Monitoring and Management of the Swedish Brown Bear (*Ursus arctos*) Population

Jonas Kindberg
Monitoring and Management of the Swedish Brown Bear (*Ursus arctos*) Population

Jonas Kindberg

Faculty of Forest Sciences
Department of Wildlife, Fish and Environmental Studies
Umeå

Doctoral Thesis
Swedish University of Agricultural Sciences
Umeå 2010
Cover: Brown bear in its habitat.
(photo: Jan van der Veen)
Monitoring and Management of the Swedish Brown Bear (*Ursus arctos*) Population

Abstract
For society, there is a constant need for scientifically based information to successfully manage bear populations. In Sweden, the brown bear (*Ursus arctos*) population is increasing and expanding after successful conservation measures were employed during the 20th century. Two important issues in management are to understand how bears use their habitat, at different spatial- and temporal scales, and to estimate size and trend of the population at various scales. The central aim of this thesis was to provide management authorities with knowledge and methods for monitoring and managing the Swedish brown bear population. We have used radio-marked bears to determine the use of habitats at two different spatial- and temporal scales. To obtain population trends we used bear observations and to estimate population size we identified individual bears from DNA in collected scats and calculated the total number of bears with Capture-Mark-Recapture methods. These data were obtained with the help of volunteers and covered, in principle, the total bear range in Sweden. We estimate the Swedish brown bear population to 3,298 (2,968-3,667) individuals in 2008, and the yearly increase in the bear population to be 4.5% during the period 1998 to 2007. We show that bears prefer forest habitat in rugged terrain >10 km from towns or resorts. Bears located within 10 km of human settlements are mainly younger individuals. Bears habitat selection differs between active and resting periods. They are more active during nocturnal and crepuscular hours and rest during the daytime. My results provide management authorities with information on distribution, population size and trends of the brown bear population in Sweden, at national as well as regional scales. We have introduced and verified a method for monitoring bears, the Large Carnivore Observation Index, based on effort corrected observations of bears during hunting. We show that the bears use habitats that are further away from humans and that their use differs between sex and age groups. I recommend that the monitoring and management of bears should be carried out from an adaptive management perspective, where methods and the effects of different decisions should be continuously evaluated. For the future management of bears in Sweden, managers need good information about bear ecology, demography, and the perception of the human dimension.

Keywords: habitat, CMR, non-invasive, survey, DNA, trend, population size

Author’s address: Jonas Kindberg, SLU, Department of Wildlife, Fish and Environmental Studies, SLU, SE-901 83 Umeå, Sweden
E-mail: Jonas.Kindberg@vfm.slu.se
Dedication

To My Family
Tamisha, Jonathan and Noah

I should never have made my success in life if I had not bestowed upon the least thing I have undertaken the same attention and care I have bestowed upon the greatest.
Charles Dickens
Contents

Monitoring and Management of the Swedish Brown Bear (*Ursus arctos*)

Population 1

List of Publications 7

1 Introduction 9
  1.1 Brown bear management 9
  1.2 The species 11
  1.3 Objectives 12

2 Material and methods 13
  2.1 Study areas 13
  2.2 Geographical data 15
  2.3 Radio-marked bears 15
  2.4 Bear observations 16
  2.5 Identified individuals using DNA from scats 16
  2.6 Population estimation 18

3 Results and Discussion 19
  3.1 Habitat use on the landscape level (Paper I) 19
  3.2 Activity and habitat selection at the local scale (Paper II) 21
  3.3 Observations as a method for monitoring bears (Paper III, Paper IV) 22
  3.4 National and regional estimates of trend and population size
      (Paper IV) 23

4 General Discussion 27
  4.1 Habitat 27
  4.2 The role of volunteers in large carnivore surveys 28

5 Conclusions 31

6 Future perspectives on management and research 33

References 35

Acknowledgements 41

Swedish summary – Svensk sammanfattning 44
List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:


Papers I, II and III are reproduced with the permission of the publishers.
1 Introduction

1.1 Brown bear management

Management of animal populations can be viewed as the desire to accomplish specific goals with a given population, with focus most often on population size. The goal can be to maintain the current population size or to increase or decrease it. Harvest of certain species is important and thus goals are set for achieving a certain yield (Caughley and Sinclair, 1994; Williams et al., 2002a).

Until recently, management of large carnivores focused mainly on efforts for protecting and saving populations, reversing trends, and restoring habitats (Noss et al., 1996). Large carnivore densities are ultimately regulated by the densities of prey species, which in turn are often regulated by humans (Carbone and Gittleman, 2002). The main threat to large carnivores is the increase and expansion of the human population, which has led to reduced availability of suitable habitats, persecution, and various conflicts with humans (Weber and Rabinowitz, 1996; Woodroffe, 2000; Gittleman and Gomper, 2001). An increasing awareness and changing attitudes in the 20th century led to conservation efforts, which have been successful in some areas, including reversal of negative trends for several of the large carnivore species (Mech, 1995; Kellert et al., 1996; Linnell et al., 2001; Enserink and Vogel, 2006).

The brown bear (Ursus arctos) declined and became locally extinct across large parts of North America and Europe during the 19th and 20th century; often due in part to state-sponsored extermination campaigns (Servheen, 1990; Swenson et al., 1994; 1998a; Zedrosser et al., 2001; Clark et al., 2002). Several bear populations are now expanding or being reintroduced across most of their former ranges, but with highly variable success.
(Swenson et al., 1998b; Zedrosser et al., 2001; Servheen, 1998; Clark et al., 2002).

In Sweden the population has increased from very low levels, estimated to be only around 130 individuals in the 1930s, to a population size that today is larger than it was more than 200 years ago (Swenson et al., 1995; Paper IV). Although this resulted in an increased distribution of bears, re-colonization, especially by females, has occurred in only a portion of the former range (Swenson et al., 1994; 1998a). This is a problem commonly encountered in most places where reintroduced or expanding populations have been monitored (Clark et al., 2002).

An expanding as well as increasing bear population introduces new challenges for the management organizations (Mech, 1995; Kellert et al., 1996; Breitenmoser, 1998; Swenson et al., 1998b). Recovering from low populations and expanding into areas where they have been absent for very long times, carnivores are once again encountering humans, with a high risk for conflicts. These conflicts range from the tangible such as lethal encounters, livestock depredation, and competition for game, to the intangible, such as fear (Linnell et al., 1999; Swenson et al., 1999b; Røskaft et al., 2003; Schneider, 2006).

Managing a bear population requires a general understanding of the species’ ecology and behavior, which means that basic ecological research is needed. Abundance estimates and trends are necessary for documenting population status, setting goals, and evaluating management decisions. Identifying habitat requirements, as well as understanding their functions, is also important, because habitat is one of the major factors that regulate bear populations.

The main objective of habitat selection studies is to identify important habitats. An animal must ensure that its basic requirements are fulfilled, such as food and protection. Because one habitat normally cannot fulfill all requirements, the selection of habitats will be a balance of different qualities. For managers it is therefore essential to know which habitats are used and why animals select some habitats over others. Habitat selection can be described as an animal’s disproportionate use of a habitat in relation to its availability, and can operate at different scales, both in space and time (Johnson, 1980; Schooley, 1994; Apps et al., 2004; Nielsen et al., 2004).
1.2 The species

The brown bear occupies a wide range of habitats throughout its range, from lowlands in desert-like conditions, through boreal forests, and up to alpine areas. It has the widest distribution of any of the eight bear species, and occurs in parts of North America, Europe and Asia (Servheen, 1990; Schwartz et al., 2003).

Brown bears are omnivorous, with an extensive variety of food sources and despite their carnivorous inclination, most of their energy is obtained from berries in addition to ants, moose (*Alces alces*), grasses and herbs, depending on the seasons. Males are 1.2 – 2.2 times larger than females (Schwartz et al., 2003) and in the spring females weigh 80–110 kg and males 180–220 kg. In the fall, bears may have increased their weight by up to 20–40%. Bears hibernate in October and remain in hibernation until April. The mating season lasts from May to June (Dahle and Swenson, 2003), when a female may mate with several males and males with several females (Steyaert et al., 2010). Females are sexually mature on average at 4.5 and 5.4 years of age in the southern and northern part of the bear range in Sweden, respectively (Swenson et al., 2001).

The Swedish bear population has colonized Sweden after the last Ice Age from two directions, based on analysis of mitochondrial DNA. The population in the southern bear range is related to bears from the Iberian Peninsula, whereas the bears in the middle and the north of the bear range came from the Finnish-Russian population (Taberlet and Bouvet, 1994).

The politically determined minimum population goal in Sweden was set in 2001 to 100 yearly reproductions corresponding to about 1,000 individuals. This was supplemented by a parliament decision in 2008 stating that the population should be maintained at about current levels at the national scale, but allowed to increase or decrease at local scales, based on the local situation regarding conflicts, e.g. livestock depredation (including semi-domestic reindeer, *Rangifer tarandus*), competition for game, and problem individuals.

Hunting of brown bears has been allowed in Sweden since 1943 in a few areas and from 1981 as quotas over larger areas (Swenson et al., 1995). Harvest quotas have increased from 55 in 1999 to 233 in 2008. From 2010 quotas are set by the county administration for each of the regions.

For more information on the Swedish brown bear population, visit the home page of the Scandinavian Brown Bear Research Project [www.bearproject.info](http://www.bearproject.info)
1.3 Objectives

In this thesis I address questions which are of importance for monitoring and managing brown bear populations: methods for monitoring population trends and assessing population size, as well as habitat requirements at two different spatial and temporal scales.

My main objectives are to:

1. Study how bears use habitat at the landscape scale in relation to human disturbance (Paper I).

2. Study temporal and spatial habitat selection at the home range scale and to understand bear behavior in different habitats (Paper II).

3. Test if a method used in ungulate monitoring could be used as an index of bear density at large scales, and to validate this with an independent density estimate (Paper III).

4. Estimate population trends and to calculate bear population size at the national as well as regional scales (Paper IV).
2 Material and methods

2.1 Study areas

Brown bears are distributed throughout the northernmost two-thirds of Sweden, ranging primarily from Dalarna and Gävleborg counties and northwards. Bears occur south of these counties too, but they are comparably few and mainly males. The landscape is mainly covered by boreal forest dominated by Scots pine (Pinus sylvestris) and Norway spruce (Picea abies); other common tree species are lodgepole pine (Pinus contorta), birches (Betula spp) and European aspen (Populus tremula). The remaining area is covered by bogs and lakes; agricultural areas are rare. The Scandinavian mountain range is situated in the west and more populated areas are located along the eastern coast.

The 12,128 km² study area in paper I was located in the southernmost portion of the bear range, mainly in Dalarna County (61°N, 14°E) (see Fig.1). The area was delineated by municipality and county borders or natural terrain features, such as ridges and hills.
Figure 1. Map of Sweden with counties marked with name and gray border. The study area in paper I has a white background and black border and is marked with an (A). The study area in paper II is marked with a (B) and each home range is shaded in dark gray.

In paper II we used the area consisting of the home ranges (100% minimum convex polygons) of six bears equipped with GPS-radio collars, located in the eastern part of Dalarna and western part of Gävleborg counties (61°N, 15°E) (Fig 1.).
In papers III and IV we utilized all of the counties, as both DNA-scat surveys (except Norrbotten County) and bear observations (LCOI, see below) were conducted at that scale (Fig 1.). We consider the same areas as registered for moose hunting, with some modification in the mountainous regions, as the area that could potentially be used by bears.

### 2.2 Geographical data

The study area for paper I comprised of 758 4 x 4 km squares classified as “forest” or “bog” if more than 50% of the coverage was forest or bog, respectively, estimated from 1:100,000 scale maps with contour intervals of 10 m. We further classified each grid cell according to a terrain ruggedness index (TRI; Nellemann and Thomsen, 1994) as well as to distance from towns and tourist resorts. There are six town and settlement areas, ranging in size from 3,000-11,000 inhabitants, and two major tourist resort areas with cabin resorts and down-hill skiing facilities, located within the study area.

In paper II we used habitat data from SMD (Svenska Markstäcke Data) with a pixel size of 25 x 25 m corresponding roughly to CORINE land cover maps, but with more detailed habitat classes (Engberg, 2002; 2003).

### 2.3 Radio-marked bears

In paper I we used a total of 106 (55 females and 51 males) brown bears, two years and older (i.e. post weaning), equipped with VHF-radio collars, and located within the study area from 1985 to 2002. We used positions approximated from weekly triangulations using standardized methods, from the ground or by air plane (Dahle and Swenson, 2003). To avoid locations influenced by denning behavior, we only used positions from June, July, August and September (Manchi and Swenson, 2005) and all positions were separated by at least 100 hours to avoid autocorrelation.

The six female GPS-collared bears in paper II were equipped with GPS-Plus-3 collars including activity loggers (five females), VHF units, and GSM modems (VECTRONIC Aerospace GmbH, Berlin, Germany). The position and activity status were recorded every half hour and every five minutes respectively, between 20 May and 24 August 2004. The activity index was an indication of the bears’ head movement during these five minutes. The activity index (measurements summed to between 0 and 510) of a bear at a site, was the mean of the six recordings during the 30-minute interval surrounding the time of the GPS location. Based on the
recommendations of Gervasi et al., (2006), we defined all periods where the bears showed a mean activity of <50 as passive periods and ≥50 as active periods. We divided the study period into the pre-berry (20 May – 6 July) (Dahle and Swenson, 2003) and berry seasons (16 July – 24 August), with a break between periods when berries started to ripen, to correct for seasonal patterns in behaviour and diet (McLellan and Hovey, 2001; McLoughlin et al., 2002).

2.4 Bear observations

We used effort-corrected bear observations made by moose hunters in papers III and IV, as an index of bear density. Since 1998, the Swedish Association for Hunting and Wildlife Management has collected observations of bears within the Large Carnivore Observation Index (LCOI) program during the first seven days of the moose hunt (starts in September or October, depending on county), as complementary information to their "moose observation" survey (Ericsson and Wallin, 1999; Sylvén, 2000; Liberg et al., 2010).

The moose hunters record bear sightings of young-of-the-year and older animals, length of daily hunting activity in hours, and numbers of hunters, based on hunting unit and day. Hunting is conducted during daytime from one hour before sunrise to one hour before sunset. The LCOI is calculated as number of bear observations per 1,000 observation hours for each hunting management unit, and it has national coverage, as moose are hunted over practically all of Sweden and in all bear habitat, except for national parks. This program generates approximately 4.5 million observation hours yearly (Liberg et al., 2010), of which more than 2 million hours are from the areas with bears.

2.5 Identified individuals using DNA from scats

In these studies (Paper I, III and IV), we used DNA extracted from scats to identify individuals, including their sex (Table 1.). Searches for bear scats were conducted for about 12 weeks in the autumn period starting in the end of August. Each of the counties with an established bear population has been sampled at least once, apart from Norrbotten. Samples were collected opportunistically, mainly by cooperating hunters, but even by other volunteers. Hunters picked up each scat sample with a stick of wood, and placed them into collection bottles. A different stick and bottle were used for each sample. For each scat sample, a sampling date, geographical
location, co-ordinates (Swedish RT90 2.5 gon V), as well as the hunting team’s name were recorded by the volunteers.

For every collected scat sample, DNA extractions and amplifications were performed at the Laboratoire d’Ecologie Alpine, Grenoble, France, as described in Bellemain et al., (2005) and in paper IV. Briefly, each DNA extract was first screened for species-diagnostic amplification with one microsatellite marker (Paetkau and Strobeck, 1994). Next, 6 microsatellite markers (Paetkau and Strobeck, 1994; Taberlet et al., 1997) and a sex marker (Bellemain and Taberlet, 2004), were amplified, following the multiplex pre-amplification method (Piggott et al., 2004; Bellemain and Taberlet, 2004). Amplifications were repeated four times, samples were grouped according to their genotype, and unique genotypes were then identified.

In paper I we used scat data from the study in 2001 (Bellemain et al., 2005) to verify bear habitat use in relation to distance to settlements obtained by VHF positioning. One randomly selected scat from each individual resulted in a total of 145 locations (88 female and 57 male locations) within the study area.

Table 1. Summary of brown bear scat surveys and genetic identification in studied counties in Sweden, i.e. the number of scat samples collected and analyzed, the number of samples successfully amplified for 5 to 7 loci (including the sex locus), sex ratio as percentage males and the number of unique genotypes identified.

<table>
<thead>
<tr>
<th>County</th>
<th>Survey year</th>
<th>Number of analyzed scats</th>
<th>Number of amplified scats</th>
<th>Percentage males</th>
<th>Number of unique genotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dalarna and Gävleborg</td>
<td>2001</td>
<td>1066</td>
<td>728</td>
<td>43%</td>
<td>311</td>
</tr>
<tr>
<td>Dalarna and Gävleborg</td>
<td>2002</td>
<td>838</td>
<td>665</td>
<td>42%</td>
<td>239</td>
</tr>
<tr>
<td>Västernorrland</td>
<td>2004</td>
<td>690</td>
<td>434</td>
<td>55%</td>
<td>140</td>
</tr>
<tr>
<td>Västerbotten</td>
<td>2004</td>
<td>940</td>
<td>524</td>
<td>63%</td>
<td>223</td>
</tr>
<tr>
<td>Jämtland</td>
<td>2006</td>
<td>*3000</td>
<td>2400</td>
<td>47%</td>
<td>684</td>
</tr>
</tbody>
</table>

* 3000 samples were randomly selected to be analyzed among the 5183 collected scats.
2.6 Population estimation

In paper IV we used capture-mark-recapture (CMR) methods (Schwarz and Seber, 1999; Buckland et al., 2000; Williams et al., 2002a; Amstrup et al., 2005) to calculate population size for different counties, from the number of individuals identified in each of the DNA-analyses. We used closed populations models in program MARK (White and Burnham, 1999) with each week (obtained from the collection date) used as a capture session in the analysis for capture and recapture rates. To choose the most appropriate among the defined models, we used model selection with Akaike’s Information Criterion (AICc) values and model averaging where appropriate (Burnham and Anderson, 2002). All high-ranking models included individual heterogeneity in capture probabilities and time effects, which means that there are differences in the probability to capture a bear, as well as variation over the sampling period. Heterogeneity in capture probabilities usually arises from different age and sex classes and also reproductive status (Boulanger et al., 2008). We can distinguish between females and males, but not age or reproductive status in the DNA-analysis, so differences among sexes is accounted for in the models.
3 Results and Discussion

3.1 Habitat use on the landscape level (Paper I)

Some of the major threats to brown bear populations are habitat loss and habitat fragmentation by infrastructure and human settlements (Servheen, 1990; Gibeau et al., 2002; Nielsen et al., 2004). We analyzed bear habitat use in a 12,128 km$^2$ area in the southern part of the bear range in Sweden, with data collected in 1985-2002 during the non denning period. We randomly selected 10 positions from each of 106 radio-collared bears (55 females and 51 males) and compared their habitat use in relation to resorts and towns, terrain ruggedness, sex and age of bears.

The area bears used during the non denning period increased substantially with increasing distances to towns or resorts ($R^2 = 0.94$, $p < 0.01$). The increase occurred regardless of the sex of the bears or if it was a resort or a town. The use of areas within 10 km from resorts or towns was significantly lower compared to what was available within the study area. Those bears which were observed in closer proximity to settlements (<10 km from resorts or towns) were, on average, 27 and 51% younger, females and males, respectively, than bears observed more than 10 km from any settlement (Fig. 2). This trend was most pronounced in males (mean 4.4 ± 0.4 versus 8.9 ± 0.8 years for males and 4.4 ± 0.4 versus 6.0 ± 0.2 for females).

The preferred habitat for bears encompassed forest and rugged terrain located more than 10 km from towns or resort. This habitat constituted 29% of the available area within the study area, yet we detected more than 74% of the females’, as well as 57% of all male bears’ locations in these areas. Flatter, forested terrain, far from human settlements, was used according to availability and all areas dominated by bogs were used less than expected by both males and females. Overall, 40% of the study area (4,864 km$^2$) was
classified as <10 km from towns and resorts, but contained only 9% of the female bear locations and 15% of the male locations. Older males (>7 years) were generally located beyond 10 km from major towns or resorts, with only 8% within 10 km. Within the rugged forested habitat, female bears utilized areas which were <10 km from towns and resorts 81-95% less often than comparable areas further away.

Recreational resorts are developing rapidly, typically near national parks, and they may thus limit the bear population’s expansion or fragment existing bear habitats. Together with active conservation, safeguarding undeveloped corridors of forest and rugged terrain may be important for the successful recolonization of the brown bear into its original range.

**Figure 2.** Proportion of locations of sub-adult (≤ 6 years) male and female, and adult (≥ 7 years) male and female brown bears along 5-km intervals from settlements and resorts, based on ten random bear locations per animal (n = 106) from June to September 1985-2003, Dalarna, Sweden (Paper I).
3.2 Activity and habitat selection at the local scale (Paper II)

We used 24-hour data from six female brown bears equipped with GPS-GSM collars incorporating activity loggers to analyze variations in habitat selection related to diel variations in activity (foraging and resting).

We found that the bears rested mainly during the daylight hours and foraged mainly during the crepuscular and nocturnal hours for both the pre-berry and berry season (Fig. 3).

The bears selected habitats differently when they were resting compared to foraging and the selection also differed between the two seasons (see Fig. 2 in Paper II). Poor conifers, open bog, and “Other” habitats were almost
always avoided, and young forest was always selected. In the pre-berry season, active bears selected forested bogs, clearcuts and young forest, however the forested bogs where only used during early day activity period. During the berry season bears selected mixed forests, short conifer, and young forest during both active and resting periods and avoided clearcuts.

We compared the diel habitat selection (active and resting) with the overall 24-hours general selection, where we did not take activity into account. The 24-hour study showed that bears used the available habitats non randomly during both seasons, but the pattern was different when compared to the diel habitat selection, as both resting and active locations were used together.

Thus, for studies of habitat selection, our results show the importance of obtaining data from all 24 hours and dividing these data into relevant categories based on the diel activity pattern of the bears to understand their needs for food and shelter. This is crucial for the management of any species with diel behavioral differences.

3.3 Observations as a method for monitoring bears (Paper III, Paper IV)

Observations are a common method in the monitoring of brown bears in different populations (Eberhardt and Knight, 1996; Mattson, 1997; Ordiz et al., 2007). However, these monitoring programs are rarely validated against true densities or other methods. Here we evaluated a method developed for monitoring populations of moose, based on voluntarily and systematically collected bear observations from hunters and corrected for effort, the Large Carnivore Observation Index (LCOI). We used regressions to obtain the relationship between bear observations per 1,000 observation hours and independent estimates of minimum brown bear densities from DNA-based scat surveys in a double sampling approach (Eberhardt and Simmons, 1987).
We found strong linear relationships between bear observations in the LCOI and the independent density estimates for bears at the scale of local wildlife management units (each about 1,000–2,000 km$^2$) in four regional study areas (adjusted $R^2 = 0.88–0.60$) (Fig. 4). However, the slope of the regression lines differed significantly between Västerbotten and the three other study areas.

We also verified that the LCOI accurately reflected the distribution and the known minimum density of brown bears in Sweden. The distribution of brown bears, based on results from LCOI, compared well with the distribution of harvested bears within Sweden during the same period (Fig. 2, Paper III).

These results suggest that systematic, effort-corrected reports of observed animals can be an alternative and accurate monitoring method for the conservation and management of large mammals occurring over large areas when large numbers of willing volunteers are available. We also suggest that the relationship between the LCOI and density must be established for each area.

3.4 National and regional estimates of trend and population size (Paper IV)

Estimations of size and trends of bear populations are important for management. For population estimations, a DNA–based scat survey has been
employed since 2001 in five of the six counties with established bear populations, and estimates have been calculated with CMR methods. The LCOI uses effort-corrected observations of bears by hunters during the moose hunt (> 2 million observation hours/year) and has shown a good correlation with relative density of bears using the DNA-based method (Paper III). We calculated population trends from the LCOI for the period 1998–2007 and we estimated the yearly increase in the bear population ($r$) to be 0.044 at the national level, using an exponential model. In the different counties, the population trend varied between zero and 0.097 (Table 2). Dalarna and Västerbotten had no significant trend, whereas Jämtland and Norrbotten had relatively high rates of increase. The highest growth rates were found in Gävleborg and Västernorrland, which also are considered to be expansion areas.

We calculated the population size in each county with the point estimates obtained from the CMR of the DNA survey and extrapolating them using the trends from the LCOI in an exponential population model. To take the variation from both methods into account we used parametric bootstrapping (10,000 runs) of both the estimate of trend and population size. For the northernmost county, Norrbotten, a fecal survey was lacking, so we used assumptions based on data from the neighboring county to estimate population size (Table 2). The total population estimate for Sweden was calculated by randomly adding together all the 10,000 county estimates. The total estimate was a brown bear population of 3,298 (2,968–3,667) for 2008.
Table 2. Results from brown bear population estimates based on DNA in scats and trends estimated from the Large Carnivore Observation Index (LCOI) surveys in the different Swedish counties. The trends are based on data from 1998-2007 (1998-2006 for Gävleborg) and figures within brackets are confidence limits (95%).

<table>
<thead>
<tr>
<th>County</th>
<th>DNA Survey year</th>
<th>DNA population estimate</th>
<th>Growth rate ($r$)</th>
<th>$p$</th>
<th>Estimated population 2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dalarna</td>
<td>2001</td>
<td>286 (251-337)</td>
<td>0</td>
<td>0.590</td>
<td>286 (251-337)</td>
</tr>
<tr>
<td>Gävleborg</td>
<td>2001</td>
<td>264 (232-311)</td>
<td>0.097 (0.036-0.157)</td>
<td>0.007</td>
<td>529 (352-759)</td>
</tr>
<tr>
<td>Västernorrland</td>
<td>2004</td>
<td>173 (148-249)</td>
<td>0.095 (0.022-0.169)</td>
<td>0.017</td>
<td>255 (171-364)</td>
</tr>
<tr>
<td>Västerbotten</td>
<td>2004</td>
<td>309 (265-401)</td>
<td>0</td>
<td>0.300</td>
<td>309 (265-401)</td>
</tr>
<tr>
<td>Jämtland</td>
<td>2006</td>
<td>906 (821-1043)</td>
<td>0.054 (0.019-0.088)</td>
<td>0.007</td>
<td>1009 (878-1151)</td>
</tr>
<tr>
<td>Norrbotten</td>
<td>(2008)</td>
<td>-</td>
<td>0.050 (0.021-0.079)</td>
<td>0.004</td>
<td>910 (713-1152)</td>
</tr>
</tbody>
</table>

The results from the population estimate show that the bear population in Sweden today is higher now than it has been for over 200 years (Swenson et al., 1995). The population continues to grow and expand, but has not yet reached its maximal historical area of distribution. Both the LCOI and the scat sampling rely on a huge effort provided by volunteers that was crucial considering the large areas to be covered. Our results suggest that reliable information about the brown bear population can be obtained from volunteers, using standardized protocols for data collection.
4 General Discussion

4.1 Habitat

In this thesis I have covered the brown bear’s habitat use at two different spatial scales and two different temporal scales. Both of these spatio-temporal scales are important for the management of brown bears (Gibeau et al., 2002; Nams et al., 2006; Ciarniello et al., 2007).

To understand the population dynamics of brown bears we need to know where they are in the landscape, in relation to resources and disturbance. This is important for predicting future expansion areas and also hotspots for conflicts, e.g. livestock depredation, competition for game species, and the fear arising from bears occurring near people (Linnell et al., 2001). Monitoring programs need information on distribution to design surveys. Bear densities can shift over short distances (Stoen et al., 2005) and not using large enough areas can bias the estimates (Woodroffe, 2000; Schwartz et al., 2003).

Human disturbance may seem low in areas with few or small towns, but the more intensive use of outdoor activities in cabin areas or resorts can equal the disturbance from a town with a much larger permanent population size (Paper I). Some habitats are not as good as others. Bears avoid open habitats and areas closer to human disturbance. Bears living in these areas might have a lower probability of survival, due to legal hunting or the higher risk of coming into conflict with humans. Human disturbance might also affect reproduction. A female that is disturbed during the denning period and leaves its den has a higher chance of losing its cubs (Swenson et al., 1997b). On the other hand, habitats closer to human settlements can be attractive both for reproducing females to avoid older males, to avoid infanticide (Mattson, 1990; Swenson et al., 1997a) and by
subadult individuals to avoid dominant adults, as well as to provide anthropogenic food resources (Mattson, 1990).

At the home range scale (Paper II) we studied how bears selected different habitats and how they used them, throughout the day and between seasons. The diel activity seems to be synchronized to avoid disturbance, with a short resting period during the night and a long during the day. The findings are in agreement with findings for adult brown bears in Slovenia and Croatia (Kaczensky et al., 2006). Habitats used during the day rest period are in denser or more protected areas (Ordiz, 2010; Martin et al., 2010). Brown bear populations in areas without or with low human disturbance in North America are more diurnal (Munro et al. 2006) than in Europe, but areas closer to humans in North America show the same nocturnal activity pattern (Gibeau et al., 2002). A similar pattern has been observed in mountain lions (Felis concolor) (Van Dyke et al., 1986). A way to explore this is to determine whether bears living in or close to national parks in Europe show a more day-active pattern. This should be possible to test in the future, as GPS-collared bears recently have been marked in these areas. For management authorities, this information is useful for informing the public about how to avoid unwanted bear contacts, for restricting activities that could cause disturbance, or to reducing the risk for livestock depredation.

Habitats are selected seasonally according to availability of food resources. In the pre-berry season, bears use clearcuts, which are a source of carpenter ants (Camponotus spp.) (Swenson et al., 1999a) and forested bogs for predation on moose calves (Swenson et al., 2007; Kindberg unpublished). In the Berry season, mature mixed conifer forests are selected. If the main goal of habitat selection studies is to find which habitats are important to bears, it is crucial to differentiate between seasonal selection for active and resting habitats.

4.2 The role of volunteers in large carnivore surveys

The monitoring of bears presented in this thesis (Paper III and IV) could not have been accomplished without the help of a large number of volunteers, in our case mainly hunters. Almost 9,000 scats have been collected to be analyzed in the DNA-scat surveys covering over 160,000 km². In addition around 1,000 bear observations are made during seven days of moose hunting each year, during more than 2 million observation hours. This has enabled us to survey most areas where bears reside, even remote ones, as this is accomplished in combination with recreational activities (hunting). The
costs for these surveys are mainly for administration and information in addition to genetic analysis (Schneider, 2006).

It is unusual for management authorities to rely on volunteers for large carnivore surveys but see Kojola *et al.*, (2006). Survey programs for other species relying on volunteers have mainly targeted bird species like the Breading Bird Survey (Johnson, 2007), large ungulates (Ericsson and Wallin, 1999; Solberg and Sæther, 1999), or, in the case of the Finnish wildlife triangles (Lindén *et al.*, 1996), both birds and mammals. It is also an advantage that an important group interested in the management of the species is directly involved in the data collection and therefore gains a higher trust in and understanding of the data (Newman *et al.*, 2003).
5 Conclusions

Based on the results from this study I conclude that:

1. The two independent methods, which we have developed and tested, are useful for monitoring the Swedish brown bear population and are able to provide management authorities with an index to follow the population trends in different areas over time and space, as well as distribution and statistically robust estimates of population size. These methods work on both a national and a regional level, the latter being where the management decisions are taking place nowadays.

2. The bear’s habitat use differs spatially and temporally, at both the landscape and home range scales. Bears avoid human disturbance at the landscape scale, using habitats that are further away from human settlements. They avoid open areas and select resting and foraging habitats differently. Their diel activity pattern seems to be tailored to minimize contact with humans by resting during the day in dense vegetation and foraging at evening and night.
6 Future perspectives on management and research

From the LCOI we can obtain population trends of the bear population in different areas. According to available data, the population has increased in several counties (Paper IV). It is important that these trends are confirmed by a second DNA survey in each of the counties in an adaptive management manner, to test the reliability of the LCOI.

At the same time that the bear population has increased, harvest quotas have increased at an even higher pace. The effect of hunting cannot be seen immediately, as the effects of reduced reproduction or infanticide take time to come into effect. As the quotas for bear hunting increase, more hunters specialize in bear hunting and may become more effective (Bischof et al., 2009). It is therefore important to target the effect of hunting on different groups of individuals, as well as where they are hunted. The presaturated dispersal in brown bears (Swenson et al., 1998a) is one explanation for the fast expansion of the brown bear population, but if females are harvested in the expansion areas this can effectively stop the expansion.

Apart from increased livestock depredation, which today is a relatively small problem (Viltskademecnter, 2010), we can expect a higher mortality in game species as adult moose in the expansion areas are more susceptible to predation (Berger et al., 2001). The Scandinavian Brown Bear Research Project has calculated the predation rate on moose calves (Swenson et al., 2007) and the effect is a reduction in the number of moose calves by 22%. However, this figure probably will change if the ratio between numbers of moose per bear is reduced.

Large carnivore management is strongly influenced by the human dimension (Linnell et al., 2001). Human attitudes are formed from several factors, usually involving education, urbanization, age, and income (Williams et al., 2002b). A generally positive attitude towards bears in
Sweden was documented in 2004, with the lowest support in rural areas and where bear densities were highest (Ericsson et al., 2008). Attitudes are more likely to change with personal experience (Williams et al., 2002b; Ericsson and Heberlein, 2003). What will happen when bears expand into the areas with higher human densities and thus directly affect a larger part of the human population (see Fig. 5)? A repeat of the 2004 attitude study, made in 2009 (Sandström and Ericsson, 2009), showed a decreased support for bears in the counties with bear populations compared to the results from 2004. The fear of bears among people also has increased; especially in areas with a high bear density and with recent expansion (Ericsson et al., 2010), suggesting that an increasing probability of encountering bears will affect the attitudes towards bears.

With bear populations expanding into areas with higher human densities, a reduced moose population, and a negative change in people’s attitudes towards bears, the conflict between bears and humans is already increasing. Perhaps it is time to determine the “conflict-based carrying capacity” of bears in Sweden and where bears should be allowed to occur in higher densities to ensure population viability and public acceptance concurrently.

Figure 5. Population expansion of brown bears in Sweden, based on effort corrected bear observations (the LCOI) for 1998-2000 (A), 2001-2003 (B) and 2004-2006 (C). Predicted suitable habitat using criteria from paper I, based on forest cover, terrain ruggedness, and areas > 10 km from villages, are shown as light gray to dark gray, where darker is better habitat for bears and areas < 10 km from villages as white (D).
References


Engberg, A. (2002) Productspecifikation av Svenska CORINE Markstäcke data. SCMD-0001. [In Swedish]


Acknowledgements

A thesis on a species like the brown bear is a product of many people. For me, it has been a long trip; visiting different parts of the scientific as well as the physical world.

I would like to thank my supervisors, Göran Ericsson and Jon Swenson for taking me in into this, supporting and encouraging me, to the end. We met long before this started and hopefully the journey does not end here. Göran, we started out as friends and ended up as colleagues. I’m equally thankful for the support in my work as for the times I spent in the spare bed in Stockholm after a night out with you and Karina. Jon, you have taken me under your wings, always trying to teach me a new aspect on science. Good thing always starts with a nice glass of whisky, as our work in the bear project.

I’m fortunate to have been a part of two research groups, with different focus, skills and views, and also belonging to two different PhD-student groups. I want to thank all the people at the department of Wildlife, Fish and Environmental studies where I was based almost to the end. We have shared the daily life at the department, from science to parties. I watched how Gert, Maria, Fredrik, Therese and Märtha all finished their PhDs. Even the newbie’s, Fredrik and Wiebke overtook me in the end but I still hope to outrun Henrik.

My other home has been the Scandinavian Brown Bear Research project where I was one of many PhD-students working on brown bears. Sven, Lena, Peter, Solbritt, Eva, Jonna, Ole-Gunnar, Andreas, Åsa, Jodie, Alice, Ali, Andrés, Richard, Marcus, Sam, Susan, Andrea, Veronica, Jon A, Pierre, Therese, Ingela, Geir-Rune, Mia, Magnus, volunteers and all others,
together we have shared discussion on bears and visits to exotic places like Deosai National Park in Pakistan, the French Alps, Asturias in Spain, Kuhmo in Finland and our study areas in Sarek and Orsa, not to forget mentioning our yearly meetings in Ås. Christian, your teaching in tactical movements is brilliant!

My co-workers at the Swedish Association for Hunting and Wildlife Management; Hans, without your patience and understanding during this period none of this would be possible. To Niklas, Göran, Markus, Daniel and Fredrik, thanks for your support in “språkgranskning” “brainstorming” “distraction” … and for keeping my spirits in good mood. To Rolf, thanks for endless discussions during our “recovering time” in the wonderful Hågådalen together with Stefán, Mats, Göran and Leif, where I learned that rubber boots rules. My friends and former collages from the research unit at Bäcklösa, in particular Tomas, Jonas and Kjell, you have played an important role in preparing me for the researcher role and you have always been there with solutions when I was faced with doubts.

I made many good friends during this period (and maybe also some enemies) but especially Christer, Ole-Gunnar and Fredrik, you have become my wingmen, in work and life!

Huge thank you to all the hunters and other volunteers for all the time you spent participating in all surveys and field work, discussions at meetings and critical evaluations. To managers at Länstyrelsen, Jägareförbundet and Naturvårdsverket for good cooperation in the strive for a better management.

My family has been very supportive. I especially want to thank the love of my life, Tamisha, your support, understanding, ……; I owe you everything you can imagine. My two man cubs, Jonathan and Noah, popped out in the middle of this chaos, unaware of a life without thesis work; you spend your days to keep me alert. Mamma och pappa, ni har alltid stöttat mig vad jag än gjort, tryggheten ni gett är grunden till mina resultat. Marcus och Daniel, att växa med två småbröder har förberett mig för det mesta i livet.

To all of you I haven’t mention; my work is the result of many people’s hard work, thank you!
I am most grateful to FORMAS, the Program for Adaptive Management of Fish and Wildlife, the Swedish University of Agricultural Sciences, the Swedish Association for Hunting and Wildlife Management, KSLA and the Scandinavian Brown bear Research Project for financial support.

All animal handling was approved by the Animal Care Committee and was carried out in accordance with the Swedish laws concerning animal research ethics. All personnel were certified according to the standards by the Swedish Animal Welfare Agency and the Swedish Board of Agriculture.
observationstimmar. Vi visar också att de bästa livsmiljöerna för björnar är områden som ligger långt bort från människor men att nytjandet av olika områden skiljer sig mellan björnarnas ålder och kön. Jag rekommenderar en adaptiv förvaltning av björn i Sverige där man kontinuerligt utvärderar resultatet av populationsövervakning och förvaltningsbeslut mot uppsatta mål. För den framtida björnförvaltningen i Sverige, behövs bra vetenskapligt baserad information om björnens ekologi, demografi, samt att man inte glömmer bort människan i systemet.
Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements


aUnited Nations Environment Programme, GRID Arendal, Fakkelgården, Storhove, NO-2624 Lillehammer, Norway
bDepartment of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway
cDepartment of Animal Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden
dDepartment of Biological and Environmental Sciences, P.O. Box 65, 00014 University of Helsinki, Finland
eNorwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway
fLaboratoire de Biométrie et Biologie Evolutive, UMR CNRS 5558 – Université Lyon 1, 43 Bd du 11 novembre 1918, 69622 Villeurbanne Cedex, France

ABSTRACT

Brown bears (Ursus arctos) are threatened by habitat loss, habitat fragmentation by infrastructure and human settlements, and have been hunted to local extinction in large areas of their former range. We analyzed the habitat use during the non denning period of 106 radio-collared bears in an expanding bear population in Sweden in relation to resorts and towns, terrain ruggedness, sex and age of bears. Bear use increased substantially with increasing distance to towns and resorts for comparable habitat and terrain types, also for independent scat surveys using DNA-analyses. More than 74% of all female bear locations were in the 29% of the terrain classified as "rugged" and located >10 km from any town or resort, whereas similar habitat closer to towns or resorts was avoided. Bears closer to larger settlements and resorts (<10 km) were on average 27–51% younger than in areas beyond (mean 4.4 ± 0.4 versus 8.9 ± 0.8 years for males and 4.4 ± 0.4 versus 6.0 ± 0.2 years for females). Sub-adult bears (<4 years) comprised up to 52% of all bear use within 10 km from resorts and settlements, likely representing exploratory dispersing individuals. These areas, however, contained only 8% of the old males (>7 years), the remaining 92% located beyond 10 km from major resorts and settlements. Recreational resorts are developing rapidly, typically near national parks, and may thus limit expansion or fragment existing bear habitats. Together with active conservation, safeguarding undeveloped corridors of forest and rugged terrain may be important for successful recolonization of the brown bear into its original range.

© 2007 Elsevier Ltd. All rights reserved.

*Corresponding author: Tel.: +47 93466713; fax: +47 61222215.
E-mail addresses: christian.nellemann@nina.no (C. Nellemann), ole.stoen@umb.no (O.-G. Støen), Jonas.Kindberg@szooek.slu.se (J. Kindberg), jon.swenson@umb.no (J.E. Swenson), ingunn@fifo.no (I. Vistnes), goran.ericsson@szooek.slu.se (G. Ericsson), jonna.katajisto@helsinki.fi (J. Katajisto), bjorn.kaltenborn@nina.no (B.P. Kaltenborn), martin@biomserv.univ-lyon1.fr (J. Martin), andres.ordiz@umb.no (A. Ordiz).
0006-3207/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
1. Introduction

Throughout its circumpolar range, the brown bear (Ursus arctos) is threatened by overhunting, habitat fragmentation and habitat loss (UNEP, 2001; Uotila et al., 2002; Waller and Servheen, 2005). During the 20th century, the development of roads, settlements, mineral exploration sites and more intensified forestry has resulted in dramatic reductions in wilderness areas and subsequent loss of undisturbed bear habitat (Gibeau et al., 2002; Kaczensky et al., 2003; Nielsen et al., 2004a,b). Anthropogenic disturbance of bears has led to avoidance of areas close to disturbance and subsequently displaced home ranges (Elgmork, 1978, 1983, 1994; Gibeau et al., 2002; Johnson et al., 2005; Rode et al., 2006). Large-scale development and associated human activity has also been documented to act as semi-permeable barriers to bear movements (Chruszcz et al., 2003). Continued fragmentation of landscapes by human activity may therefore result in small and demographically isolated carnivore populations (Tallmon et al., 2004; Proctor et al., 2005).

The brown bear became locally extinct across large parts of North America and Europe in the 19th to 20th century, often even the result of state-sponsored extermination campaigns (Elgmork, 1988, 1996; Swenson et al., 1994, 1998; Zedrosser et al., 1998; Clark et al., 2002). Bear populations are now expanding or being reintroduced across most of their former ranges, but with highly variable success (Zedrosser et al., 1998; Clark et al., 2002). In Sweden, like in many of the ranges across the Northern Hemisphere, extensive conservation and protection efforts have increased bear numbers, here from approximately 300 bears in 1930 to about 2550 in 2005 (Swenson et al., 1998; Kindberg et al., 2006). Although this resulted in an increased distribution of bears, recolonization, especially by females, has occurred in only a portion of the former range (Swenson et al., 1994, 1998), a problem encountered commonly in most places where reintroduction or expanding populations have been monitored (Clark et al., 2002).

Human-caused habitat fragmentation may potentially influence the recolonization of former bear habitat (Gaines, 2003; Apps et al., 2004; Johnson et al., 2004; Proctor et al., 2005). Currently, little is known about how the large-scale development of outdoor recreational resorts and construction of second-home cabins may be influencing the availability and quality of bear habitat (Elgmork, 1978, 1983, 1994; Mattson et al., 1992; Mace and Waller, 1996; Olson et al., 1997; Gibeau et al., 2002; Boyce and Waller, 2003; Apps et al., 2004). Studies from 1949 to 1978 in Norway clearly suggested lower abundance of bears near cabin development in a declining population (Elgmork, 1978, 1983), but little is known whether this pattern also applies to the growing bear populations observed today. Cabin development is a potential growing problem in Scandinavia, because more than 2000 recreational cabins are constructed annually in Sweden (Statistics Sweden, 2003), and more than 5000 annually in Norway (Nelleman et al., 2003), but also in other parts of Europe and North America.

Hence, an understanding of bear habitat use in increasingly human-dominated landscapes is important for conservation and efforts to further develop networks of protected areas (Powell et al., 1996). In this study we compare bear densities across various terrain and vegetation types during the non denning period in relation to distance from resorts and towns.

2. Methods

2.1. Study area

The 12,336 km² large study area was located in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (61° N, 18° E; Fig. 1). The outer boundary was delineated by municipality or county borders or natural terrain features, such as ridges and hills. The rolling landscape in this area is covered with coniferous...
forest, dominated by Scots pine (Pinus sylvestris) and Norway spruce (Picea abies). Over 95% of the study area is forest covered. There is an extensive road system consisting of small closely spaced graveled logging roads and paved public roads with more traffic. Road density including minor gravel logging roads is ca. 0.3 km/km², varying from 0 to 1.5 km logging roads per km². There are six town and settlement areas, ranging in size from 3000–11,000 inhabitants, and two major tourist resort areas with cabin resorts and downhill skiing facilities, located within the study area. The resorts have only 100–500 permanent residents, but a very large number of tourists. In 2001, the largest resort had 1,000,000 visitor nights, distributed throughout the year with peaks in late winter, mid-summer and fall (Statistics Sweden, 2003). Adjacent to this resort the creation of the Fuluufjellet National Park (380 km²) in 2002 caused an increase in the number of visitors to the park by 40% from 2001 to 2003 (53,000 visitors in summer 2003; European Tourism Research Institute, 2005). Bears have been abundant in the study area for more than 30 years and the numbers have been fairly stable during the last decade, although increasing the study area for more than 30 years and the numbers have been increasing at the western, eastern and southern edges, and due to good survival bears have been emigrating out of the study area (Bellemain et al., 1998; Solberg et al., 2006). Bear density is estimated at ca. 30 bears per 1000 km² (Bellemain et al., 2005). As an additional measure to distance to settlements.

2.2. Habitat classification

The study area was divided into 771 4 × 4 km squares completely covering the study area. This scale was selected, because it best identified the variation in the ruggedness across the landscape, as described in the guidelines for optimizing analysis of terrain ruggedness on topographic maps in different landscapes (Nellemann and Fry, 1995). Thirteen grid cells covered by water and mountains above 1000 m were excluded, leaving 758 grid cells with Norway spruce, birch (Betula pubescens) and Scots pine forest and bogs and semi-open meadows. Squares were classified as “forest” or “bogs” if more than 50% of the coverage was forest or bogs, respectively. We further classified each grid cell according to terrain ruggedness index (TRI; Nellemann and Thomsen, 1994). The method has been used to help identify terrain and habitat selection of large ungulates such as reindeer (Rangifer tarandus tarandus), caribou (Rangifer tarandus granti), muskoxen (Ovibos moschatus) and African elephants (Loxodonta africana) (Nellemann and Cameron, 1996; Nellemann and Reynolds, 1997; Vistnes and Nellemann, 2001; Nellemann et al., 2002), and small predators like the Arctic fox (Alopex lagopus; Eide et al., 2001). In brief, terrain ruggedness is calculated as a function of changes in terrain aspects (“ups and downs”) and contour densities along 4 km transects within each grid cell, using 1:100,000 scale maps and contour intervals of 10 m (see details in Nellemann and Thomsen, 1994). Sites were classified as rugged (TRI > 2.5), or flatter terrain (TRI < 2.5).

We also classified all grid cells according to distance from towns and tourist resorts and compared the use by bears at 0–4.9 km, 5.0–9.9 km and for areas >10 km from resorts or towns using radio locations. We further compared the use of habitat and terrain types >10 km from towns and resorts with use of comparable habitat nearer (<10 km) towns and resorts. Reviews of disturbance studies have revealed that the majority of animals impacted by human activity primarily are disturbed within 10 km from infrastructure (Nellemann et al., 2003).

3. Brown bear habitat use

To estimate the bear use of the area within the grid cells, we randomly selected locations of radio-collared brown bears within the study area. From 1985 to 2002 a total of 55 female and 51 male brown bears 2 years and older (i.e. post weaning) carried radio collars within the study area (Støen et al., 2005). The ages of bears not followed from birth were estimated by counting the annuli in a premolar root, which was done in Matson’s Laboratory, Milltown, Montana, USA. (Matson et al., 1993). The radio-collared bears were located approximately weekly using standard triangulation methods from the ground or homing from the air (Dahle and Swenson, 2003). To eliminate auto-correlated data, we only used locations separated by at least 100 h, which corresponds to the minimum time between the weekly localizations of the bears. To avoid locations influenced by denning behaviour, we only used positions from June, July, August and September (Manchi and Swenson, 2005). Using these criteria, we obtained 4150 radio locations of female bears and 2323 radio locations of male bears. From these locations we selected 10 positions randomly from each individual, i.e. 550 female locations and 510 male locations, based on a random digit generation procedure. Of these, 515 female locations and 324 male locations were within the 758 squares. We measured the distance from each selected bear location to the nearest state road, nearest resort (centre) and nearest town (centre). The number of bear locations was used as a measure of bear use and the relationship between distance to resorts and towns and number of number of bear locations was analysed using polynomial regression between distance and number of observed bear locations in 1 km distance intervals out to 26 km distance.

The size of the bear population based on a DNA analysis of non-invasive sampling of scats was estimated in the study area in 2001 (Bellemain et al., 2005). As an additional measure of bear use, we selected the location of one random scat from each identified individual, which gave 88 female and 57 male scat locations within the 758 squares. As potential bias in sampling of scats may have resulted in a sex-biased distribution (Bellemain et al., 2005), these scat locations were used only to obtain an additional measure of bear use in relation to distance to settlements.
4. Statistical analyses

Statistical analyses were performed in Sigmastat (Kuo et al., 1992). Data were first subjected to a Kolmogorov–Smirnov test for normality. Comparisons of bear locations were made using the non-parametric Kruskal–Wallis analysis of variance with Dunn’s tests for multiple comparisons. Use versus availability was tested using the chi-square test. If significant differences were found, the Bonferroni $z$-statistic test was used to determine differences in use versus availability of the individual habitat types (Neu et al., 1974). P-values less than 0.05 were considered statistically significant.

5. Results

5.1. Bear use in relation to human settlements

Bear use by both males and females increased with increasing distance to both towns ($R^2 = 0.74, P < 0.01; R^2 = 0.73, P < 0.01$, respectively) and resorts ($R^2 = 0.64, P < 0.05$; and $R^2 = 0.89, P < 0.01$, respectively) (Fig. 2). Increasing use was strongest when females and males were combined and distance to any settlement (whether resort or town) was used ($R^2 = 0.94, P < 0.01$).

Use by bears in relation to area was significantly lower than expected from availability within 0–5 and 5–10 km from both resorts and towns compared to areas >10 km (Table 1). However, there was no significant difference between use by bears within 0–5 km and 5–10 km. In the following we compare differences in bear use <10 km from settlements with bear use at distances >10 km for comparable habitat categories to identify possible effects of habitat and bear age on the distribution of bears.

5.2. Sex and age of bears in relation to distance to resorts and settlements

Bears of both sexes that were observed closer to settlements (<10 km from resorts or towns) were, on average, younger than bears observed >10 km from any major settlement (Table 2). Bears closer to settlements were on average 27 and 51% younger for females and males, respectively. This trend was most pronounced in males (mean 4.4 ± 0.4 versus 8.9 ± 0.8 years for males and 4.4 ± 0.4 versus 6.0 ± 0.2 for females; $P < 0.01$). Sub-adult bears (<4 years) comprised up to 52% of all bear use within 10 km from resorts and settlements, likely representing younger dispersing individuals. These areas, however, only contained 8% of the old males (>7 years), the remaining 92% located beyond 10 km from major resorts and settlements. Hence, the proportion of young bears in areas within 10 km was significantly higher from the proportion observed in areas >10 km from settlements ($P < 0.05$; Fig. 3). Distribution of both old and juvenile bears were significantly lower than expected from availability of area closer to resorts and settlements ($P < 0.01$; Fig. 3).

5.3. Bear use in different terrain and forest types

The distribution of bears in relation to distance to resorts and towns was not a function of apparent differences in terrain or forest type, although a clear preference for undisturbed rugged terrain was found. The number of female and male bear locations in forested rugged terrain far from human settlements and resorts was significantly higher than in any other habitat type ($P < 0.05$; Fig. 4). Within areas >10 km from towns and/or resorts, the use by female bears was significantly greater in rugged forested terrain (0.108 ± 0.008 locations/km²) than in flatter forested terrain (0.036 ± 0.006 locations/km²) or in bogs (0.016 ± 0.003 locations/km²), both $P < 0.01$. Use was significantly higher than expected from availability in rugged forested areas far from human settlements for both female

<table>
<thead>
<tr>
<th>Table 1 – Bear use of areas at 0–4.9 km, 5–9.9 km and &gt;10 km from major resorts and towns (based on 10 random locations from 55 radio-collared female and 51 male brown bears June–September 1985–2003, Dalarna, Sweden)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of bear locations/km²</td>
</tr>
<tr>
<td>0–4.9 km from towns</td>
</tr>
<tr>
<td>Males</td>
</tr>
<tr>
<td>Females</td>
</tr>
<tr>
<td>Total</td>
</tr>
</tbody>
</table>

Fig. 2 – Mean bear use of 1-km distance intervals from resorts (“females-resort/males-resorts”), towns (“females-towns/males-towns”), and nearest settlement, whether a town or resort (“any settlement”) (based on ten randomly selected positions from each of 55 radio-collared female and 51 male brown bears June–September 1985–2003, Dalarna, Sweden).
and male bears (Figs. 4 and 5A–D). These areas comprised 29% of the study area, but contained 74% of all female and 57% of all male bear locations. Flatter, forested terrain far from human settlements was used according to availability by both females and males (Fig. 4). All areas dominated by bogs were used less than expected by both males and females.

Both males and females used all areas <10 km from both towns and resorts less than expected from availability (Figs. 4 and 5A–D). The largest resort had 1 million visitor nights, but bear use was similar within 10 km from this resort as from towns with 3–10,000 permanent residents. There was no statistical difference between use by bears of rugged forested terrain in areas near resorts compared to similar habitat near towns (P = 0.11; Fig. 4). Rugged, forested terrain near towns and resorts comprised more than 20% of the study area, but contained less than 7% of all female bear locations and 10% of all male locations. Overall, 40% of the study area (4864 km²) was classified as <10 km from towns and resorts, but contained only 9% of the female bear locations and 15% of the male locations. Within rugged forested terrain, use by female bears <10 km from towns and resorts areas was 81-95% lower than for areas far (>10 km) from towns and resorts (0.021 ± 0.004 and 0.005 ± 0.002 locations/km² <10 km from towns and resorts, respectively; compared to 0.108 ± 0.008 locations/km² in areas far from them; P < 0.05). Hence, when excluding bogs, flatter forested terrain and areas <10 km from resorts or towns, the remaining patches of rugged terrain corresponded closely to the distribution of recorded bear locations (Fig. 5A–D).

6. Results based on non-invasive sampling of scats

Corresponding patterns of habitat use and avoidance of areas <10 km from human settlements were also found with the distribution of individual bears as determined from DNA in collected scats. Of 145 locations of individual bears, 61% of

Table 2 – Use of areas by sub-adult and adult male and female bears and mean ages of bears in relation to distance to resorts or towns (based on 10 random locations from 55 radio-collared female and 51 male brown bears) June–September 1985–2003, Dalarna, Sweden

<table>
<thead>
<tr>
<th>Distance to towns or resorts (km)</th>
<th>No. of locations</th>
<th>No. of locations</th>
<th>No. of locations</th>
<th>Mean age (Years ± s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;10 km</td>
<td>No. of locations</td>
<td>No. of locations</td>
<td>No. of locations</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>19 (40%)</td>
<td>19 (40%)</td>
<td>10 (20%)</td>
<td>4.41 ± 0.47</td>
</tr>
<tr>
<td>Females</td>
<td>23 (52%)</td>
<td>10 (23%)</td>
<td>11 (25%)</td>
<td>4.38 ± 0.37</td>
</tr>
<tr>
<td>&gt;10 km</td>
<td>80 (28%)</td>
<td>81 (29%)</td>
<td>123 (43%)</td>
<td>8.94 ± 0.84</td>
</tr>
<tr>
<td>Females</td>
<td>185 (39%)</td>
<td>110 (23%)</td>
<td>182 (38%)</td>
<td>6.0 ± 0.19</td>
</tr>
</tbody>
</table>

Fig. 3 – Proportion of locations of sub-adult (<6 years) male and female, and adult (>7 years) male and female bears along 5-km intervals from settlements and resorts, based on ten random bear locations per animal (n = 106) from June–September 1985–2003, Dalarna, Sweden.

Fig. 4 – Use (mean ± 95% C.I.) by 55 radio-collared female (closed dots) and 51 male brown bears (open triangles) and the proportion of nine different forest habitat types available in the study area (bars) (10 random positions per animal in June–September 1985–2003), Dalarna, Sweden.
the females and 47% of the males were located in the 29% of the landscape constituting rugged forested terrain >10 km from towns and resorts, significantly greater than expected from availability (P < 0.05 for both females and males). A combined regression based on use of the different habitat categories for males and females combined revealed a close relationship (R² = 0.96, P < 0.01).

7. Discussion

7.1. Effects of human activity

Towns and resorts were generally avoided by bears. Avoidance by bears of the areas of greatest human activity is well known from North America (Mace and Waller, 1996; Mace et al., 1996; Vander Heyden and Meslow, 1999; Gibeau et al., 2002; Boyce and Waller, 2003; Chruszcz et al., 2003; Johnson et al., 2005; Waller and Servheen, 2005; Rode et al., 2006). Avoidance and low use by bears of areas surrounding major roads and human settlements has been described in numerous studies in recent years from North America, Asia and Europe (Clevenger et al., 1992; Huygens et al., 2001; Wielgus et al., 2002; Kaczensky et al., 2003; Preatoni et al., 2005). Avoidance of human disturbance is also well known for some other species of wildlife, including birds and ungulates (Reijnen et al., 1996; Forman and Alexander, 1998; UNEP, 2001; Vistnes et al., 2001; Nelleman et al., 2003). A few studies have previously assessed the effects of cabin resorts on brown bears. Elgmork (1978, 1983) found that the number of bear observations across several decades declined with growing development of recreational cabins and logging roads. These studies found highly significant negative relationships between abundance of bears and cabin development, attributed mainly to growing human activity around cabins.

Although resorts have only 5–30% as many permanent residents compared with towns in the area, most of the people visiting the resorts go there primarily for outdoor recreation activities. The number of visitor nights in the largest resort was 1 million per year, which corresponds to 2739 every day on average, but with peaks in later winter, mid-summer and early fall. The towns, in comparison, have 3–10,000 permanent residents, but quite different traffic patterns, in general more confined to the road system. In contrast, the traffic patterns around recreational resorts in summer and fall are a product of off-road activities, such as hunting, fishing and hiking, a large share following an intensively used network of trails through the woods. Whereas the resorts and settlements physically cover only <1% of the study area, the 0–10 km “recreational” zone covered nearly 40% of the study area and was used actively for various human activities including running, hiking and hunting. The distance at which bears are potentially disturbed, is likely dependent upon age and sex (Figs. 2–5, Tables 1 and 2) and possibly the previous experience of the individual bear with humans.

7.2. Sexual and age differences in sensitivity to disturbance

Whereas bear use clearly increased with increasing distance to resorts and settlements, also for comparable habitat types, it is important to notice the differences in age composition of bears. Areas within 10 km from resorts and settlements had a relatively higher proportion of sub-adults, with an age of only 4.4 years, which suggests that these areas were primarily...
used by young, immigrating dispersing bears (Schwartz and Franzmann, 1992; Mueller et al., 2004). Juvenile bears leave their mother already at 1–3 years age in Scandinavia (Stoene et al., 2006). The older bears that are more abundant in the more remote area may pose a risk to sub-adult bears by predation (Swenson et al., 2001). Bears in the study area typically give birth for the first time at 4–5 years of age, by 7 almost all female bears are reproductive. Hence, most of the younger bears appear to move out of the high-density bear areas and into nearby large “empty” areas surrounding the nearby resorts and towns, generally unoccupied by older bears. Similarly, Rode et al. (2006) found that sub-adult brown bears foraged more closely to experimentally introduced human bear-viewers than other age groups at Douglas River, Alaska. We found that that older male bears appear to be more, or at least just as, sensitive to disturbance than reproductive females. Rode et al. (2006) concluded that adult male brown bears would be most likely to be displaced from human activities in areas with alternative food resources available away from humans. This is the case in our study area. Hence, the distribution of bears in relation to disturbance appears to be a function of variation in sensitivity influenced by sex, age and social organisation.

7.3. Use of rugged forested terrain

Both radio-telemetry data and scat data revealed that rugged forested terrain >10 km from towns and resorts was the most preferred habitat for both male and female bears in the study area. Males used areas >10 km from town and resorts more than any habitat <10 km from towns and resorts, even for flat forested terrain. Rugged terrain may provide particular benefits to bears. Terrain ruggedness influences plant composition and plant phenology (Nellemann and Thomsen, 1994). The frequent changes in aspect also may influence the availability of denning sites (Linnell et al., 2000), food plants and the abundance of ant hills by providing numerous south-facing slopes (Lyons et al., 2003; Nielsen et al., 2004a,b,c). Previous studies have shown preferences for rugged terrain by bears (Apps et al., 2004; Nielsen et al., 2004b). Rugged terrain may also provide better cover and lower human access (Nielsen et al., 2004a). However, in spite of the large availability of rugged forested terrain near human settlements, these habitats were only used as or less than expected based on availability, and generally below that of undisturbed flatter forested habitat (Fig. 4).

7.4. Implications for dispersal and population expansion

Although the bear population in Sweden has grown (Bellemain et al., 2005; Kindberg et al., 2006), the density of brown bears in the study area has been fairly stable for the past 10 years, in spite of good production of cubs (Solberg et al., 2006). Dispersal in brown bear populations is sex-biased, with most of the females establishing their breeding home ranges or adjacent to their natal areas and males dispersing longer distances from their mothers’ home ranges (Glenn and Miller, 1980; Blanchard and Knight, 1991; McLellan and Hovey, 2001). In Scandinavia, however, more than 40% of the females disperse from their natal areas and dispersal probability and dispersal distances are inversely density dependent in both males and females (Stoene et al., 2006). Because the bear population in our study area remained stable in spite of good production, juveniles have probably emigrated from the study area (Swenson et al., 1998; Solberg et al., 2006; Stoene et al., 2006), rather than settled in the more disturbed areas within the study area. The abundance of towns and farmland increases substantially to the south, east and west of the study area with few undisturbed corridors available to migrating bears. This may restrict population expansion in the future.

7.5. Implications for conservation

The success of natural expansion or reintroduction of bears depends upon a series of factors, including survival, social organisation, genetics of founder populations, poaching, habitat and range fragmentation (Clark et al., 2002). As juvenile female bears often disperse in Scandinavia, habitat fragmentation is probably a major obstacle to the successful recolonization of historic bear ranges now isolated by settlements, farmland and developing large-scale resorts. Resorts apparently had a significant influence on bear habitat choice and movements. Currently, more than 7000 new recreational cabins are built in Norway and Sweden every year and recreational resorts are also increasing many places in the United States, Canada and particularly in Central-Europe. In many cases, they form resorts with shops, hotels and extensive trail systems, and in some cases, smaller previously disconnected resorts merge and generate long corridors of development, typically in the low-alpine zone and in the boreal forest. Safeguarding corridors of undeveloped forest sections, particularly of rugged terrain, will likely be a management challenge in the future in order to secure further recolonization by bears and limit further range fragmentation. This should also be considered in areas where there are plans to reintroduce bears.

Acknowledgements

This study was funded by the Norwegian Directorate for Nature Management, the Swedish Environmental Protection Agency, the research programme “Adaptive management of fish and wildlife populations”, WWF Sweden, the Research Council of Norway, and the Norwegian University of Life Sciences. We thank the personnel in the Scandinavian Brown Bear Research Project for their assistance in the field and Orsa Communal Forest for field support. We also thank Pierre Taberlet and Eva Bellemain for the genetic results. All capture and handling of bears reported in this paper complied with the contemporary laws regulating the treatment of animals in Sweden and Norway and were approved by the appropriate management agencies and ethical committees in both countries.

REFERENCES


human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biological Conservation 120, 101–113.
Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos)

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

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

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

[Intraduit par a Rédaction]

Introduction
Habitat selection is an animal’s disproportionate use of a habitat in relation to its availability, and can operate at different spatial and temporal scales (Johnson 1980; Schooley 1994; Mysterud et al. 1993; Apps et al. 2004; Nielsen et al. 2004a). Throughout its life, an animal must satisfy its basic needs, such as food, cover, water, and pre-berry opportunities. Because usually a single habitat can satisfy all these needs adequately, the animal’s habitat selection will reflect a trade-off among them. In the management of a species, it is thus essential to know which habitats are used and why animals select some habitats over others (Manly et al. 2002).

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

An animal’s needs and behaviour change throughout the day. Studies on both brown bears (Servheen 1983; Bieden and Fiolm 2002; Nielsen et al. 2004a) and cervids (Mysterud et al. 1999) have indicated that habitat selection also varies according to the time of day. Beyer and Haufler (1994) stressed the need for habitat studies to consider a
species' daily activity pattern. However, earlier habitat-
selection studies have rarely taken this into account.
Monitoring these finer spatiotemporal trends will be important
in future studies for the conservation of animals, as it ena-
bles us to draw more biologically relevant conclusions
(Johnson 1980; Beyer and Haufier 1994; Mysterud et al.
1999; Apps et al. 2004a; Nielsen et al. 2004a).
Most previous habitat studies on large mammals have
been conducted by equipping the animal with very high fre-
quency (VHF) transmitters. Triangulation from the ground is
labour intensive and has mainly been restricted to the day-
light hours. With the introduction of GPS-GSM (global
positioning system and global system for mobile communi-
cation) collars and the NAVSTAR GPS (satellites and
ground receiving system), it is now possible to locate the an-
imal's position with very high accuracy. Also, the collars can
be programmed to produce a large amount of locations,
independent of time and remoteness (Obeda et al. 1998;
Arthur and Schwartz 1999). This new technology thus gives
us the possibility of very small-scale habitat selection stud-
ies in both time and space (Rodgers et al. 1999, Aradados
et al. 2003).
In this paper, we explore the habitat selection of six fe-
male brown bears in Sweden. They were all equipped with
GPS-GSM collars, as well as activity loggers. From this we
determined their coordinates and activity status (foraging
or resting) at each site. Because the needs of a foraging bear
(foods) are not the same as the needs of a resting bear
(shelter), we expected (i) differences in the habitat selection
of foraging bears compared with those of resting bears.
From this we also expected that (ii) the bears' habitat
selection would vary on a diel scale. Finally, we con-
ducted a 24 h habitat selection study, and based on the pre-
vious three hypotheses, we expected to find (iii) a difference
between the diel habitat selection and the overall 24 h habi-
tat selection.

Study area
The study was conducted in the counties of Dalarna and
Gävleborg, Sweden (61°N 15°E), an area near the southern-
most distribution of the Scandinavian brown bear popula-
tion. The area is mainly forested, 80% being covered by highly
managed productive forest. Bogs and lakes cover the remain-
ing area, and the human settlements consisted of a few scat-
tered villages. The forest turnover time is 90–100 years, with
<60% of the forest being older than 35 years (Swenson
et al. 1999). Gravel roads crisscross the entire study area.
Combined with the always ongoing tree cutting, this makes
the landscape a patchwork of different habitats with a me-
dian patch size of 22,500 m² (mean 80,600 m²). The terrain
is gently undulating with altitudes ranging 200–700 m
above sea level. No area rise above the timberline.

The dominating tree species is Scots pine (Pinus silvestris
L.), with Norway spruce (Picea abies (L.) Karst.), larchpole
pine (Pinus contorta Doug. ex Loud., non-native), birches
(genus Betula L.), and European aspen (Populus tremula
L.) covering the remaining area. Important field-layer veg-
etations include myrtle blueberry (Vaccinium myrtillus
L.), lingonberry (Vaccinium ilicis-idea L.), black crowberry
(Empetrum nigrum sup. hermaphroditum (Lange ex Ha-
gerup) Böcher), some forbs, and heather (Calluna vulgaris
(L.) Hull). The ground layer consists of mostly lichens and
mosses. The estimated winter population of moose (Alces
alces (L., 1758)) was about 920 individuals per 1000
km² (Swenson et al. 2007) and the estimated brown bear popu-
lation was about 30 bears per 100 km² (Belleman et al.
2005). Snow covers the ground from the end of October
until early May and the mean temperature ranges from a
minimum of −7 °C in January to 15 °C in July (Swenson
et al. 1999).

Materials and methods
Data collection and GPS radiotelemetry
We studied six sexually mature female brown bears with
cub cubs of the year, ranging 3–10 years old. All were equipped
with GPS-Plus-3 collars, as well as activity loggers, VHF
units, and GSM modules (VEKONIC Aerospace Umsch Berlin,
Germany). For procedures on capture and marking see
Aradados et al. (2006). The coordinates and activity status (N
= 19,209) of the bears were recorded every half hour (48 time
day) between 20 May and 24 August 2004. The coordi-
nates and time of day were obtained by the NAVSTAR glob-
all positioning system (Rodgers et al. 1999). To correct
for seasonal patterns in behavior and diet (McLellan and
Hovey 2001; McLoughlin et al. 2002), the study period was
divided into the pre-berry (20 May – 6 July) (Dahle and
Swenson 2003) and berry (16 July – 24 August) seasons with
a break when berries started ripening.

The location error in this study was relatively small, a
maximum approximately ±10 m. One of the transmitted
partly malfunctioned, resulting in a general loss of positions
and (or) no positions at all for several days or weeks. Recog-
nizing that this was a technical problem that would not
lead to any habitat biases, we chose to include the available
data from this bear in our analyses. A more serious problem
was loss of data owing to a sporadic lack of contact between
the GPS collars and the satellites. Several factors have been
suggested as the cause of this, e.g., animal behavior, the
position of the array inside the collar, the number of sat-
ellites available, weather conditions, habitat density, and
topography (Dussault et al. 1999; Bowman et al. 2000;
Moen et al. 2001; D’Eon et al. 2002; Aradados et al. 2003)
When studying habitat selection, this can be a serious prob-
lem, as it can lead to erroneous conclusions (D’Eon 2003).

For example, loss of data in dense forests will underestimate
this habitat. Although this study did not focus on habitat
selection per se, we did examine the GPS-fit success rate and
located what activity showed the lowest success rate.

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

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

© 2007 NRC Canad
Table 1. Habitat categories within the home ranges of six female brown bears (Ursus arctos) in Dalarna, Sweden, 2004.

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

Note: SMD (Swedish landuse data) habitat classes are from the Swedish landcover data (Engberg 2003).

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

Activity sensors

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

Statistics

Because our study included only six bears and three of these were related (mother and two independent daughters), we chose to use χ² goodness-of-fit tests, with individual observations as sample units and not the individual bear. Although this method has been criticized (Aebischer et al. 1993; Allredge and Griswold 2006; Thomas and Taylor 2006), we felt that the method was justified because our primary goal was to compare habitat use in different periods of the day. To determine whether habitat use was spatially autocorrelated owing to restrictions on bear movement, we also analyzed the movement of the bears (calculated as the straight-line distance between subsequent GPS positions) to find their ability to move between different habitat patches within the scope of two preceding observations. The χ² tests were performed with MINITAB® version 13.0 (Minitab Inc. 2000), and when they showed that the bears used their home-range habitats nondominantly (P ≤0.05), we used the method described by Krebs (1999: pp. 480-481) to determine which habitats were selected or avoided. A selection index was the proportion of habitat used divided by the proportion available, with a value of 1 indicating no selection, indices significantly <1 indicating habitat avoidance, and indices significantly >1 indicating habitat selection. Running several tests on the same sample and using nonindependent habitat availability measures (risking unit = sum constraints) increased the risk of making type I errors (Aebischer et al. 1993; Manly et al. 2002; Nakagawa 2004). To reduce this probability, we performed a Bonferroni adjustment when calculating the 95% confidence intervals (α level/n = 0.05/9). We considered two categories to be significantly different from each other when their confidence intervals did not overlap. This was a conservative assumption (Krebs 1999) and it might have decreased the power of our tests (Nakagawa 2004). However, the main goal of this study was to show the different habitat-selection patterns of studies using different temporal scales. Since all our tests were run using this same method, an absolute accuracy of which habitats were significantly selected or avoided was not necessary to adequately test our hypotheses.

Results

Methodology

A median patch size of 22,500 m² gave an average maximum exit distance of 85 m; 160 m calculated from the mean (80,600 m²). To determine whether the bears were actually able to move between the habitats within the 30 min available between each GPS fix, we calculated their straight-line movement in metres per 30 min. Fitting the seasons and using all sites where the bears has been active (mean activity ≥50), the median movement was 361 m/30 min (N = 8948, quartile 1 = 180, quartile 3 = 604) and the maximum distance walked in 30 min was 2515 m. Less than 0.1% of the habitat patches exceeded 2 km across.

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

Did activity periods

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

© 2007 NRC Canada
Fig. 1. Mean activity for each half-hour period (local mean time) during the diel cycle for five female brown bears (Ursus arctos) in Dalarna, Sweden, during the (A) pre-berry and (B) berry seasons of 2004. Shaded bars are active periods (mean activity ≥ 50; \( N_{	ext{pre-berry}} = 3662; N_{	ext{berry}} = 4246 \)) and solid bars are passive periods (mean activity ≤ 30; \( N_{	ext{pre-berry}} = 6285; N_{	ext{berry}} = 3343 \)).

![Graph A](image)

![Graph B](image)

bears during the two seasons (Fig. 1) — (1) night rest (NR): 0030–0239 pre-berry season, 0000–0329 berry season; (2) early-day activity (EDA): 0300–0829 pre-berry season, 0330–0839 berry season; (3) day rest (DR): 0830–1739 pre-berry season, 0900–1729 berry season; (4) late-day activity (LDA): 1800–0029 pre-berry season, 1750–2359 berry season.

Diel habitat selection in relation to diel activity periods

There was a significant difference in use of habitats during the different activity periods for both seasons (pre-berry: \( \chi^2_{[3]} = 508.9, p < 0.001 \); berry: \( \chi^2_{[3]} = 174.9, p < 0.001 \); Fig. 2). Poor conifers, open bog, and other habitats were almost always avoided, whereas young forest was always selected. But these four habitats were significantly more avoided (less selected) by resting than by foraging bears (except young forest during the berry season). Tall conifers, mixed forest, and forested bog were generally more selected by resting than by foraging bears. Short conifers were selected only by resting bears during the pre-berry season, but also by foraging bears during the berry season. Clearcut was avoided by both resting and foraging bears during the berry season, but significantly more so by resting bears. During the pre-berry season, clearcut was a selected habitat for foraging but not for resting.

Overall 24 h habitat selection compared with diel habitat selection

We also conducted an overall 24 h habitat-selection study to determine whether this gave the same results as dividing the habitat selection according to diel activity. The 24 h study showed that bears used the available habitats nonrandomly during both seasons (pre-berry: \( \chi^2_{[1]} = 1291.7, p < 0.001 \); berry: \( \chi^2_{[1]} = 972.8, p < 0.001 \); Table 2). As the bear selected habitats differently when they were foraging than when they were resting (Fig. 2), there were bound to be differences between the diel habitat selection and the 24 h habitat selection. During the pre-berry season, there seemed to be a general selection of short conifers and mixed forest based on the 24 h habitat selection, but these habitats were not selected during the active periods. Clearcuts also seemed to be selected based on the 24 h habitat selection, but they were not selected during the day-rest period. Tall conifers were also selected during the day-rest period of the berry season, but it was not a selected habitat based on the 24 h habitat selection of the berry season.

Discussion

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

Methodology

We wanted to determine whether using positions 30 min apart would cause a problem of spatial autocorrelation (Niel et al. 1974, Aeberscher et al. 1992). To this end, we explored the bears’ movement between subsequent GPS fixes and compared it with the average distances within the habitat of this patchy area. The average maximum estrus distance of a patch was 85 m, with < 0.1% of the habitat patches exceeding 2 km across. Considering that the bears walked a median straight line distance of 361 m during the time available and sometimes as much as 2.5 km, the bears should be able to walk both out of and into all available habitats between each subsequent GPS fix, thus decreasing the problem of spatial autocorrelation.

The average success rate for GPS fixes was 76%, which was dependent on the activity of the bear. Almost 80% o
Fig. 2. Selection indices (+95% confidence intervals) of habitats used during different activity periods by six female brown bears in Dalarna, Sweden, during the (A) pre-berry (N = 10881) and (B) berry (N = 6585) seasons. There were no observations in the habitat category "other" during day rest in the berry season.

(A) 

(B) 

© 2007 NRC Canada
the failed fixes occurred when the bears were passive. The success rate has also been found to be behaviour-dependent in white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) (Bowman et al. 2000). The difference in fix rate between behaviours is probably due to one or both of two factors. First is the position of the antenna inside the collar. Resting bears might lie on their side or near a rock or other object. This might prevent the transmitter from having a clear line of contact with the satellites and might lead to an undersampling of resting sites. This would, however, not be a great problem, as we divided habitat selection into periods of resting and foraging. Second is the habitat choice of passive versus active bears. Resting bears seem to select denser habitats, and Dussault et al. (1999) and D’Eon et al. (2002) have found that a higher percentage of canopy cover and mature stands limit the transmitter’s ability to contact the satellites. This problem should also be even more when segregating between habitat selection of foraging bears than of resting bears. But it might still have led to an undersampling of sites in denser habitats.

### Diel activity periods

From the activity data, we found that the bears rested and were active at particular times of the day (Fig. 1). Resting was mainly restricted to the daylight hours, whereas activity was restricted to the crepuscular and nocturnal hours. This corresponded well with the findings of Kazzensky et al. (2006) for adult brown bears in Slovenia and Croatia. Gervasi et al. (2006) found that one could differentiate between resting and active bears from the activity data, but could not differentiate between foraging and other active behaviours. To examine whether the habitats used during the active periods of the day were important foraging habitats, our field crew visited 105 randomly selected bear sites to look for any sign of foraging (data not shown). Confirming the study of Gervasi et al. (2006), we found that the bears avoided foraging during the day-rest period and that there were significant signs of foraging during the late active period of the post-berry season. We did not find signs of foraging for the remaining active periods, but this lack of foraging signs did not necessarily reflect an actual lack of foraging during these periods, because of the difficulty of finding any sign of foraging on berries. Jhansen (1997) found that almost 50% of the bears’ assimilated energy came from berries in this area, and MacHutchon (2000) argued that brown bears spend most of their active time foraging.

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

### Diel habitat selection in relation to diel activity periods

There were large differences between the habitats selected during the resting compared with the active periods of the day (Fig. 2). Generally, resting bears seemed to avoid open habitats more than foraging bears. This was particularly obvious for elements during both sexes. Also, tall conifer was an avoided habitat during most active periods, but it was in fact a selected habitat during the day-rest period. Sverdrup (1983) observed a similar trend for bears feeding on agricultural lands in Montana; they avoided using these open habitats during the daylight hours, but foraged there during the night. The same was true for the bears Nielsen et al. (2004a) studied in Alberta, which used elements more often during the crepuscular and nocturnal hours than during the daylight hours. Horner and Powell (1999) studied habitat use in relation to activity of black bears (*Ursus americanus* Pallas, 1780) in North Carolina and differentiated between moving, foraging, and resting bears. In contrast to our findings, their results suggested no differences in habitat use between these activities. However, their analyses only includes the most frequently used sites. Also, their method of defining resting and foraging activities from collar activity sensor levels was not verified with field observations. Gervasi et al. (2006) found that, although it was possible to differentiate between active and passive status of brown bears equipped with activity sensors, it was not possible to differentiate among active behaviours such as walking and foraging.

From our results, we can conclude that if the objective is to study all habitats that are important for an animal, then it is crucial to include observations from all 24 h of the day.
We divided the day into categories based on diel activity rather than activity per se. But we also tested the habitats selected by active (activity level ≥50) versus passive (activity level <50) bears regardless of time of day (data not shown), and the same pattern emerged as in Fig. 2. There were two main reasons why we chose to divide the categorizes according to the time of day. First, we wanted to examine whether studies based on observations from different times of the day were comparable, and our results clearly show that this might not be the case. Second, finding a diel regular activity pattern could be useful for future studies. According to our results, it should now be possible to program collars to take coordinates more often or seldom at particular times of the day based on animal behavioral patterns. For instance, in studies focusing on foraging bears it would be possible to decrease the interval between subsequent GPS fixes attempts (or stop altogether) during the daylight hours. This would increase the longevity of the batteries and thus save both money and animal stress as a result of being captured less often.

Overall 24 h habitat selection compared with diel habitat selection

Comparing our findings of the bears' 24 h habitat selection (Table 2) with diel habitat selection (Fig. 2) revealed another important pattern. Based on the 24 h habitat selection, clearcut appeared to be highly selected during the pre-berry season. However, the bears did not select this habitat when they were resting (Fig. 7). From the 24 h habitat selection, it also appeared that the bears avoided or did not select tall conifers. However, they significantly selected this habitat when resting. These findings show the serious biases that can result from drawing conclusions based on the bears' 24 h habitat selection. Beyer and Haftel (1994) and Belant and Follmann (2002) emphasized the problems of using only observations from a particular time of day. But as we have seen, it can be equally erroneous to use overall 24 h data sets too. This becomes especially evident when dealing with habitats that are chosen differently for foraging and resting activities, as opposite selections might lead to an average of no selection at all. If the main goal of habitat-selection studies is to find which habitats are important to bears, then it is crucial to differentiate between foraging and resting habitat selections.

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

Acknowledgements

This study was conducted as 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, and the Norwegian Research Council. Claudio Signer, Kent Ove Moren, Jorn Grotenhjøk, and Vincenzo Gervasi assisted with GPS and field data collection.

References


Environmental Systems Research Institute, Inc. 2002. ArcView®.

© 2007 NRC Canada
Moe et al.


© 2007 NRC Canad.
Monitoring rare or elusive large mammals using effort-corrected voluntary observers

Jonas Kindberg\textsuperscript{a,}* \ G"oran Ericsson\textsuperscript{a} \ Jon E. Swenson\textsuperscript{b,c}

\textsuperscript{a}Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden
\textsuperscript{b}Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, NO-1432 Ås, Norway
\textsuperscript{c}Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

\begin{abstract}
Populations of rare or elusive large mammals are difficult to monitor, because they usually are secretive, solitary, occur at low densities, and have large home ranges. The global trend of generally decreasing large carnivore populations necessitates new, feasible, reliable, and cost-effective monitoring methods. We evaluate an index method developed for monitoring populations of moose (Alces alces) based on voluntarily and systematically collected observations from hunters, corrected for effort, for use in monitoring populations of large carnivores in Sweden. For our evaluation, we used independent estimates of minimum brown bear (Ursus arctos) densities from DNA-based scat surveys and brown bear distribution from mandatory reports from successful bear hunters. We verified that the index correctly reflected bear distribution. We also found strong linear relationships between the indices and the independent density estimates for bears at the scale of local management units (about 1000–2000 km\textsuperscript{2}) in all three regional study areas (adjusted $R^2 = 0.88–0.60$). Our results suggest that systematic, effort-corrected reports of observed animals can be an alternative and accurate monitoring method for the conservation and management of large mammals occurring over large areas when large numbers of willing volunteers are available (effort >30,000 h).
\end{abstract}

\section{Introduction}

Monitoring can be defined as the process of gathering information about variables in some systems, such as a population, at different points in time and space to characterize their status (Yoccoz et al., 2001). Density and distribution are considered key parameters for the conservation and management of most animal species (Wilson and Delahay, 2001). Large carnivores are typical examples of rare and elusive mammals that are vulnerable or endangered with declining habitat or numbers (Weber and Rabinowitz, 1996; Gittleman and Gomper, 2001). Their secretive characteristics and low abundance make monitoring a difficult task for this group (Kendall et al., 1992; Linnell et al., 1998; Thompson, 2004).

Although there are many available methods for monitoring (Schwarz and Seber, 1999; Williams et al., 2002), few are suitable for low-density mammals or other elusive species (Mills et al., 2000). Many of these methods either are too expensive or not suitable to cover large areas, at least on a regular basis (Link and Sauer, 1997; Schwarz and Seber, 1999; Zhou and Griffiths, 2007). Because it normally is difficult to determine absolute densities, managers often must rely upon indices to determine abundance and trends (Eberhardt and Simmons, 1987; Skalski et al., 2005). When detection...
probability is unknown, counts are normally treated as indices. Indices are usually cheaper than other methods of monitoring trends, and can be very useful for managing populations, if they accurately reflect relative abundance. Several studies have shown that indices can be highly correlated with abundance (Hochachka et al., 2000; Slade and Blair, 2000; Wilson and Delahay, 2001; Romain et al., 2004), but indices also have received much criticism (Anderson, 2001).

In Scandinavia direct or indirect observations of primarily family groups, and snow tracking, have been used to monitor lynx (Lynx lynx) and wolf (Canis lupus) populations (Andrén et al., 2002). These methods are often time consuming, costly, may have serious biases, and/or rely on favorable weather conditions (Elgmork, 1991; Linnell et al., 1998; Andrén et al., 2002). Analyses of standardized observations of female brown bears (Ursus arctos) with cubs made by approved observers have been used successfully to estimate the minimum population size and population growth rate in the Yellowstone Ecosystem, USA (Knight et al., 1995; Eberhardt and Knight, 1996; Mattson, 1997; Keating et al., 2002; Harris et al., 2007; Schwartz et al., 2008). However, Solberg et al. (2006) evaluated observations of female brown bears with cubs that were reported by the general public (i.e., not an organized effort) to the hunters’ organization in Sweden and found that it greatly underestimated the population size. Solberg et al. (2006) considered compiling unorganized reports of females with cubs by the general public, as practiced in Sweden, to be inadequate for population monitoring. In addition, brown bear litter sizes reported by the general public in Sweden were lower than those documented in the same area by researchers (Zedrosser and Swenson, 2005).

A simple, straight-forward method, such as observations combined with a measure of effort, has been used to monitor moose (Alces alces) populations since the mid-1970s in Norway, mid-1980s in Sweden, and in parts of North America (e.g. Ericsson and Wallin, 1999; Solberg and Sæther, 1999). Substantial research effort has been invested in testing and verifying the theoretical and the practical assumptions of observation indices. For example, we know that effort-corrected observations of moose accurately, and linearly, reflect annual reproduction or recruitment (Fryxell et al., 1988; Crête and Courtois, 1997; Ericsson and Wallin, 1999; Solberg and Sæther, 1999; Sylvén, 2000).

A similar method could potentially give valuable information about population size, distribution, and trends of large rare or elusive mammals (i.e., large carnivores). Although Elgmork (1991) and Swenson et al. (1994) suggested using effort-corrected bear observations collected by hunters during moose hunting as a method for estimating relative densities of bears that was independent of harvest data, the applicability of this method remains to be verified with independent data.

The large carnivore observation index (LCOI) was introduced in Sweden in 1998 as an add-on module to the nationwide monitoring program for moose (Linnell et al., 1998). During the first 7 days of the moose hunting season (during September–October), hunters register observed large carnivores (i.e., brown bears, lynx, wolves, and wolverines [Gulo gulo]) and the total observation effort in hours. We evaluate the general applicability of these systematically and effort-corrected observations as a means of monitoring populations of large rare or elusive mammals. As a case study, we use observations of brown bears from the LCOI program in Sweden. We focus on two central questions; can the LCOI be used as an accurate index of the density and of the spatial distribution of brown bears? We test these questions using independent data from on-going research and management.

2. Materials and methods

2.1. Study areas

We used data from the provinces (läns) in Sweden with established bear populations and with available independently collected density estimates (Fig. 1). We analyzed data at the scale of the local management unit (LMU), which is the scale where hunters collect data and implement general wildlife management strategies decided by the regional authorities. A LMU usually consists of >1 parishes within a municipality or an en-

Fig. 1 – The map of Sweden (light gray) showing province (läns) borders. The large carnivore observation index data for brown bears used in this study were from the provinces marked with hatched lines; Dalarna (W), Gävleborg (X), Västernorrland (Y), and Västerbotten (AC).
tire municipality. The study provinces were Dalarna and Gävleborg (combined), with 48 LMUs and an area of 47,747 km² (mean size of 995 ± 831 km² (SD), Västernorrland with 19 LMUs and 21,499 km² (1131 ± 582 km²), and Västerbotten with 21 LMU and 54,002 km² (2572 ± 1615 km²). Reported areas are the areas available for moose hunting (primarily forest), with a smaller adjustment in Västerbotten to remove inaccessible mountain areas without observations or scat sampling.

The habitat consists mostly of managed boreal forest, mainly coniferous, and an increase in alpine areas towards the western border to Norway. The road network is well developed and the area has a generally low human population density (4.7–15.2 inhabitants/km² in the study provinces). For a more detailed description of the habitat see Dahle and Swenson (2003).

### 2.2. The large carnivore observation index

The LCOI methodology is simple and easy to use, with its basic design following that of Ericsson and Wallin (1999) and Solberg and Sæther (1999). In Sweden the management authorities use the about 200,000 organized moose hunters to voluntarily monitor large carnivores. Moose hunters usually hunt together in a stable party and rent a specific hunting area for many years (Thelander, 1992; Heberlein, 2000). The season starts in September or October depending on province, and is conducted during the daytime from one hour before dawn to 1 h before dusk. During the first 7 days the moose hunters are hunting, they record all sightings of moose, in addition to those of brown bears, wolves, lynx and wolverines. The reports record sightings of young-of-the-year and older animals, length of daily hunting activity in hours, and numbers of hunters, all by hunting unit and day. From this, we calculated an index (observations per 1000 h). The LCOI allows almost national coverage, as moose are hunted over practically all of Sweden and in all bear habitat except for national parks. This program generates around 4.5 million observation hours yearly (J. Kindberg, unpublished data) with about 2.5 million hours in the areas with bears and an average of around 1000 bear observations annually.

### 2.3. Independent data

The independent data on brown bear distribution and population size come from population estimates based on the DNA-based identification of individual bears from hunter-collected bear scats in the provinces of Dalarna and Gävleborg in 2001 (Bellemain et al., 2005) and from similar surveys in Västerbotten and Västernorrland provinces in 2004 (Bellemain, 2005; Kindberg and Swenson, 2006) (Table 1, Fig. 1). The participating hunters were primarily moose hunters who collected scats throughout the entire provinces during the entire fall hunting season. Thus, the sampling included areas where bears were rare and areas where bears were relatively numerous (Bellemain et al., 2005). We used these data sets to determine the known minimum number of individual bears obtained from the DNA analysis in each LMU. The index was calculated as the number of unique bears per square kilometer, found in each of the LMUs. In cases where an individual was encountered in more than one LMU, it was assigned to each of them. We did not find any patterns suggesting a positive correlation between estimated search effort (h per km²) and density of detected individual bears (r = 0.40).

In addition, the distribution of bears was estimated from the locations of hunter-killed bears. Bear hunting is allowed for all qualified hunters, with no license restrictions or number of bears that an individual hunter can kill, but family groups are protected. Bear harvest is limited by a quota for each province. Due to the lack of a specific license requirement to kill a bear, 55% of the bears are harvested by hunters hunting primarily for other species (Bischof et al., 2008). Thus, potential bear hunters are not just concentrated in areas with high bear densities. Successful bear hunters are required to submit an extensive report about the harvested bear, including coordinates of the kill site (Bischof et al., 2008). From that database we produced a map of harvested bears from 1998 to 2006 and compared that with the average observation rate of bears the LCOI from the same period.

### 3. Statistics

We performed all statistical analyses in SAS software and we considered results to be significant at α ≤ 0.05. For regressions we used Proc GLM and for tests of differences among areas we used it with the Contrast statement. All reported correlation coefficients were adjusted for sample size. For estimating variance in bear observations in relation to effort, we used all observational data from Dalarna province (2001) and calculated confidence intervals for 1000 randomizations (Manly, 1997).

### 4. Results

The LCOI accurately reflected the distribution and the known minimum density of brown bears in Sweden. The distribu-
tion of brown bears, based on results from LCOI, compared well with the distribution of harvested bears within Sweden during the same period (Fig. 2). Secondly, and more importantly, we found a strong statistical relationship between densities of individually identified bears in each LMU and the LCOI for all three study areas. The regression results had a high explanatory power for Gävleborg and Dalarna in 2001 ($P < 0.0001$, $R^2 = 0.82$, $N = 48$ LMUs); for Västernorrland in 2004 ($P < 0.0001$, $R^2 = 0.60$, $N = 19$ LMUs); and for Västerbotten in 2004 ($P < 0.0001$, $R^2 = 0.88$, $N = 21$ LMUs). Thus, the known density of bears explained between 60% and 88% of the observed variation in observation per hour at the lowest spatial scale, i.e., the LMU (Figs. 3–5). However, the slopes of the relationships between observations/1000 h and minimum bear density differed significantly among the three regions. A trend towards a difference was found between Dalarna–Gävleborg and Västernorrland ($P = 0.11$), but Västerbotten was highly significantly different from the other two study areas (both $P < 0.001$).

Furthermore, we found that the LCOI stabilized at the scale of larger LMUs, at around 30,000 observation hours (Fig. 6). However variance was still high, ±40%, at 130,000 observation hours.

5. Discussion and conclusions

Monitoring programs are crucial for adequate conservation and management of most species, because baseline information is needed to understand their status. For species that are rare, elusive, and occur over large areas, large sample sizes are required for density or abundance estimates. However, this makes more preferred methods, such as capture-recapture or distance-based methods, very expensive. In some situations, an index method could be the solution to provide information about density and distribution for these species. However, to be useful for managers, index methods must have sufficient statistical power to detect significant changes...
in population size (Clevenger and Purroy, 1996; Field et al., 2005; Brodie and Gibeau, 2007). We used effort-corrected observations of brown bears from organized volunteer hunters and found that the resulting index accurately reflected distribution and relative local densities. We suggest that the LCOI, as used in Sweden, allows the possibility for continuous monitoring, even with scarce resources. Nevertheless, some methodological aspects must be addressed.

First, when using observations, it is important to know that there is considerable variance in the estimation of the parameters related to effort (Harris et al., 2007). Thus, one needs many observers to actually have the statistical possibility to detect a change. Hochachka et al. (2000) showed that relatively few hours (average 7700 h yearly) were sufficient for trend and density estimates of common species, but suggested that the method possibly would not work for uncommon species. We have shown that, with enough observation effort, we can estimate a density index for an elusive species (brown bear) at a scale that is useful for management. To obtain such an effort almost requires the use of voluntary input, as was possible in Sweden.

A few studies have investigated what actually causes the variance when using volunteers, such as hunters and bird watchers, as reporters in monitoring programs (Link and Sauer, 1997; Newman et al., 2003). Ericsson and Wallin (1999) and Sylvén (2000) have shown that most of this variation is due to variation among the individual observers. Ball et al. (1999) showed that also extreme (warm–cold, dry–wet) weather situations may temporarily change the behaviors of the hunters and thus create outliers in a monitoring time series.

Because of the relatively large variation in our data, especially on the local scale, we suggest that the LCOI needs a considerable minimum observation effort and should be used with caution at scales smaller than provinces. Also due to this variation, combined with the possible effect of extreme events in a single year, we recommend that one be cautious in drawing conclusions about population trend based on results from a few years. Therefore, we stress that, if observation programs are implemented to monitor trends of large and elusive mammals, a long-term commitment is essential.

We believe that a major strength of an observation program for monitoring purposes, such as we describe, is that the managers obtain annual data, which can allow the detection of a trend relatively quickly. Even in a situation with perfect data, managers will not react immediately. Solberg and Sæther (1999) found that it took managers approximately 2 years to change moose hunting quotas as a response to either an increasing or decreasing trend. Thus, an inexpensive monitoring program using effort-corrected observations may alert management faster than expensive monitoring methods that are conducted less often.

There are several problems associated with relying on voluntary work for wildlife monitoring. First, the observers must be in the habitats where the animals occur. Second, be-

Fig. 5 – Regression between the number of brown bear observations per 1000 observation hours by big-game hunters (LCOI) and the minimum number of bears (identified from DNA in scats) per 100 km² in local management units (LMUs) in Västerbotten Province, Sweden, 2004. The dotted line shows the 95% CI.

Fig. 6 – Results of a stabilization test of brown bear observations per hour for groups of observation hours as the mean and 95% CI for 1000 re-sampling events, using the data from Dalarna province, Sweden, in 2001.
cause of individual variation, the number of observers must be large. Third, the observers must carry out the observation program in a systematic and comparable fashion year after year. Fourth, the observers must be linked to an organization that mediates the data to nature-resource managers. Fifth, and this is crucial for an observation method and the ability to detect a change, is that the observers must record their observation effort accurately (Link and Sauer, 1997; Hochachka et al., 2000). The method should be carried out in a manner that allows one to detect and correct for spatial differences in effort and changing effort and area use between years. Systematized observations could be used in many areas and utilize different groups of people as a base for monitoring trends of elusive large mammals. In national parks or recreational areas, tourists and guides could be used and in more managed areas perhaps wardens.

A general problem with index methods in wildlife monitoring is the question of their comparability among areas and habitats (Eberhardt and Simmons, 1987; Slade and Blair, 2000; Williams et al., 2002). Our results showed a linear relationship between observations and density within the range of data we obtained, but that the slopes of these relationships differed among provinces. As pointed out by Ericsson and Wallin (1999), the regional differences in the relationships are not crucial per se, at least for monitoring population size within a region. However, to convert observation values into relative or estimated densities, for example to compare among regions or make a national estimate, it is necessary to understand the factors causing the regional differences in slopes. Future studies should investigate both this and the consistency of the relationship between the methods over years in the same province. This will be possible in the near future, because the management authorities plan to repeat the scat surveys.

Acknowledgements

We thank the hunters for collecting scat samples and reporting bear observations, the Swedish Association for Hunting and Wildlife Management for providing bear observation data, the natural-resource managers in the provinces of Västerbottens and Västernorrland for data on their DNA-based population estimates, and M. Wallgren and W. Neumann for quality control of observational data, P. Taberlet and E. Bellemain at the Laboratoire d’Ecologie Alpine, Grenoble, France, for DNA analysis. The study was financed by the Swedish Environmental Protection Agency and the Swedish Association for Hunting and Wildlife Management. J.K. and G.E. gratefully acknowledge FORMAS and the program Adaptive Management of Fish and Wildlife for support.

References


Estimating population size and trends for the Swedish brown bear (*Ursus arctos*) population

Jonas Kindberg¹, Jon E. Swenson²,³, Göran Ericsson¹, Eva Bellemain⁴, Pierre Taberlet⁴

¹ Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.
² Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Box 5003, NO-1432 Ås, Norway.
³ Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway
⁴ Laboratoire d’Ecologie Alpine (LECA), Génomique des Populations et Biodiversité, CNRS UMR 5553, Université Joseph Fourier, BP 53, F-38041 Grenoble Cedex 9, France

Abstract

Estimating population size and trends are key issues in the conservation and management of large carnivores. The rebounding brown bear (*Ursus arctos*) population in Sweden is monitored by two different systems, both relying on voluntary resources. Population estimates have been calculated with Capture-Mark-Recapture methods, based on DNA-based scat surveys in 5 of the 6 counties with established bear populations. A total of 1,358 genotypes were identified using DNA extracted from collected scats. An independent ongoing program, the Large Carnivore Observation Index (LCOI), was started in 1998. The LCOI uses effort-corrected observations of bears by hunters during the moose (*Alces alces*) hunt (>2 million observation hours/year) and has shown a good correlation with relative population density of bears using the DNA-based method. From this, we have calculated population trends during the period 1998-2007. We estimated the yearly increase in the bear population to be 4.5% at the national level, varying between 0 and 10.2% in different counties, using an exponential model. We used the regional population estimates and the trends from the LCOI, taking the variation from both systems into account using parametric bootstrapping, to calculate the regional, as well as national population size in Sweden in fall 2008. In one case (the northernmost county, Norrbotten) a DNA-scat survey was lacking, so assumptions based on data from the neighboring county were used to estimate population size. We estimated the Swedish brown bear population to be 3,298 (2,968-3,667) individuals in 2008. Our results suggest that reliable information, necessary for the management of the brown bear population can be obtained from volunteers using standardized methods.

Key words: Survey, observations, monitoring, genetic, DNA, scat, feces, volunteers
Introduction

Estimating population size and trends are important parameters for the management and conservation of large carnivore species (Kendall et al., 1992; Mowat and Strobeck, 2000). These parameters are used to assess population status, decide quotas for harvested populations, evaluate the effects of management measures or decisions (Wilson and Delahay, 2001), or obtain parameters for conservation principles, including the IUCN criteria for Red-listing evaluations (Vié et al., 2009). This is even more important for low-density populations of rare and elusive animals that are long lived and with relatively low reproduction rates; in addition these species are particularly difficult to monitor (Thompson, 2004). The brown bear (*Ursus arctos*) is a typical example of a cryptic animal with these characteristics and they occur in relatively low densities even within established areas and avoid humans (Nielsen et al., 2004; Nellemann et al., 2007). The public often demands an accurate knowledge of population size. Thus, managers are faced with challenges to estimate population sizes and trends and evaluate the population’s response to hunting and other management measures, often within short time spans.

Current methods for monitoring brown bears range from field observations to intensive collection of material for identification of individual bears by DNA analysis (Linnell et al., 1998). Observations are used both for estimation of population size and trends (Mattson 1997, Kojola et al., 2006; Schwartz et al., 2008; Kindberg et al., 2009) and most observation-based methods focus on females with cubs (Eberhardt and Knight, 1996; Harris et al., 2007; Ordiz et al., 2007; Schwartz et al., 2008), because they are easier to recognize in the field and are the most important segment for a populations stability. Observations can also be used in combination with other methods, e.g. in mark-resight studies, where radio-marked bears are used in combination with aerial surveys (Swenson et al.,
The introduction of non-invasive DNA-methods in the 1990s (Taberlet et al., 1999; Mills et al., 2000; Paetkau, 2003) led to the possibility to accurately distinguish individuals in an area without the need to capture and handle them. The prevailing methods for non-invasive DNA sampling are hair snagging using baits (Boulanger et al., 2002; Kendall et al., 2009) and collection of scats (Bellemain et al., 2005). Population size estimations have benefitted from the development of analysis methods using Capture-Mark-Recapture (CMR) software (White and Burnham, 1999) and better field methods for improving capture rates (Woods et al., 1999; Mowat and Strobeck, 2000; Kendall et al., 2009).

The brown bear population in Sweden was constrained to a few remote areas in the 1930s after centuries of persecution, with an estimated lowest population size of 130 individuals (Swenson et al., 1995). After effective conservation measures were implemented in the early 20th century, several population estimates showed a steady increase in population numbers and distribution (Swenson et al., 1995). However, these population estimates were made using different methods, mainly based on inquiries of presence or various methods of estimation and also lacked variance estimates, so they could not be compared or used to determine population trends. The first population estimate made by the Scandinavian Brown Bear Research Project (SBBRP) used several methods, including observations of marked and unmarked bears from helicopter surveys during the mating season and among harvested bears (Swenson et al., 1994). Today methods are based on systematic effort-corrected observations of bears by moose (Alces alces) hunters, introduced in 1998 (Kindberg et al., 2009), and DNA-based surveys using hunter-collected bear scat, introduced in 2001 (Bellemain et al., 2005). Together with data from harvested bears and research bears in the SBBRP, these are the main sources of information used for the management of the bear population in Sweden.

In this paper, we describe how we have combined cooperation with organized hunter teams to collect bear scats that we used for modern DNA-based population estimates and a standardized protocol for bear observations made by moose hunters to estimate the trend of the brown bear population throughout Sweden. We have also used these data to estimate population size even where DNA surveys had not been conducted. This has been extremely useful for bear managers in Sweden and perhaps can be used as a model for bear managers in other countries or jurisdictions. Here we report estimates of population trends and the population size of brown bears in 2008 in Sweden and the individual counties.
Material and Methods

Study area
Brown bears are unevenly distributed in the northernmost two-thirds of Sweden (Fig 1.) The population is expanding from four former core areas (Swenson et al., 1998; Manel et al., 2004), which results in a skewed sex ratio in the expansion areas (Swenson et al., 1998; Kindberg et al., 2009). The habitat is mainly boreal forest with the Scandinavian mountain range in the west and the more populated areas along the eastern coast. Large carnivore management is mainly administrated at the county level, and therefore most surveys are conducted or reported at that scale.
Figure 1. Map of Sweden with the different counties and the distribution of bears as an index of average bear density from the LCOI (1998–2006) in gray shading (higher densities with darker colors).

Collection of scats and genetic analysis

Searches for bear scats were conducted within counties throughout the study area except for the northern most county (Norrbotten) (Fig. 1), even where bears were very rare or nonexistent. Samples were collected opportunistically by cooperating moose hunters, volunteers, and personnel from the SBBRP. Hunters picked up each scat sample with a stick of wood and put 1 cm³ of it into a 20-ml collection bottle. A different stick and bottle were used for each sample. For each scat sample, the volunteers recorded sampling date, geographical location, the hunting team name, and coordinates (Swedish RT90 2.5 gon V).

For every collected scat sample, DNA extractions and amplifications were performed at the Laboratoire d’Ecologie Alpine, Grenoble, France, as described in Bellemain et al., (2005). Briefly, each DNA extract was first screened for species-diagnostic amplification with one microsatellite marker (G10P, Paetkau and Strobeck, 1994). Next, 6 microsatellite primers (Mu10, Mu23, Mu50, Mu51, Mu59, G10L; Paetkau and Strobeck 1994; Taberlet et
al., 1997) and a sex marker (Bellemain and Taberlet, 2004), were amplified, following the multiplex preamplification method (Piggott et al., 2004; Bellemain and Taberlet, 2004). The detection and sizing of fragments was performed in an ABI Prism 3100 DNA sequencer (Applied Biosystems, Foster City, California). Amplifications were repeated four times. We typed samples as heterozygous at one locus if both alleles appeared at least twice among the four replicates and as homozygous if all the replicates showed identical homozygous profiles. If neither of those cases occurred, the alleles were treated as missing data. The gels were analyzed using Genemapper (version 3.0) software package (Applied Biosystems, Foster City, California). Samples were grouped according to their genotypes and unique genotypes were identified.

Table 1. Summary of brown bear scat surveys and genetic identification in the studied counties in Sweden, i.e. the number of scat samples collected and analyzed, the number of samples successfully amplified for 5 to 7 loci (including the sex locus), and the number of unique genotypes identified.

<table>
<thead>
<tr>
<th>County</th>
<th>Survey year</th>
<th>Number of analyzed scats</th>
<th>Number of amplified scats</th>
<th>Number of unique genotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dalarna &amp; Gävleborg</td>
<td>2001</td>
<td>1066</td>
<td>728</td>
<td>311</td>
</tr>
<tr>
<td>Dalarna &amp; Gävleborg</td>
<td>2002</td>
<td>838</td>
<td>665</td>
<td>239</td>
</tr>
<tr>
<td>Västernorrland</td>
<td>2004</td>
<td>690</td>
<td>434</td>
<td>140</td>
</tr>
<tr>
<td>Västerbotten</td>
<td>2004</td>
<td>940</td>
<td>524</td>
<td>223</td>
</tr>
<tr>
<td>Jämtland</td>
<td>2006</td>
<td>*3000</td>
<td>2400</td>
<td>684</td>
</tr>
</tbody>
</table>

* 3000 scats were randomly selected to be analyzed among the 5185 collected scats.

Population trends

Since 1998, the Swedish Association for Hunting and Wildlife Management has collected observations of bears within the LCOI program during the moose hunt, as complementary information to their "moose observation" survey (Ericsson and Wallin, 1999; Sylvén, 2000; Liberg et al., 2010). The LCOI is based on bear observations made by moose hunters during the first seven days of the hunt and is corrected for effort using man-hours. The index has been evaluated and observations corrected for effort are closely correlated with relative bear density, as determined from individuals genetically identified during the population censuses, see below (Kindberg et al., 2009). Because the monitoring is carried out yearly, it has been used to calculate growth rate in each county, as well as for Sweden as a whole.
Population growth rate was calculated as the "instantaneous rate of increase" ($r$) for the period 1998-2007 using an exponential growth model, except for Gävleborg County where we used the period 1998-2006. The reason for the shorter period is that data collection changed in parts of Gävleborg County in 2007. Thus we cannot be certain that the 2007 stratum is comparable with earlier data. With regard to the national growth rate, these areas in Gävleborg County were removed (for the entire period 1998-2007), so that only areas that continuously submitted reports using the same protocol were used for the national growth rates.

**Population estimates**

*Counties with DNA-based estimates.* Population estimates of brown bears at the county level in Sweden have been based on the opportunistic collection of scats by volunteers (mainly hunters) during the early fall hunting season. Individual bears were identified using DNA analysis and the data were used in a CMR analysis to estimate total population size in the county. The method has been evaluated and appears to give a reasonable estimate of population size (Bellemain *et al.*, 2005; Solberg *et al.*, 2006). Estimates of this type have been conducted once in each of the counties with an established bear population, except for the northernmost county of Norrbotten, which also has the largest area and lowest human density. The counties of Dalarna and Gävleborg were surveyed in 2001 and 2002 to evaluate the technique and were followed by Västernorrland and Västerbotten in 2004 and Jämtland in 2006. Västerbotten was resurveyed again in 2009 but the data have not yet been analyzed.

The population estimates from the scat surveys in each of the counties (Table 2) were calculated using CMR methods available in program MARK (White and Burnham, 1999), with each week used as a session for capture and recapture. We used closed population models and model selection using Akaike’s Information Criterion (AICc) values and model averaging where appropriate (Burnham and Anderson, 2002). For the counties of Jämtland and Västerbotten, only the top models ($M_{th2}$) were used, as they were the only models with a delta AICc less than 2 (Burnham and Anderson, 2002). For Västernorrland two models were included in the model averaging and, because the lower bound confidence limit was less than the number of identified individuals, confidence limits were calculated by hand (Williams *et al.*, 2002). All high-ranking models included individual heterogeneity in capture probabilities and time effects. This seems to be reasonable, because search effort varied among capture sessions, with the highest effort attained.
during the first week of the moose hunt (Bellemain et al., 2005). Heterogeneity among individuals can arise due to factors that cannot be recognized from DNA, such as age and reproductive status (Boulanger et al., 2008). We modeled heterogeneity using two mixtures (Pledger, 2000; White, 2008).

The estimate for Dalarna and Gävleborg in 2001 (Bellemain et al., 2005) also had time and heterogeneity in the selected model. For that survey, it was necessary to divide the original population estimate to obtain the population size for each of the counties. We assumed that the population was distributed between the two counties in the same way as the identified genotypes, which gave a 52/48% split of the joint population of 550 bears (52% in Dalarna). Only 4% of the genotypes were found in both counties.

With the surveys spread over a 5-year period, it was not possible to analyze overlap between adjacent populations in different surveys. However, an analysis of all available genotypes (including the 2002 survey in Dalarna and Gävleborg) in 2008, found that 2.8% of the genotypes were present in more than one county (Bellemain unpublished).

County without a DNA-based estimate. No DNA-based population estimate has been conducted in Norrbotten County, although one is scheduled for 2010. We estimated the brown bear population for Norrbotten based on the LCOI in 2004 (to compare with adjacent Västerbotten in 2004 when the scat survey was made), the relationship between LCOI and the relative density of bears previously found for Västerbotten (Kindberg et al., 2009), and the estimated density of brown bears in Västerbotten from the DNA-based population estimate. The estimate of the 2004 population for Norrbotten was calculated using an area equivalent to the registered moose areas determined by the Norrbotten County Board (ca. 78,800 km²). This method entailed the assumption that the relation between the LCOI and bear density was similar to an adjacent county with comparable forest density and structure. This is an important assumption, because the slope of the relationship varies within Sweden (Kindberg et al., 2009). To improve our confidence in using the relationship from Västerbotten as a proxy for Norrbotten, we compared the relationship in Jämtland with that found in Dalarna-Gävleborg and Västernorrland. These counties also have a similar forest density and structure, but the relationship between the LCOI and population density in Jämtland was not included in the study by Kindberg et al., (2009). If the slope of the relationship were similar in these counties, it would strengthen our assumption that it would also be similar for Norrbotten and Västerbotten.
Statistics

To calculate the uncertainty in the estimates that included both the population size calculations based on DNA and population growth rates according to the LCOI, we used parametric bootstrapping to create 10,000 values of both population estimates and growth rate, using the same mean and variance as our results. We used the \texttt{rlnorm} and \texttt{rnorm} functions in the statistical software R 2.8.1 (R Development Core Team). We averaged the standard errors from the somewhat skewed confidence limits from the MARK estimates, which usually were smaller in the lower bound, because the population cannot be lower than the of the number of identified individuals. We used the lognormal distribution to improve the variance estimate of the population size, as it is has been suggested to be close to this type of confidence limits (Chao, 1989). Regardless of the lack of a perfect fit, the mean of the estimates will be the same and this only minimally affects only the size of the variance. The mean of the 10,000 population values gives the estimated population for each county in 2008 and the 95% confidence limits were calculated using the 2.5 and 97.5 percentiles. The total number for Sweden was estimated by randomly adding the 10,000 county estimates and calculating the mean and confidence, as described above.

To evaluate if the relationship between the LCOI and the minimum density of bear from the DNA-scat surveys were different, we tested the regression slopes between Jämtland and Västernorrland as well as among all the five counties (Dalarna and Gävleborg was combined) using analysis of co-variance. We considered results to be significant at a $p \leq 0.05$. 
Results

Genetic identification of individuals

Table 1 summarizes the number of scat samples collected and analyzed in the laboratory, the number of samples successfully amplified for 5 to 7 loci (including the sex locus) as well as the number of unique genotypes identified.

Relationships between the LCOI and minimum bear density

There was no significant difference between the slopes from the regression of observations/1000 h and minimum bear density from the DNA-scat survey in Jämtland and Västernorrland \( (p = 0.46) \), see (Fig. 2). We also tested the slopes from all the counties and only the slope of Västerbotten was significantly different \( (p < 0.001) \).
Population trends

The LCOI indicated that the bear populations had a significantly positive growth rate during the period 1998–2007 in all but two counties, Västerbotten and Dalarna, which showed no significant trend (Table 2). The highest growth rates were found in Gävleborg ($r = 0.097$, $p < 0.007$), based on data from 1998-2006, and Västernorrland ($r = 0.095$, $p < 0.017$), which are both considered to be expansion areas. In the counties of Jämtland and Norrbotten, which include several core areas of reproduction, the growth rates were lower ($r = 0.054$, $p < 0.007$ and $r = 0.050$, $p < 0.004$, respectively), but still are judged to be relatively high. The total Swedish bear population had a positive trend with an instantaneous rate of increase ($r$) of 0.045 ($p < 0.008$) as calculated from the LCOI.
Population estimates

The counties of Dalarna and Västerbotten had no significant population trend and therefore the population estimates and confidence limits (95%) for 2008 were the same as calculated from the scat surveys, 286 (251-337) for Dalarna in 2001 and 309 (265-401) for Västerbotten in 2004. The other populations had a significant observed population trend and bootstrapped estimates of initial population size and trends were used in an exponential model to estimate the population size for 2008 with 95% confidence limits. The Jämtland population was estimated to be 1,009 (878-1,151) bears in 2008. Gävleborg and Västernorrland, which had the highest observed growth rates, were estimated to have 529 (352-759) and 255 (171-364) bears, respectively, in 2008. The estimated population size in Norrbotten was calculated to be 910 bears (713-1,152) in 2008, using the relationship between observation rate and population density in Västerbotten.

The total population estimate for Sweden was calculated by randomly adding the 10,000 county estimates. The total estimate was a brown bear population of 3,298 (2,968-3,667) for 2008.

Table 2. Results from brown bear population estimates based on DNA in scats and trends estimated from the Large Carnivore Observation Index (LCOI) surveys in the different Swedish counties. The trends are based on data from 1998-2007 (1998-2006 for Gävleborg) and figures within brackets are confidence limits (95%).

<table>
<thead>
<tr>
<th>County</th>
<th>DNA Survey year</th>
<th>CMR population estimate</th>
<th>Growth rate (r)</th>
<th>p</th>
<th>Population estimate 2008</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dalarna</td>
<td>2001</td>
<td>286 (251-337)</td>
<td>0</td>
<td>0.590</td>
<td>286 (251-337)</td>
</tr>
<tr>
<td>Gävleborg</td>
<td>2001</td>
<td>264 (232-311)</td>
<td>0.097 (0.036-0.157)</td>
<td>0.007</td>
<td>529 (352-759)</td>
</tr>
<tr>
<td>Västernorrland</td>
<td>2004</td>
<td>173 (148-249)</td>
<td>0.095 (0.022-0.169)</td>
<td>0.017</td>
<td>255 (171-364)</td>
</tr>
<tr>
<td>Jämtland</td>
<td>2006</td>
<td>906 (821-1043)</td>
<td>0.054 (0.019-0.088)</td>
<td>0.007</td>
<td>1009 (878-1151)</td>
</tr>
<tr>
<td>Västerbotten</td>
<td>2004</td>
<td>309 (265-401)</td>
<td>0</td>
<td>0.300</td>
<td>309 (265-401)</td>
</tr>
<tr>
<td>Norrbotten</td>
<td>(2008)</td>
<td>-</td>
<td>0.050 (0.021-0.079)</td>
<td>0.004</td>
<td>910 (713-1152)</td>
</tr>
</tbody>
</table>
Discussion

In this paper we used two independent methods that we have developed and tested for monitoring the Swedish brown bear population. These provide management authorities with an index to follow the population trends in different areas over time, as well as distribution, and with statistically robust estimates of population size. All the counties in Sweden with an established bear population, except the northernmost county Norrbotten, have been surveyed between 2001 and 2006 to obtain population size using DNA from collected scats and CMR methods. These surveys cover more than 160,000 km² and encompass almost all areas where we can expect bears, apart from the mountain range. In addition the LCOI has provided yearly indices of bear density since 1998, covering all counties in Sweden with bears as well as those counties without a current bear population.

A common limitation in bear monitoring is that it is difficult to obtain large enough samples for CMR estimations, due to resource limitations and the huge area that must be covered (Mills et al., 2000). Here the role of volunteers is important, to keep costs low, but also to allow the survey of the huge areas needed (Newman et al., 2003). Another important advantage of using volunteers is that involving them in the monitoring process increases their knowledge and understanding of the procedures (Newman et al., 2003). The interest among volunteers must be maintained, with feedback as one of the most important factors, in order to obtain the long data series, 8–10 years, required for trend estimations (Maxwell and Jennings 2005, Harris et al., 2007). The use of LCOI as an add on to the ongoing moose observations system will help to keep this interest, as the moose is the motivation for most hunters. However, this means that the system is somewhat dependent upon the moose hunting situation.
The politically decided minimum population goal in Sweden was set in 2001 as 100 yearly reproductions equaling about 1000 individuals. This was supplemented in a government decision in 2008 stating that the population should be maintained at about current levels on a national scale, but allowed it to increase or decrease at local scales, based on the local situation regarding conflicts, e.g. livestock depredation (including semi-domestic reindeer, *Rangifer tarandus*), competition for game, and problem individuals.

Our objective was to provide estimates of brown bear population size by county, because bear management operates at that scale in Sweden. That means that the spatial structure of bear population management does not correspond with the current bear population distribution (see Fig. 1). This will have an impact on the results, such as a violation of population closure assumptions, as parts of the same population will be surveyed at different times in different areas.

There are a number of confounding factors for both methods. For scat surveys, these can occur during the collection of scat samples (unevenly distributed or that some areas are completely missing, see Bellemain *et al.*, 2005), the handling of samples, the analysis of DNA, and the choice of models for estimating population size. We used closed capture models for estimation population size, as these are better suited for estimating the number of individuals (Amstrup *et al.*, 2005), but bears move across large areas and therefore some bears can appear in several counties, violating closure assumptions (Miller *et al.*, 1997; Schwartz *et al.*, 2003). We believe that this is minor issue, as the sampling takes place on a limited period (maximum 12 weeks) during the hyperphagia period, when there is little immigration/emigration and also that the surveys cover large areas, thus encompassing most of the individuals (Kendall *et al.*, 2009).

Using observations for estimating population size has been criticized, with several studies showing these to underestimate population size (Swenson *et al.* 1995; Schwartz *et al.*, 2008; Kendall *et al.*, 2009), but for estimation trends of population size, they seem to give comparable estimates to demographic methods (Harris *et al.*, 2007; Brodie and Gibeau, 2007) but see Fernandez-Gil *et al.*, (2010). This, in addition to our evaluation of the LCOI (Kindberg *et al.*, 2009), supports our assumption that we can use the LCOI to obtain trends in the population. The conditions in each area should also be as similar as possible throughout the period. If changes occur in e.g., the manner in which the hunting is conducted, the reporting protocol, the areas involved, or the composition of the brown bear population, it could affect the LCOI.
We calculated population growth \( (r) \) as exponential growth. It is very likely that this model is not valid in a stable bear population because it, for example, does not include density dependent effects, although it does not require any other assumptions. The difference between different growth models should be small in our case and we only included the years for which we have data.

Harvest rates have increased rapidly in recent years (quotas increased from 55 in 1999 to 233 in 2008) and all the effects of the most recent quotas cannot be fully seen in the calculated growth rate, which is based on data from the entire period. This means that the projected growth that we have used may be somewhat higher than it actually was at the end of period. The estimated sustainable harvest in the Swedish population has been estimated to be 11.2% of the females (C.I. 8.2–13.5%) based on long-term monitoring data from the study area in central Sweden (Bischof and Swenson, 2009). Future trend estimations, when more data are available, should include curvilinear models in competition with the current model as used elsewhere see (Harris et al., 2007).

The estimate for Norrbotten was largely dependent on assumptions based on the survey in Västerbotten. It is most likely that the relationship between the number of bears and the LCOI is more similar to the situation in the adjacent Västerbotten than in the other counties. But inside Norrbotten we find two former core areas for female bears, whereas Västerbotten only shares one with Jämtland (Manel et al., 2004). The same assumption was made between the Jämtland and the adjacent Västernorrland in an earlier estimate, before Jämtland was surveyed. Here we were able to verify this assumption (Fig 2.). Nevertheless, we must await the first scat survey in Norrbotten to test the assumptions we used here. Until then, this population estimation for Norrbotten should be used carefully.

The LCOI shows a clear linear relationship when compared to the relative density of bears in DNA surveys (Kindberg et al., 2009), but the relationships are different in different areas, as with moose (Ericsson and Wallin, 1999). However, these relationships might change both over time and with changing bear density. One should therefore periodically, perhaps every 5–7 years, correct bear observations with other surveys (DNA scats) to reduce the risk of over- or underestimates. The need for a complementary DNA-survey can be accelerated if the LCOI indicates a major change in the population trend, especially a decline (Hauser et al., 2006). It is also important that the method of collection bear observations is implemented in the same way over time.
Initially, a population survey using DNA should be conducted in Norrbotten to determine the population size and the relationship to the LCOI. It is important to conduct new estimates in the other counties, with Dalarna and Gävleborg having the oldest estimates. One should consider conducting the surveys to include the entire subpopulation of bears (Manel et al., 2004) to avoid violations of the assumptions of closed population models. It is important to continuously evaluate our models against estimates from future DNA-based scat surveys to test the accuracy of the estimates and verify the trend calculations from the LCOI to learn from the process, i.e., adaptive management.

Our calculations have not taken immigration, emigration or deaths into account, but they should be considered for future surveys. A common database has recently been constructed, containing all bears that have been sampled and analyzed, which will contribute to that. Bears that are located south of Gävleborg and Dalarna counties have not been considered in our national estimate, because they represent a relatively small part of the Swedish population. Other elements that should be included in future analysis (as discussed above) are the effects on growth rate caused by hunting, both short- and long-term, various growth models, and diffusion and density. Heterogeneity in capture probabilities may occur because some individuals are located in less accessible areas. A solution to this might be to model distance to roads as a covariate for individuals (Huggins, 1989). The sex ratio of the population should be followed, as a change in the ratio might indicate a shift from an expansion area (with fewer females, Swenson et al., 1998) to a more stable population structure with more reproducing females.

The use of the two independent methods we have developed and tested for monitoring of the Swedish brown bear population provides management authorities with an index to follow the population trends in different areas over time, as well as distribution and statistically robust estimates of population size. It is of course crucial that the scat surveys are repeated at reasonable time intervals to confirm trends obtained by the LCOI and to verify population sizes, in combination with data on harvest and other mortality. It is also important to be able to adjust the established relationships between the two methods in different areas, as these may change over time.
Acknowledgements

We thank the participating hunters collecting scats and making observations, the county boards of Jämtland, Västerbotten and Västernorrland, the Swedish Association for Hunting and Wildlife Management, WWF Sweden, FORMAS, Swedish EPA and the program for Adaptive Management of Fish and Wildlife Populations. We thank G. Bergqvist, C-G. Thulin and F. Widemo for comments on an earlier draft of the manuscript.
References


