into day-beds (124 plots, n = 17-30 per bear) and night-beds (34 plots, n = 1-16 per bear). The habitats used for day-beds were significantly different from those used for night-beds ($\chi^2 = 32.56$, df = 5, $p \leq 0.001$, Fig. 4). Especially the Mature forest was more favoured as a night resting habitat, whereas the Pre-Commercial Thinning (PCT), Mid-aged (Mid) and Deciduous dominated forest (Dec) were more used during the day rest. Only three beds were found in the Clear-cut (Cc) habitat, all these were night-beds. Thus my predictions that bears would choose denser habitats while resting during the daytime, and more open areas while resting during the night time, were confirmed.

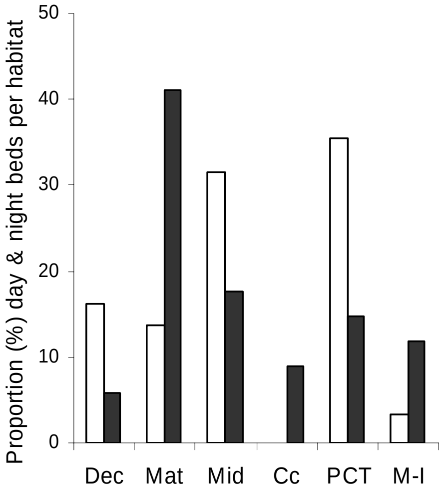

Fig. 4. Habitats used by brown bears in central Sweden for resting, separated into day- and night-beds (white and black columns respectively). Dec = Deciduous (n = 22), Mat = Mature forest (n = 31), Mid = Mid-aged forest (n = 45), Cc = Clear-cut +/- re-growth (n = 3), PCT = Pre-Commercial Thinning (n = 49), and M-I = Mire-Impediment (n = 8).

3.4 Observed food abundance in habitats

I used signs left by bears while foraging for ants from tree stumps and anthills, and the presence and abundance of berries in our field observation plots to indicate food abundance in the different habitat categories, as these were the most obvious indicators of typical bear-food abundance. Most tree stumps opened by bears (with fresh and old bear signs) were found in the Pre-Commercial Thinning forest (5.1 ± 0.4, mean number of opened tree stumps per plot ± SE), followed by Clear-cut +/- re-growth (3.8 ± 0.8) and Deciduous forest (2.9 ± 0.8). The mean number of opened tree stumps in the remaining three habitats was less than 0.9 per plot. The mean number of anthills used (with fresh and old bear signs) did not differ much among the habitats, ranging from 0.5 - 0.2 per plot (Mire-Impediment and Deciduous forest respectively). We found the occurrence of berries to be rather widespread and the richness varied greatly from plot to plot. As a whole the highest berry abundance was found in Mature forest and Clear-cut +/- re-growth, followed by the Mid-aged forest. The Deciduous forest had the poorest availability of berries.

3.5 Performance of GPS

The GPS-GSM technology generally worked well, and we received data from most bears on a daily basis. Of the programmed 48 fix attempts per day 47.9±0.04 (mean ± SE) were received for five of the six bears. The GPS-GSM collar on the sixth bear (W 0209) periodically malfunctioned seriously. Only 25.3±1.93 (mean ± SE) fix attempts per day were taken on this bear, including a three-week period with almost no fix attempts. Thus she was excluded from all analyses.

We detected fresh bear signs at 67 % of the 1057 field plots, centred around a bear's GPS relocation, throughout the whole field study. Separating the period into mating, intermittent period and berry season we found fresh signs at 67, 74 and 64 % of the plots, respectively. The proportion of successful GPS fixes decreased significantly during the study period (Kruskal Wallis: $p < 0,001$. Fig. 5). During the whole study period the overall success rate was 76±0.36 (% mean ± SE). Separated into periods the success rate was 85 %, 74 %, and 68 % during mating season, intermittent period (27 days), and berry season, respectively. The fix success varied some among the individuals, and the range in success rate during mating season, intermittent period and berry season was 78 – 88 %, 72 – 77 %, and 65 – 73 %, respectively. As bears' activity level influenced GPS success rate, I summarized the mean proportion of active states for all bears during the three periods: mating season, intermediate period and berry season (Fig. 6). There was a tendency for a difference among seasons (Kruskal Wallis: $p = 0.08$), with a lower proportion of active status during mating season compared with the other periods.

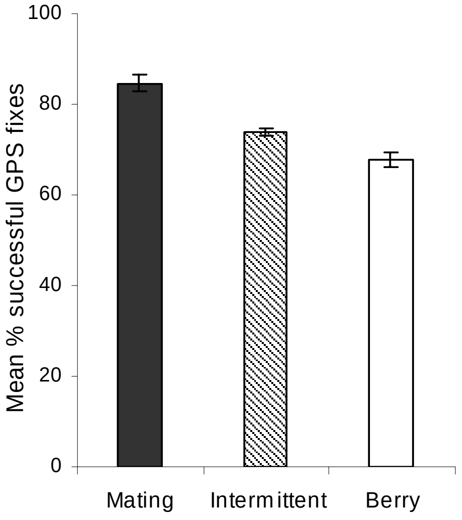

Fig. 5. The proportion of successful fixes, as a mean from five brown bears in central Sweden, decreased significantly during the study period. The length of the mating season (black column), intermittent period (dashed column) and berry season (white column) were 35, 27 and 34 days respectively.

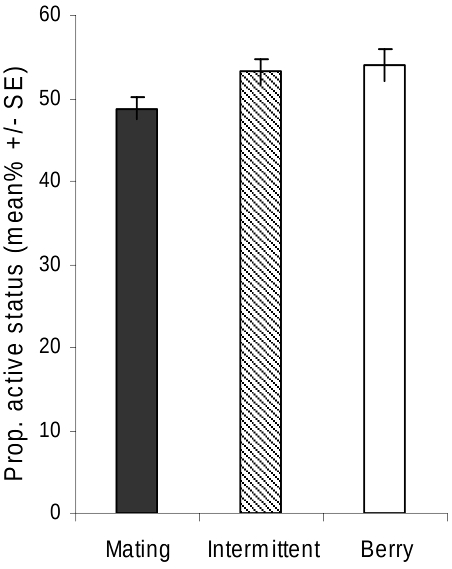

Fig. 6. Registration of active status as a proportion of the three types of activity modes: passive, active and un-defined activity state, during each season as a mean from five brown bears in central Sweden. The length of the mating season (black column), intermittent period (dashed column) and berry season (white column) were 35, 27 and 34 days respectively.

There was a strong relationship between bears' level of activity and the success GPS fixes, where bears were mostly passive during the occasions when a fix attempt failed. Activity data was obtained in 90 % of the 5 minute intervals surrounding a fix attempt. These activity data showed that bears were passive in 83±3.6 (% mean ± SE) of the occasions when a GPS fix attempt failed (including W 0209, the value was 78±5.6 %). The success rate followed the bears' activity pattern during a 24-hour day. Activity data indicated a cyclic activity pattern, with a shorter passive period after midnight and a longer passive period during the middle of the day. During the two periods in-between, the bears were more active (Fig. 7). This pattern was similar among individuals and between seasons, though the dominating active and passive bouts were more conspicuous during the berry season.

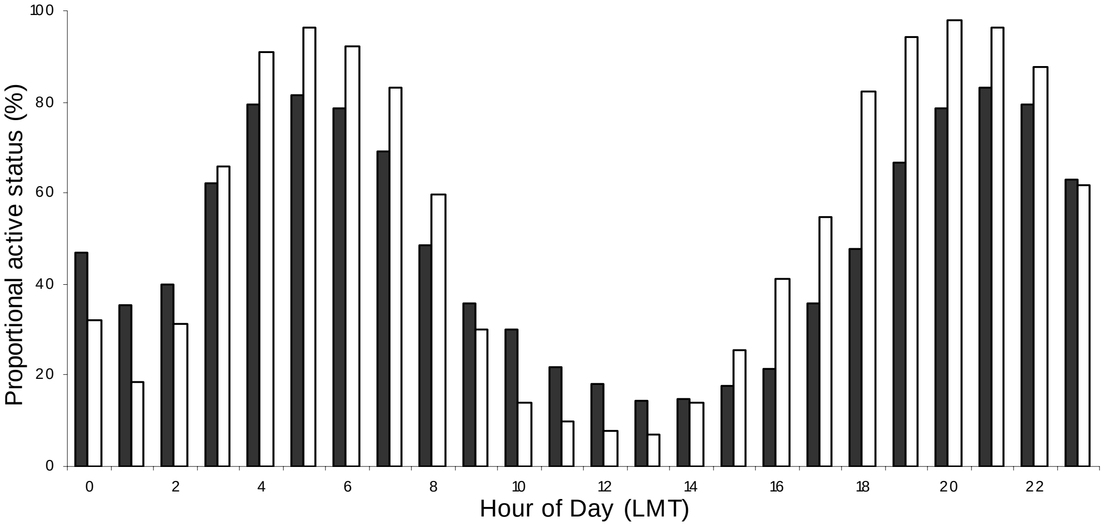

Fig. 7. The activity status of brown bears in central Sweden during each hour of a 24-hour day as a proportion of the three activity modes from all five bears combined. The proportion from the un-defined activity mode was negligible (≤ 5.8 %, mean 3.7 %) and varied little among the hours. The black and the white columns show the mating and berry season, respectively.

4 Discussion

Bears used habitats within their home ranges non-randomly, and their use of habitats varied between seasons, which confirmed my predictions based on earlier studies of animals in general, and bears in particular. The selection I found by these bears in central Sweden confirmed earlier predictions from the same area; that bears in general tend to avoid mires and prefer forest (Katajisto, Moilanen and Swenson, unpublished manuscript, Swenson and Sandegren 2000). Bears showed some selectivity for habitats with richer food abundance, though the selection for shelter (mainly expressed as avoidance of open habitats) appeared to be a stronger decisive factor for bears' choice of habitats. Bears appeared to be less selective during the mating period than during the berry season, which confirms my prediction based on variations in major diet and behaviour during the two seasons. Frequent relocations allowed an analysis of differences in habitat use depending on the time of day, and as predicted the bears' habitat use during the four diel periods differed. Bears were most selective during the longer day rest period, when especially selection against more open habitat types was obvious. Additionally, I found that bears used different habitats for their day versus their night resting sites, and, as predicted, the habitat used most frequently for day-bed sites are those that offered better shelter. This confirmed my predictions, based on known ecology of the bear as a shy, omnivorous species that seeks shelter when resting (e.g. Sandegren and Swenson 1997, Servheen et al 1999)

There were large variations among the bears in this study which made it difficult to detect important habitats and resources for bears in general when sampling just a few individuals. These variations cannot be explained by the proportional habitat availability in their home ranges, which Mysterud and Ims (1998) have suggested as a cause for variation in observed selectivity. Nor can it be explained by sex or reproductive status as the bears belonged to the same sub-group within a population; lone, sexually mature females. Similar to this study McLellan and Hovey (2001) found no effect of sex and age on grizzly bears' habitat selection, but instead found a large individual variation. Large individual variations in bears have been commented on by others, e.g. Craighead (1998) and Nielsen et al. (2002). In this study four out of the five bears used habitats non-randomly during both the mating and the berry season, and all of these bears selected against mires. The individual bears' selectivity for the other habitat categories showed little consistency, and in comparison the selectivity were more similar during the berry season than during the mating season.

Bears' non-random use of the their habitats was also documented in all the habitat selection studies of bears I have reviewed; Servheen 1983, Waller and Mace 1997, Craighead 1998, Kobler and Adamic 2000, McLellan and Hovey 2001, Stratman et al. 2001, Belant and Follmann 2002, Nielsen et al. 2002, Lyons et al. 2003, Wielgus and Vernier 2003, Apps et al. 2004. Six of these studies also compared seasonal habitat use, and all of those documented different use of habitats between seasons, similar to results from my study. All these studies relate the selection of habitats to food availability and many also discuss the habitats value for the cover it provides. The general selection I found, based on mean preference indices from the five bears, revealed the same patterns. However, the results from individual bears' habitat use during the active parts of the day - times when bears would be most actively feeding - showed only a significant selection *for* habitats for one bear (which selected for clear-cut in the *evening active* period, during the mating season). Hence, bears' choice of habitats appeared less based on food availability. This is also what one would expect from bears as omnivores, utilising a number of different food sources of which many are widespread throughout a number of habitats. The lack of significant selection for habitats can also have been an effect of the selection analysis method, where a habitat that is dominantly used will not be regarded as selected for if it is also a dominant habitat within the study area (Mysterud and Ims 1998). Or perhaps the limited selectivity indicates that, as a whole, bears do not perceive any great variation in the habitats available within the boreal forest landscape in this study area in central Sweden.

4.1 General habitat selection – mating season

In general, the bears showed a selection for Young forest and a selection against Mire in the mating season. This is a period when ants (Swenson et al. 1999) and moose calves dominate bears' diet in this region (Johansen 1997, Dahle et al. 1998). Bears forage on ants in tree stumps and in anthills. Ants that inhabit tree stumps and other woody debris (including the preferred *Camponotus* spp.) are common on clear-cuts, with highest ant density in clear-cuts aged 10-20 years (Bauhaus 2003). This is consistent with our findings of the highest density of bear-opened tree stumps in Pre-Commercial Thinning forest, followed by Clear-cut +/- re-growth (matching the Young forest and the Clear-cut from the vegetation map). The mean number of opened anthills was rather similar throughout the habitat types. Most of the Young forests in this region are replanted clear-cuts, with trees between 2-5 m height, habitats that are often dense - very dense. Hence this habitat provides bears with both a rich supply of ants and shelter. The observation of a relatively higher use of Young forest during the active periods of the day during the mating season suggested its importance as a feeding habitat during the early spring-summer. Bears avoidance of mires was probably due to both lack of food and shelter. Though not so numerous, the highest mean number of opened anthills per plot were found in Mire-Impediment habitat. However, bears never seemed to have made any major foraging effort on the relatively small anthills present in Mire-Impediment, which leads me to the assumption that ant species commonly inhabiting mires are less preferred by bears. Clear-cuts are often reported as a habitat avoided by bears (e.g. McLellan and Hovey 2001, Bauhaus 2003, Wielgus and Vernier 2003). My result from the mating season contradicted these findings somewhat, as some bears showed a slight preference for clear-cuts. The use of clear-cuts occurred mainly during the night (the *night rest* and *evening active* periods), and very likely it was the abundant supply of ants that attracted the bears, but the lack of shelter led bears to avoid this habitat during day time.

4.2 General habitat selection – berry season

In general, bears showed a selection for Conifer-short and a selection against Clear-cut and Mire. There were also weak tendencies towards a selection for Mix-Deciduous and against Conifer-poor. As berries are such an important food supply during late summer and autumn, bears would presumably spend much time in habitats with a high abundance of ripe berries. A study of berry abundance and bears' consumption of berries in central Sweden (Jigsved 2003) showed that plots visited by bears had a richer berry supply than random plots. We observed the highest abundance of ripe berries in the Mature forest, Clear-cut +/- re-growth and Mid-aged forest (in that order), which is similar to the observations by Kardell (1980) and Jigsved (2003), except for their documentation of lower berry abundance on clear-cuts. The Conifer-short was significantly more preferred during the berry season than during the mating season, presumably due to the berries it provides in the later season. The habitats with a rich supply of ripe berries - Conifer-tall and Conifer-short (matching best to the Mid-aged forest in the observed habitat category) were more evenly used during the 24 hour day in the berry season that during the mating season. I propose this was because these habitats provide both food and shelter during the berry season. Contradictory to my prediction of selection for berry-rich habitats, bears appeared to select against Conifer-poor (matching best to the Mature forest in the observed habitat category) and Clear-cut during the berry season. Bears used the Conifer-poor habitat mainly during the night rest period. Bears' use of Clear-cut occurred mainly during the *morning active* and the *night rest* period, presumably when foraging for berries in that berry rich and open habitat. The use of Mires followed the same pattern as for Clear-cut. The tendency towards a selection for Mix-Deciduous (a predominantly dense - very dense habitat) cannot be explained by berry abundance. As bears predominantly used this habitat during the day-rest period, its importance was likely due to the shelter it provides to a resting bear.

4.3 Degree of selectivity – mating vs. berry season

With a roaming behaviour, a bear would presumably be encountered more often in any habitat that it is not specifically selecting for, as it traverses the area in search of food and/or partners. In this study I found the female bears to be less selective and to use larger home ranges during the mating season compared to the berry season. I also observed that bears made more long distance movements during the mating season than during the berry season. This supports the expectation of a greater roaming behaviour during mating season. I suggest this was largely due to the seasonally dominating diets; ants and moose during the mating season and berries during the berry season. Ants and moose are rich in digestible energy, but these food items are patchily distributed in the landscape and often in limited quantities, requiring the bear to roam over larger areas in search of food. This is especially true for the predation of moose. MacHutchon (2001), who studied 5 grizzly bears by direct observation, noted that bears who fed primarily on caribou (*Rangifer tarandus*) tended to spend less time foraging and more time travelling or resting than bears who fed mostly on plant food. During the berry season the major food, berries, are widespread and often abundant, hence there is less need for bears to travel far in search of food. Also the lesser selectivity and the larger home range size used during mating season supported the conclusions by Dahle and Swenson (2003b, c) that estrous females extend their ranges during the mating season as they actively search for males to mate with. They may do so with the purpose of finding a (preferred) male to mate with, and/or because they aim to mate with a number of males. Promiscuity in females is one of the counter-strategies females use to avoid sexually selected infanticide (Hrdy 1979, Ebensperger 1998), a documented behaviour of the brown bear (Swenson et al. 2001).

4.4 Diel period habitat use

As argued by Palomares and Delibes (1992), the division of data into different diel periods and/or activities revealed different patterns of use that could not be detected from aggregated data. For example, Mire and Clear-cut were generally avoided, but the diel period analysis revealed tendencies of importance of these habitats nocturnally and during active feeding periods, particularly the Clear-cut habitat during the mating season. As in the aggregated data, bears' diel period habitat use varied much among individuals, though bears were clearly more selective during the *day rest* period. During the mating season the Clear-cut was relatively less used during the *day rest* and the Young forest was used relatively more during the *evening active*. During the berry season Clear cut and Mire were relatively more used during the *morning active* and Mix-deciduous was relatively more used during the *day rest* period. The findings both on a general and on an individual level indicated a selection against open habitats during the *day rest* period. This avoidance was not found during the *night rest* period. As noted from the proportion of active status (Fig. 7), bears were less passive during the *night rest* compared to the *day rest* period. Hence, it is likely that bears also foraged a great deal during the *night "rest"*. The findings also confirmed the frequently documented behaviour of bears' avoidance of detection during hours when humans are more active, i.e. day time (e.g.

Swenson and Sandegren 2000, Belant and Follmann 2002). I found few other studies that had divided the habitat selection into different periods. Horner and Powell (1990) did not detect any use of specific areas for certain activities (resting, foraging and traveling) within home ranges of black bears (*Ursus americanus*). As discussed by Johnson (1980), selection may differ among spatial scales. This may be the reason why my results differed to those by Horner and Powell (1990), as they compared habitat use at a larger scale (areas of intensive use to the home range). My results of relatively less avoidance of open habitats during the night were instead similar to the findings of Belant and Follmann (2002) and Servheen (1983). The former compared diurnal and nocturnal habitat use and found significant differences for some of their observed black and brown bears. Their results revealed a relative importance of more sparsely vegetated areas during the night for black bears, and brown bears' relatively higher use of deciduous habitats over shrub habitats during the day. Servheen (1983) reported from a short intensive night tracking of grizzly bears that bears traversed and foraged in open agricultural lands, a habitat they completely avoided during daytime.

4.5 Bed site habitat use

From the observation of sites visited by bears, I found that bears selected for Deciduous forest and against Clear-cut +/- re-growth and Mire-Impediment for the choice of bed sites, which conforms to the results of the day-period habitat use. Dividing these bed sites into day- and night-beds for a habitat comparison clearly indicated that Deciduous, Mid-aged and Pre-Commercial Thinning forests (all of them in general dense - very dense habitats) were more important for the day rest, as found in the results of *day rest* habitat use (see above). The Mature forest was a favored night resting habitat, as was indicated in the diel period habitat analysis, in which Conifer-poor had a tendency to be preferred during *night rest*. The typical mature forest has sparsely growing mature trees, and is thus a more open habitat with higher visibility then the habitats more favored as day-bed sites. My finding contrasts somewhat to those of Mysterud (1983), who reported proportionally more day-beds (49 %) in mature forest (aged 80 - 160 years), and secondly in the young forest (aged 30-80 years, 19 % of the beds). Mysterud (1983) detected the beds by tracking bears with a dog, thus I suspect that he could not have distinguished a night-bed from a day-bed. Many day-beds that we found were placed within immensely dense tree stands - perhaps the dog was more reluctant to lead his owner into this habitat? My results confirm the findings of Katajisto (2001), who reported differences in day-bed site selection between females with and females without cubs of the year. Her findings were that females without cubs did not select mature stands for their day-beds during the mating season, as those with cubs did, and that the bears selected areas for day-beds with relatively greater cover and visibility both during and after the mating season.

4.6 Experiences of bear behaviour study through indirect observation

The study design we used for this study enabled us to physically observe sites a bear recently had visited. Finding out *why* (i.e. for what activities) visited habitats are used, e.g. for finding certain important food types or for resting, can hopefully give more insight to the values of different habitats to a bear. The disadvantages with this method are the subjective interpretation of a bear's activity from the detected bear signs, and that the probability of detecting signs depends on the activity of the bear, vegetation at the site, and the weather between the bear's visit and the observation. We experienced that bear signs were easier to detect in dense vegetation, as hairs get caught in the vegetation, and paths become visible through more herbaceous and grassy ground layers. At the same time vegetation obscures signs that are better visible in sparsely covered areas, like bear scats. Signs of berry feeding and signs in drier habitats with sparse undergrowth were especially difficult to confirm and/or detect. Often we observed that berries had been eaten, but if the consumer had been a bear, a fox, humans or other creatures could be impossible to tell. In the beginning and the end of the study period we found fewer signs than during the middle period. I believe this was due to the seasonally dominating diets of a bear, with feeding signs easiest to detect from the typical diets of early - mid summer. The easiest feeding signs to detect were when bears had fed on carcasses, and when they had opened tree stumps to search for ants. Most foraging signs in anthills were also obvious, as were diggings in the ground, especially when they had dug out nests from ground wasps (*Hymenoptera* spp.), as wasps were still active in the disturbed nest. Detecting footprints was difficult, as many vague prints on the forest floor were impossible to confirm as bear footprints. The bears' bedding effort and type of ground layer vegetation influenced detectability of resting beds. At some of the resting sites it was clear that the bear had made an effort to make the bed, either by gathering moss, branches and other vegetation or by scraping away the vegetation to lay on bare soil. At other resting sites the bear had just simply laid down on the ground, without making a bedding effort, but the depression in the vegetation was still such that we could conclude that the bear had rested there.

4.7 GPS performance

The amount of successful relocation attempts in this study was compatible with other studies using GPS receivers. The studies of Belant and Follmann (2002) and Schwartz and Arthur (1999), using GPS receivers on brown and black bear, both reported an overall mean success rate of 67 %, with large variations among the individual bears and between years (range10-93 and 13-96 % respectively). Bears were passive during most of the occasions when a GPS fix attempt failed, as was observed in the study by Belant and Follmann (2002), indicating that the animals' behaviour and/or habitat influenced GPS success rate. Moen et al. (2001) noted lower success rate for GPS fixes when GPS-equipped moose were active. That their results differed from the findings of this study may be an effect of the animals' behaviour (moose vs. bear) on the position of the antenna, which has a major influence on the GPS reception of satellite transmission. When a bear is resting, it often lies curled up against an object like a tree, stone or log. Thus the antenna, positioned on the top of the collar, may have limited access to signal transmissions. There was a significant decrease in GPS fix success rate during the study period from spring to late summer, a finding also reported from Belant and Follmann (2002), and Schwartz and Arthur (1999). Bears were proportionally more active later on in the study period, which contradicts behaviour as the only factor to affect fix success. Instead it supports the habitats' impact on fix success, as the vegetation grows increasingly dense as the summer goes on, and as bears were observed to use different habitats between seasons.

We found fresh bear signs from about a third of the visited plots (n=1057, including the data from the W 0209). However, during the intermittent period (June-July), when a bear's dominating diet resulted in the most obvious foraging signs, we detected fresh bear signs in 74 % of the visited plots. The reason for not finding signs could be either because we simply did not detect the signs, the bear had just passed and left no signs, or that the GPS fix was erroneous and the search area was too small to contain an imprecise GPS fix. Most beds we detected were obvious, though we may have missed as much as 30 % of the beds on sites were the activity data implied a resting period. Gervasi (unpublished manuscript) reported a lower precision of position data when bears were passive. Possibly this effected the precision of the GPS fix precision so that our 30-metre radius search areas were too small to include some of the resting beds. D'Eon et al. (2002) reported a GPS positioning accuracy ± 31m, 95 % of the time, for all fixes (i.e. for both 3D and 2D fixes). In general I believe we received a good GPS precision of the relocations in our data set, because when we found beds in bears' resting sites, the beds were usually within 10 metres from our located zero-points.

The precision of a GPS and the frequency of positioning at regular intervals are far superior to the traditional methods of radio-tracking, which is limited in both precision and frequency, and in most studies restricted to daytime relocations. Especially it allows for, or improves, studies of animal ecology and behaviour at smaller and more detailed scales. However, GPS positioning is not un-biased, and certain behaviours and habitats are under-sampled. If I (instead of selecting relocations every 5th hour and interpolating missed fixes) had used all successful relocations in my habitat selection analysis, it is very likely that the resulting selection would have been biased against the day resting habitats, when GPS fix success was the lowest. This risk of bias also has been reported too by D'Eon (2003).

4.8 Conclusions

For practical implementation in the aim to conserve a species, managers are mainly interested in the behaviour, e.g. habitat use, of the whole population. From this study I cannot draw any reliable conclusion for the bear population as a whole, as so few individuals were used. However, the results showed some general trends that I suggest should be explored in more detail. Bears' use of the habitats within their home ranges was non-random and varied between the mating season and the berry season. Also bears' use of habitats varied among different diel periods, related to their predominant active or inactive status. The bears' selective habitat use did not indicate a particularly strong selection for food-rich habitats. However the pattern of habitat use during mating season (a period when ants are an important food item) implied a selection for habitats with the richest supply of ants of the most preferred *Camponotus* genera. The wide distribution of berries in the Swedish boreal forests may be the reason why no habitat in particular was selected for during the active periods during the berry season. Habitats with highest berry abundance were the most common habitats, hence may not have appeared as selected for in the analyses that I used, even if there were preferences for these habitats. The selection appeared especially driven by bears' need of a sheltered resting site. Bears were notably more selective during the day resting period, when most bears selected against the most open habitats; clear-cuts and mires. More specifically, for their day-bed they selected for the habitats that generally gave the best shelter, whereas night-beds were more often placed in mature forest stands that offer a relatively good visibility.

4.9 Suggestions for future studies

As the bears in this study were found to use habitats differently between seasons and among different periods of the day, I suggest that also future studies of bears' habitat selection take this into consideration when possible. Normally radio tracking data are limited to daytime positions. This regular, infrequent positioning may result in large biases if animals use habitats differently depending on the time of day (Palomares and Delibes 1992), as was noted in my and in Belant and Follmann's (2002) studies. With too infrequent locations important information, especially on smaller scale habitat use, may not be detected. The advancement of the GPS technique opens up new dimensions for wildlife research, especially for more in-depth, fine scale studies of the animals' behaviours and habitats use. As an example it allows for indirect observations studies of shy animal like the bear, in landscapes were they otherwise are rarely seen. A field inventory of bear visited sites can give many new insights on bears' use of habitats and specific habitat characteristics, such as vegetation density and visibility at a smaller scale, like the patch scale. However, the interpretation of a bears' activity from indirect observations of signs in the field may be biased against certain activities and certain habitats, and would have to be considered if comparing type of activity to habitat.

The use of point data to analyse habitat selection is questionable, especially when the data contain substantial relocation errors (less problematic in studies using GPS), the habitat patch sizes are small, and where animals select for mosaics of habitats. Rettie and McLoughlin (1999) discussed this subject, and recommended the use of buffers around relocations to describe selected habitat. Habitat compositions within buffers can be analysed for example in the compositional analysis (Aebischer et al. 1993), a method that is increasingly used for habitat analysis today. A distance-based analysis of habitat use (Conner et al. 2003) is another method, particularly promising for the detection of animals' habitat use in relation to edges and distribution of habitats in the landscape. A characteristic feature of the harvested forests in Sweden is high patchiness and high edge density. Many plants and animal species are strongly influenced by and often attracted to edges, as edge habitats usually provides higher productivity and light infiltration, i.e. more food, and more protective undergrowth for shelter then more interior areas. Our experience from this summer was that bears often keep to edges between mires or clear-cuts and maturing forest stands. Lyons et al. (2003) made the same observation, often locating bears near edges of closed canopy classes during their aerial surveys of black bears. However, Poppelwell et al. (2003) reported a higher bear density in areas with lower mean edge density and greater mean patch size, which suggests selection against edges, at least on a landscape scale. I would recommend a habitat selection by bears in central Sweden to be analysed with methods that considers patch composition and edge effects. Although it has been shown that the χ^2-test (Neu et al. 1974) is well compatible with other habitat selection analyses (White and Garrott 1990, Alldredge et al. 1998, McClean et al. 1998), it can only compare data with one habitat category per relocation. I was restricted to the type of analysis I could use, as both the compositional and the distance-based habitat selection analyses use the animals as the sampling unit (Aebischer et al. 1993, Conner et al. 2003), and requires larger sample sizes than I had available for this study.

During the last centuries most boreal forests of central Sweden have gradually been converted into a mosaic of small-sized single-aged stands (mainly planted) and many clear cuts through intensification of the forest industry. Many forest-dwelling species perceive this as more or less dramatic habitat degradation. The recovery of the bears in Sweden occurred during the time of increasing forestry, hence it is very likely that the bears do not perceive the changes in the forest landscapes as negative (Swenson et al. 1998). In fact, the unusually high population growth rate observed (10 – 15 % annually, Swenson et al. 2000) in the bear population of central Sweden leaves little doubt that the habitats have provided well for the bears in this landscape. Still, there is a need to increase our knowledge about how the bears perceive the landscapes they live in, in order to find out which, if any, habitat characters limit or enhance their productivity and their expansion. For this we need data that reflect the whole population of bears, not just a few individuals from a subgroup of the population. As the variation among individuals is so large in this species, many individuals are required to receive a reliable indication of their general habitat use. Perhaps a combination of data from many individuals using infrequent and coarse-grained relocation by radio-tracking, with data from a few animals using more frequent, regular, and precise GPS-tracking, will be the most promising set-up for future studies of brown bear habitat use.

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Skoglig zooekologi

Examensarbeten (under institutionsnamnet Viltekologi)

1993:1 Olsson, Ulf. Bopredation i olika häckningsbiotoper och dess betydelse för kullstorleken hos skogshöns.
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1994:1 Seebaß, Armin. Habitat selection by common buzzards (*Buteo buteo L.*) in central Sweden.
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1995:1 Hjelm, Birger. Barkgnag och övriga stamskador förorsakade av älg i tallplanteringar.

Examensarbeten (under institutionsnamnet Skoglig zooekologi)

1995:1 Lundin, Lilian. Source-sink dynamics: a study of bank vole, (*Clethrionomys glareolus*), in wet and dry forest habitats during 1990-1994.
1995:2 Lindberg, Niklas. Skogsstrukturens betydelse för mönster i nordligt boreala fågelsamhällen samt något om fåglars lämplighet som signalsystem för biologisk mångfald.
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1998:2 Rooke, Tuulikki. Responses to simulated browsing in five savanna shrubs.
1998:3 Engman, Maria C. Patterns of activity and movements in a female lynx, (*Lynx lynx*), during early nursing season in Lappland, northern Sweden.
1999:1 Sundström, David. Factors affecting tree recruitment of aspen (*Populus tremula*) in northern Sweden - the importance of browsing.
1999:2 Lodin, Lars. Morphological responses to simulated browsing on conifer seedlings and subsequent browsing by large herbivores.

1999:3 Dahl, Fredrik. Survival and spatial characteristics of wild and released mountain hares (*Lepus timidus*).
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2000:3 Näslund, Peter. Moose, (*Alces alces*) perception of aspen (*Populus tremula*) in a northern Swedish landscape – an applied test of aspen stands as patches.
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2001:4 Scheurer, Maik. Evaluation of habitat quality for moose (*Alces alces* L.) in northern Sweden.
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2002:4 Carlsson, Annica. Resting site patterns and hiding cover of female capercaillie (*Tetrao urogallus. L.*) with or without brood in the Scandinavian mountain region – diurnal perspective.
2002:5 Sandström, Frida. The effect of wildfire on flat bugs, *Aradidae* (Hemiptera, Heteroptera), in interior Alaska.
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