Habitat use and population dynamics of brown bears (*Ursus arctos*) in Scandinavia

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Academic dissertation

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The thesis is based on the following articles, which are referred to in the text by their Roman numerals:


The following table shows the major contributions of authors to the original articles

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Aristotle said ‘For the things we have to learn before we can do them, we learn by doing them’
Summary

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“Arguably, no group of organisms offers more challenges to conservation biology and conservation politics than large carnivores. These animals, in accord with how they make their living, are big and fierce.”

(Noss et al. 1996)

1. Introduction

1.1. Conservation and management of large carnivores

Humans are increasingly entering carnivore habitats and at the same time populations of large carnivores recovering from past extirpation efforts are becoming involved in mutually threatening interactions with humans. Many populations of large carnivores escaped extinction during the twentieth century owning to legal protection, habitat restoration and changes in public attitudes (Breitenmoser 1998, Treves et al. 2004). Successful management has resulted in gradual recovery and return of carnivores to their original habitats, which has lead to carnivore-human conflicts and damages to livestock in many areas worldwide (Mech 1995, Mattson et al. 1996, Breitenmoser 1998, Servheen et al. 1999, Kojola & Kuittinen 2002, Garshelis & Hristienko 2006). For large carnivores to have a long term future we have to allow them to reoccupy some of their former habitats, which means integrating them into the landscapes where humans live. This makes the conservation of large carnivores particularly challenging.

Major threats or obstacles for bears and large carnivores in general are negative attitudes, human-caused mortality and deterioration of habitats (Swenson et al. 2000). Together with legal harvest and poaching vehicle collisions are a significant source of human-caused mortality (Revilla et al. 2001, Hebblewhite et al. 2003). Roads also hamper animal movements, decrease the habitat quality and increase the accessibility of poachers to wild animals (Mace et al. 1996, Noss et al. 1996, Merrill et al. 1999, Cramer & Portier 2001, Revilla et al. 2001, Kerley et al. 2002, Kramer-Schadt et al. 2004). Negative attitudes towards predators originate mainly from conflicts with domestic animals, mostly sheep and semi-domestic reindeer as well as hunting dogs (Sagør et al. 1997, Breitenmoser 1998, Naughton-Treves et al. 2003, Ogada et al. 2003). Additionally, poaching is primarily motivated by damage to domestic animals together with perceiving carnivores as competitors for ungulate game (Andren et al. 2006). Large carnivores are also often perceived as a threat for human safety. A key for conservation of large carnivores seems to be reduction in damages to livestock as well as better understanding of the values, beliefs, and demands of those who are involved or affected (Breitenmoser 1998, Woodroffe 2000, Bowman et al. 2004, Mattson et al. 2006).

Various methods for human coexistence with large carnivores have been suggested, ranging from barriers and repellents based on unpleasant olfactory or visual stimuli to translocation of carnivores (Linnell et al. 1997, 1999, Musiani et al. 2003, Treves & Karanth 2003). Wildlife management is often viewed as a discipline oriented towards seeking
Brown bears are solitary carnivores that use large areas during their lifetime. Adult bears establish lifetime home ranges that may overlap to varying degree depending on the sex and relatedness of the individuals, and home ranges of males are larger than those of females (McLoughlin et al. 1999, Dahle & Swenson 2003a, b, Støen et al. 2005b). The size of a bear’s annual home range in Scandinavia varies from 200 km² for adult females to over 1000 km² for adult males (Dahle & Swenson 2003a, 2003b). A majority of the males disperse from their natal areas, whereas females are more philopatric and often establish home ranges that overlap or are adjacent to their natal areas (Blanchard & Knight 1991, McLellan & Hovey 2001, Kojola et al. 2003, Støen et al. 2005a). However, in an expanding population also females have been shown to disperse, although not as far as males (Swenson et al. 1998b, Kojola & Laitala 2000). In Scandinavia, males generally disperse at the age of two years, whereas females tend to leave at the age of three years (Støen et al. 2005a).

The age of sexual maturity for both sexes varies between 4 – 6 years (McLellan 1994, Zedrosser et al. 2004). The earliest recorded age at first reproduction is 3 years (Zedrosser et al. 2004). During the mating season in mid-May to early July bears increase their range size and females may mate with several males as well as males with several females (Craighead et al. 1995, Dahle & Swenson 2003b, Schwartz et al. 2003). The ovulation of female bears is induced by behavioural, hormonal or physical stimulus (Boone et al. 1995, Craighead et al. 1995). The litter consisting of 1-3 and occasionally 4 cubs is born in the winter den in January to March. Cubs typically follow their mother over the next wintering period and separate from the mother during the following spring, sometimes rarely females keep their litter even as long as 3.5 years, although in Scandinavia only maximally for 2.5 years (McLellan 1994, Swenson et al. 2001, Schwartz et al. 2003). Bears may live older than 30 years, but reproductive senescence occurs in females at an age of around 27 years (Schwartz et al. 2004).

Only females take care of the offspring and when accompanied by a litter they are not receptive to males, which leads to a minimum interval of two years between successful litters. Consequently, male bears may benefit from the killing of the young by gaining a mating opportunity with the mother, thereby exhibiting sexually selected infanticide (SSI).
Box 1. Return of the bear

The recent history of the Scandinavian brown bear goes from near extinction to population recovery and expansion through successful management (Swenson et al. 1994, 1995, 1998a). The current population size estimate in Sweden is 2350 - 2900 individuals (Kindberg & Swenson 2006). The development of the nearby Finnish population follows about the same pattern (Nyholm & Nyholm 1999, Kojola & Laitala 2000). Based on bounty data there were 4000 – 5000 bears on the Scandinavian Peninsula around 1850, and over 1000 bears in Finland. As the policy at that time was to exterminate bears, by 1930 bears were virtually extinct from Norway and only 130 individuals had survived the overexploitation in four small remnant areas in Sweden (Swenson et al. 1995, 1998a). As the turn of the century, national parks were established and killed bears became Crown property in Sweden, which removed the economic incentive to kill them. As a response to reduced mortality, the population grew quickly and expanded in spite of continuing habitat change due to intensive forestry (Swenson et al. 1998a).
Summary

Infanticide is classified as SSI if the perpetrator is not the father of the young it kills, if killing of the young shortens the time to the female’s next oestrus, and if the perpetrator has a high probability of siring the female’s next litter (Hrdy & Hausfater 1984). These three requirements have been documented in brown bears in Scandinavia (Bellemain et al. 2006), and the occurrence of SSI or counter-strategies related to it have been documented in various brown bear populations (Wielgus & Bunnell 1995, Swenson et al. 1997, 2000, 2001). Female brown bears have counter-strategies to avoid SSI, such as multi-male mating and use of suboptimal habitats, together with movement and activity patterns that differ from those of males (Wielgus & Bunnell 1994, 1995, 2000, Swenson 2003, Ben-David et al. 2004, Bellemain et al. 2006).

Feeding habits of bears vary between seasons. Although during spring bears are significant predators of ungulates in some areas, the main source of yearly energy consumption are berries which constitute most of their diet in the autumn before hibernation (Dahle et al. 1998, Persson et al. 2001). Also ants form a significant portion of bears food in boreal forests (Swenson et al. 1999).

1.3. Scandinavian Brown Bear Research Project

The Scandinavian Brown Bear Research Project (SBBRP) collared its first bear in 1984 with an objective to study the basic ecology of brown bears. To date the project has followed more than 400 bear individuals, many from birth to death. This material

Figure 1.

How some of the central topics studied within Scandinavian Brown Bear Research Project are shared between students (ellipses). Common for all the topics is that they all aim to better understand the factors determining the distribution of bear populations that is essential for sound scientifically based management of bears. The green ellipse points up themes that have motivated this thesis (see 1.5.).
has been utilized in investigations regarding many aspects of the life-history, behaviour, genetics and population biology of bears as a model for large carnivores. The SBBRP has contributed significantly to the conservation and management of brown bears at the European level, and has also collaboration with North American research projects. Most of the knowledge about bears presented above is due to the SBBRP. Several PhD and MSc projects form the backbone of the research currently done in the project. Although these projects also have their own objectives, they aim to build on the previous research in the project, so that each student with a different background adds to the knowledge of bear biology and to the understanding of population ecology and management of large carnivores in general (Fig. 1). The main areas of focus in the SBBRP currently are: (i) the consequences of harvesting on population dynamics, and (ii) its role as a selective pressure in bear life history, (iii) habitat selection and the effects of forestry, (iv) density-dependent population regulation, (v) genetic components of fitness, and (vi) development of population monitoring techniques. The common goal is to understand factors affecting population distribution, which is essential for the successful management of bear populations and avoidance of conflicts with humans, also outside Scandinavia.

1.4. Study areas and data collection

The Scandinavian Brown Bear Research Project has conducted intensive radio tracking in two study areas, one located in northern Sweden (67°N, 18°E, 8000 km²) and the other in central Sweden and south-eastern Norway (61°N, 18°E, 13000 km²) (Swenson et al. 1998b, Dahle & Swenson 2003a, b). Boreal coniferous forests with Scots pine (Pinus sylvestris) and Norway spruce (Picea abies) dominate both study areas, although lakes and bogs cover large areas especially in the south. Mountains with subalpine habitats with birch (Betula pubescens) cover parts of the northern area. Elevations range from 200 m in the south to above 2000 m in north. Both study areas are sparsely populated by humans. For a detailed description of the study areas see (Zedrosser et al. 2006). Legal harvest has been allowed within both study areas throughout the study period, but the northern area includes three national parks, in which hunting is prohibited. Harvest season is in the autumn from 21 of August until 15 October (or 15 September in the north). The total harvest is limited by a quota set by the authorities for each of the ten counties where hunting is allowed. All hunters must report bears that are killed or wounded within 24 hours. When the quota is met, the season is closed with a 24-hour notice. Females that are accompanied by a litter are protected from the harvest. Hunters report the location, sex and weight of the killed bear. Hair samples and a premolar tooth from all hunter-killed bears are sent for further DNA analysis and age determination (Matson et al. 1993).

Bears were captured in the spring shortly after den emergence by immobilizing them from a helicopter using a remote drug delivery system (DanInject®). The drugs and protocol used in immobilization are described in Arnemo (2005) and Arnemo et al. (2006). Adult individuals were equipped with neck-mounted VHF radio transmitters (Telonics®). A sterile radio transmitter was implanted in the peritoneal cavity of yearling females following a well established biomedical protocol (Arnemo 2005). Thus the female young of marked mothers were followed from the birth. All captured bears were weighted and measured, and blood, hair and tissue samples were taken for the later analysis. For animals that had not been followed from birth, a premolar tooth was removed for age determination (Matson et al. 1993). Radio-marked bears were located on average once a week from an aircraft or from the ground using receivers and handheld or aircraft-mounted antennas during their entire active period from April to October (Dahle & Swenson 2003a, 2003b). The reproductive state of radio-tracked females, i.e. the number and age of cubs following the female, was systematically monitored from an aircraft or the ground after females emerged from their winter dens, after the end of the breeding season (early July) and before entering the den. Bears were normally monitored until death or transmitter failure. All capture and handling conformed to the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämnden i Uppsala).

1.5. Questions that have motivated this thesis

The conclusions of previous studies from the SBBRP describing the pattern of population expansion discovered the need to investigate the role of space-use and population dynamics in the ecology of Scandinavian bears. Coming from a department with a strong background in spatial ecology and population modelling, the obvious choice for my
PhD project was to address large-scale spatial aspects and to use modelling as a tool for answering some of the hottest bear management issues in Scandinavia today. These include questions such as what is a suitable habitat for a bear? How are these habitats distributed and are there still suitable unoccupied areas for bears? Is the bear population more vulnerable to increased harvest of some particular kinds of individuals? In order to assess these issues I aimed at developing and parameterising an individual-based model for simulating bear population dynamics, which could later be expanded to a spatially realistic predictive model.

2. Main results and discussion

2.1. Habitat use


Space use by an animal is described by its home range or utilisation density distribution (UD); an area with a spatially defined probability of occurrence of the animal during a specific time period (Powell 2000, Kernohan et al. 2001). Home ranges estimated from radio location (or GPS) data often form a framework for analysis of animal movements and habitat selection, and good estimates of home ranges can thus provide interesting insight into many basic topics in animal ecology. Chapters I, II and III in my thesis deal with landscape-level habitat assessment for bears and the development of improved kernel methods for estimating home ranges.

The brown bear population in Scandinavia has been increasing and expanding its range during the last decades (Swenson et al. 1994, Swenson et al. 1995). Consequently, it is important to evaluate the distribution of areas suitable for bears, occupied and yet unoccupied by the population. Brown bear home ranges are not randomly distributed over the landscape, but occur mainly in forested areas with a low level of human influence, as defined by the human influence index we developed for Scandinavia (I). Avoidance of humans is apparent both in the northern and southern study areas in Scandinavia, even though the general level of human influence is much lower in the north (I). This suggests, that instead of having a strict threshold, bears avoid humans relative to the level of surrounding human influence, at least in the case of an expanding bear population and Scandinavian levels of human influence. The best 50% of the habitats based on the quantitative habitat model for bears (I) cover approximately 115 000 km² of the Scandinavian peninsula (Fig. 2). Based on bear observations and our habitat model, bears apparently already occupy most of the areas with good habitat in Sweden, except an isolated area in southern Sweden that is separated from the occupied area by a dispersal barrier formed by large lakes and high human influence (Fig. 2). There are large areas of suitable unoccupied habitats in south-eastern Norway.

Radio-telemetry data obtained by traditional triangulation methods (Box 2) often contain periods of frequent observations within a time series of temporally more isolated and independent observations. The utilisation density distribution (UD) is an estimate of the proportion of time spent at any location inside an animal’s home range. Consequently, using such partially temporally aggregated data overemphasises areas of frequent sampling in the UD estimate. On the other hand, loss of data results if data is standardized into regular temporal intervals by resampling only locations that have at least a given time interval between them (II)(Rooney et al. 1998). Instead, data can be weighted so that if an independent observation temporally distant from other observations is given a relative weight of one, then observations in a temporally aggregated cluster are given weights less than one. However, the total weight of such a cluster exceeds one, as it contains more information than just an individual observation would (II, III) (Fig. 3). Simulation experiment with known UDIs shows that such a
weighted kernel estimate performs better than an estimate that uses resampled data (II).

In addition to having problems with temporally autocorrelated data, kernel estimates are sensitive to the degree of smoothing that has been chosen (Silverman 1986, Worton 1989, Seaman & Powell 1996). A too wide kernel width spreads the estimate and conceals details of the internal structure of the home range, whereas narrow smoothing results in unrealistic peaks and leads to a discontinuous estimate. Furthermore, kernel estimators have been criticised for ignoring sharp edges and spreading the home range unrealistically to unused habitats, and thus, overestimating the size of the home range (Seaman et al. 1999). The latter problem can be overcome by modifying the kernel with a preference multiplier for each habitat type (III).

Using a novel likelihood-based Bayesian approach in estimating these habitat multipliers simultaneously with the kernel width from the location data provides a way of incorporating effects of habitat quality and parametric uncertainty into home range estimates (III). Habitat multipliers reflect the animal’s habitat preference accounting for habitat availability. Additionally, a Bayesian estimate of the home range structure is obtained. When applied to brown bears, our approach results in smaller estimated effective home range sizes and apparently more realistic home range layouts (III, Fig. 3). This is because the UD does not spread into presumably poor habitats adjacent to animal observations, such as agricultural land and barren terrain bordering forest. Instead, the estimated UD concentrates more into preferred habitats, such as forest.

**Summary**

Box 2. Traditional triangulation

Most of the location data were obtained using standard triangulation (White & Garrott 1990, Rodgers 2001), i.e. the location of the bear with the transmitter was estimated by taking at least three directional bearings from known locations (normally from roads) and the animal was assumed to be located at the intersection of the bearings (or within the middle of the formed triangle) (see the figure below). The error in the localisation depends on the habitat (topography etc.), distance from the transmitter, and the movements of the individual between the measurements. The mean error in the positions obtained with triangulation in this study was 452 m ± 349 m (SD), when the bearings were taken from 400 – 2200 m distance from the transmitter (B. Dahle unpublished data).

**Figure B1.**

An example of how the bearings are taken to locate the radio-marked bear.

The main limitation of the triangulation technique is the signal range of the transmitter, which varies from a couple of kilometres to about 20 km depending on the landscape. Because bears move over large areas, locating bears by triangulation is limited by searching time and access to remote areas. Consequently, it is virtually impossible to collect location data with regular time intervals or simultaneously for many bears, and obtain equal representation of all the individuals in the data. Also, costs increase with increased frequency of the localization. For some specific studies more frequent data was collected for fewer individuals. Conventional methods of analysis have been limited in overcoming the challenge posed by such diverse records following from inherent shortcomings in the tracking protocol.
SUMMARY

example of the performance of both novel home range calculation methods developed during the course of this thesis is given in Fig. 3.

Figure 2.
Distribution of predicted suitable habitat for bears in Scandinavia based on the model developed in chapter I. The classification is based on predicted values within estimated bear UDs (described in chapter I), the more green the area the more suitable is the habitat.
2.2. Population dynamics

The Brown bear population in Scandinavia has increased both in numbers and range after a population bottleneck in the early 1900s, even though conservative harvest has been allowed since 1943 (Swenson et al. 1994, 1995, 1998b). Sæther (1998) estimated an annual population growth rate of up to 16%. Concerns about the threats that an increasing bear population causes to humans and livestock have increased the pressure for controlling the population by raising the level of harvest.

The effects of harvest on population dynamics depend partly on the interaction between hunter selectivity and the mating system of the target species (Greene & Umbanhoward 1998). In polygynous species, such as bears, the strategy of selectively harvesting males has been considered to increase the sustainable yield (Swenson et al. 1997; Sæther et al. 2004). This is particularly widespread in the management of ungulates (McLoughlin et al. 2005). However, in some species, male-biased harvest may disturb the social structure of the population and induce sexually selected infanticide (SSI), reducing the survival of the offspring (Hrdy 1979, Whitman et al. 2004). Chapters IV and V cover quantification of the effect of SSI on litter survival and evaluation of different harvest schemes while accounting for SSI in Scandinavian brown bear population.

Large male bears are a popular trophy, which might skew hunting mortality in bears towards males.
3. Synthesis and perspectives

In this thesis I have assessed the distribution of suitable areas for bears at the scale of Scandinavia and investigated their population dynamics, in addition to developing improved methods for analysing space-use and home ranges of animals. These studies show that unoccupied areas still exist for bears in Scandinavia (I) and that the population is likely to continue to grow in numbers as it is estimated to tolerate relatively high rates (10%) of harvest (V). One remaining question is whether the population will expand to unoccupied areas and how large populations could be sustained taken the habitat distribution. Our ability to answer this question is at the moment limited by inadequate knowledge about density-dependency in the population dynamics of the bear.

Bayesian estimation of home ranges (III) helps in determining effective areas of habitat needed for bear home range establishment. Other studies in the SBBRP have indicated that not only the age and sex of the individual influences the probability of dispersing, but also population density is likely to play a role (Støen et al. 2005a, 2005b). Obviously such social aspects of use of space should be linked with the surrounding habitat structure to really understand the mechanisms of population expansion. Further development of the Bayesian home range estimation by the inclusion of continuous variables, such as distance to other individuals, would enable studying the effect of other individuals in the formation of home ranges. Such improvements in understanding of density-dependent population processes could eventually help in evaluating spatially targeted harvest as a tool for controlling the population.

Traditional radio-tracking data motivated the development of new tools for analysis of habitat use, but it did not allow a detailed study of bear movement paths and dispersal. This is because of the relatively infrequent observations and because dispersing bears were likely to move outside the study area. Thus, an obvious continuation of this work is study of bear dispersal using newly available GPS locations, where the temporal resolution of data is much higher than with radio-tracking. A realistic model of sex-specific dispersal behaviour is one critical missing piece needed for a spatially explicit population model. The individual-based
model of study V would serve as a platform into which spatial elements could be built into.

Topics addressed in this thesis are all essential components to build a spatially explicit population model for brown bears in Scandinavia. It is of interest for management to be able to project the future distribution of the population while taking into account the development of human activities. The approach of individual-based modelling was chosen particularly because of its potential to incorporate the structure of the landscape and the complicated behaviour of individuals, such as SSI (IV), into the model of population dynamics (Grimm 1999, Akçakaya & Sjögren-Gulve 2000, Cramer & Portier 2001, Grimm & Railsback 2005). The harvest model presented here demonstrates the usefulness of simulation models for evaluating effectiveness and likely consequences of different management actions. Combined with the recent developments in techniques for monitoring the bear population size (Bellemain et al. 2005), such models become useful tools for adaptive management. In adaptive management, new data will be collected on a regular basis and the model would be re-evaluated and updated based on new information (Mattson et al. 1996).

Although habitat models, together with population models, help us determine the feasibility and consequences of different management goals, the question of what exactly are the goals remains political. Management of human-bear conflicts depends on the political landscape as much as the physical landscape. This work provides grounds for determination of these physical requirements and on further development of a quantitative spatially realistic management-oriented population model of bear dynamics in Scandinavia and Finland.

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Although I was not the most frequent participant in the Wednesday morning coffee, I enjoyed the lively group of PhD students, and those that will always behave as they still were students, in the department. Some days were considerably improved by nice comments about the green skirt (Vesa and Sampa) or loud jokes than can be heard to the other end of the corridor (Suski L and Johan). I particularly enjoyed organising Spring Symposium with Henna and Heikki –Mei to fôörs pîit juu voreveer! My warmest thanks to Henna and Katja for being great friends and “vertaistuki”. Thank you Hippo, Ilkka T, LUOVA-coordinators and Veijo for your help with practical issues and patience with my studies.

Preparing thesis practically means no other life. I’ve still managed to keep some good friends outside the department that have supported me through this experience. Friendship of Mirkka, Mimmu and Jodie has been very important and refreshing. I especially want to thank Riikka for not giving up with me, always believing in my skills, for your point of view. I thank the Kuhistelijat, especially Suski R, for pretty much taking care of my social life.

Kiitos Äiti ja Isä mittaanamottoma tuestanne tänä aikana. Kiitos, että olette uskoneet kykyihini ja puskeeteet minua eteenpäin. Kiitos myös Katajiston perheelle ja kaikille karvakamuille. There are no words to express my gratitude to Pekka. Your love and friendship have carried me through. You have put things in perspective when I totally lost the scale. You are my rock.

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Summary

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Central Research Station., St. Paul, MN.


Summary


Landscape-level habitat use by brown bears (*Ursus arctos*) in relation to human distribution in Scandinavia

Jonna Katajisto, Atte Molanen & Jon Swenson

- Submitted
Landscape-level habitat use by brown bears (Ursus arctos) in relation to human distribution in Scandinavia

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ABSTRACT

Assessment of large-scale habitat suitability is essential in planning the management of the expanding brown bear (Ursus arctos) population in Scandinavia. We built a quantitative habitat model using utilization distributions (UD) estimated with the kernel home range method for 73 female bears in two study areas in Scandinavia. Prior analysis of the habitat composition of home ranges ensured that the large-scale variables used in the model selection were biologically relevant. Bears were found mainly in forested areas with a low level of human influence relative to surrounding human activity. A strong correlation between the predicted habitat suitability and the distribution of hunter-killed bears indicated good performance of the model. The quantitative habitat model provides a helpful tool for bear management, as it can be used to identify and visualize suitable habitats for brown bears, as well as to estimate the potential future distribution of the currently expanding population in Scandinavia.

Keywords: Brown bear, Habitat model, Utilisation distribution, Ursus arctos

1. Introduction

The distribution of suitable habitat largely determines the distribution of wildlife (Krebs 1994, Scott et al. 2002). Because humans alter the environment continuously, species with large requirements for space, such as large carnivores, have to cope with multi-use landscapes at a broad scale (Noss et al. 1996, Linnell et al. 2000, Schadt et al. 2002). This may result in direct and indirect conflicts between humans and carnivores (Breitenmoser 1998). Consequently, a large-scale habitat suitability assessment is necessary for the conservation and management of large carnivores. Habitat models are a useful method to synthesise and apply current knowledge about habitat relationships to management and conservation questions (Schadt et al. 2002, Fernández et al. 2003, Larson et al. 2003, 2004).

After a population bottleneck in the early 1900s the Scandinavian brown bear (Ursus arctos) population has increased both in number and range (Swenson et al. 1994, 1995, 1998b). At the same time the human use of former bear habitats has increased (Linnell et al. 2000), which has raised concerns about human bear conflicts. On the other hand, brown bears are endangered in many areas in Europe (Swenson et al. 2000), which increases the conservation pressure in Scandinavia. The use of quantitative habitat models to evaluate the large-scale distribution of suitable habitats is an important step in planning conservation and management of this expanding population.

Brown bears use large areas during their lifetime. Adult bears establish lifetime home ranges that vary little in size and centre between years. The median size of bear annual home ranges in our southern study area is 217 km² for adult females and 1055 km² for adult males, and 280 km² and 833 km², respectively in the northern study area (Dahle & Swenson 2003a). Both sexes establish home ranges at maturity, at the age of 4 - 5 years. For bears, human activity is likely to affect their habitat selection and distribution, because bears are hunted...

To assess the suitable areas for brown bears in the Scandinavian Peninsula, we constructed a quantitative habitat model in two steps. In order to include only biologically relevant variables in the model selection, we first analysed whether the individual home ranges were randomly distributed in relation to habitat classes and the degree of human influence. Then, we developed a regression-based habitat model using variables that were found relevant in the first step in order to identify suitable areas for bears in Scandinavia, as well as those areas with potentially suitable habitat that are yet unoccupied by bears, but that might be occupied in the future if the population continues to expand.

Both analyses were based on utilization distributions (UD) estimated for radio-tracked bears with the kernel method.

2. Material and methods

2.1. Study areas and bear data

We used radio location data from adult female bears from two study areas, one located in northern Sweden (67°N, 18°E) and the other in central Sweden and south-eastern Norway (61°N, 18°E) (Swenson et al. 1998b, Dahle & Swenson 2003a, b) (Fig. 2). Both study areas are situated within the core areas of the current bear distribution. We followed 47 females in the southern study area, and 26 in the northern study area during 1996 – 1999 at least biweekly through their entire active period from April to October from an aircraft or from the ground using receivers and handheld or aircraft-mounted antennas (Dahle & Swenson 2003a).

To avoid biases due to occasional periods of intensive tracking, only locations at least 100 hours apart were used in the analysis. This interval has been used previously with the same data (Dahle & Swenson 2003a, 2003b), and it corresponds to the estimated time used by a bear to travel across its home range with mean speed, and to the time between weekly observations often available for bears (Wielgus & Bunnell 1994, Waller & Mace 1997, Arthur & Schwartz 1999, Dahle & Swenson 2003a).

Bear harvest is allowed in Sweden during a restricted season in the autumn from 21 August until 15 October. The total harvest is currently limited by a quota set by the authorities for each of the ten counties where harvest occurs. All hunters must report the sex, weight and location of bears that are killed. Females that are accompanied by a litter are protected from the harvest. We used an independent data set of all hunter-killed bears reported during the study period (total 706 locations) for evaluating the habitat model. Because the study bears were concentrated in two relatively small areas within the core of the current distribution of bears, this independent data set allowed better evaluation of the model performance on a larger scale.

2.2. Habitat data and human influence index

For habitat information we used the Pan-European Land Cover Monitoring (PELCOM) that was available for the entire area of the Scandinavian peninsula (Mücher et al. 2001). Habitat data were divided in 1100 m grid cells, which were each assigned to one of the 8 habitat classes: forests, semi-open land, agricultural land, barren terrain, permanent snow, bogs, open water and urban areas. We also had information about the human density in Scandinavia at the same scale (Statistics Norway and Statistics Sweden, provided by Norwegian Institute for Nature Research), but data on roads were not available. The same grid cell size of 1100m was used for all variables in both the analysis of home range composition and in building the habitat model. Because human influence is not limited to the immediate location of habitation, we spread the effect of habitation according to a decreasing-by-distance influence function (Merrill et al. 1999). We calculated a human-influence index \( H_i \) for each grid cell \( i \) in the map using a kernel calculation (Kot et al. 1996) based on the negative exponential distribution and weighted with human densities:

\[
H_i = \sum_{j=1}^{n} D_j \exp(-\alpha d_{ij}),
\]

(Eqn 1)

where \( D_j \) is the density of humans in grid cell \( j \), \( d_{ij} \) is the distance between cells \( i \) and \( j \), and \( \alpha \) is a parameter describing the spatial scale of the spread of human influence. We considered levels of a corresponding to half of the human influence being...
limited to within 2, 5, 10 and 20 km of the point of spread, and selected $a=0.1$ for further analyses (corresponding to 10km).

The level of human influence in Scandinavia decreased clearly from south to north and from the coast to the mountains. This trend is problematic, because human density throughout the southern study area is much higher than the density around the northern study area, which makes it difficult to include both study areas simultaneously in joint statistical analysis (locations closest to human habitation in the north have even lower human influence values than locations farthest from human habitation in the south). In order to remove this trend to better compare the two study areas, we calculated a relative human influence index ($R_i$) for each grid cell. $R_i$ was calculated as $R_i = H_i / G_i$, where $G_i$ is the broad-spectrum human influence, calculated using $a=0.01$ corresponding to a spread of 100 km. Our argument is that bears experience the human influence in relation to their surroundings rather than absolutely (especially in an expanding population) and would prefer locations where the relative human influence is comparatively low.

2.3. Home range calculations

Because we were interested in suitable areas for bears to establish their home ranges, we estimated adult female home ranges for the entire period of analysis to approximate the lifetime home range. Home ranges were estimated from radiolocation data using 99% kernel estimates (Worton 1989). In our calculations we used a normal distribution kernel with a spatial smoothing of 1500 m. Kernel method provides an estimate for the utilization distribution (UD) that depicts the probability of an animal occurring at each location within its home range. Instead of assuming uniform use of habitat within the entire home range or arbitrary selected contours, as is typically done with home range estimates (Marzluff et al. 2004), we used the UD values directly. For each bear to contribute equally to the analysis, we standardized each individual UD to sum up 1. We used the B-Range software for UD calculations and random sampling schemes (Katajisto & Moilanen 2006).

Random home ranges were sampled from within an area of 50 km from the outermost bear locations to estimate the availability of habitats at the landscape scale (Katnik & Wielgus 2005). We used 50 km to ensure that the sampled area was within dispersal distance for bears. The longest recorded dispersal distance for female bears in Scandinavia is 90 km, but on average they disperse 28 km (Stoen et al. 2005). For each female home range we sampled 10 random ranges (UDs) of the same configuration as real home ranges in order to have the same spatial autocorrelation (e.g. due to constraints of movement) in both the empirical data and random samples.

2.4. Statistical analysis

2.4.1. Home range selection

For animals that have established home ranges, the composition of available habitats may be more important than the distribution of individual habitat types. We used the utilization distribution (UD) by weighting the amount of habitat inside the home range, or the value of $H_i$ and $R_i$, with the corresponding UD values. At the landscape scale, non-selective individuals should locate their home ranges independently of the habitat distribution. To test this, we compared the total human influence ($H$), total relative human influence ($R$) and UD weighted habitat compositions of real home ranges with randomly located ranges. $H_i$ and $R_i$ were calculated by summing $H_i$ and $R_i$ values weighted with UD over the entire home range.

We tested home range selection using multivariate analysis of variance (MANOVA), with the UD weighted habitat composition as a response. If the habitat composition was significant in the analysis, the univariate analysis of variance (ANOVA) was used to identify which habitat classes contributed most to the difference (Arthur et al. 1996). Concerning the human influence, the comparison of real home ranges with random ranges was made using the nonparametric Wilcoxon rank sum test (equivalent to the Mann-Whitney test). Individuals were considered as sampling units in these analyses. The statistical environment R was used for all statistical analyses (R Development Core Team 2006).

2.4.2. Habitat model

Utilization distribution (UD) provides a probabilistic measure of use that can be related directly to categorical and continuous resources using multiple regression (Marzluff et al. 2004). Therefore, we apply here a novel approach based on UD values estimated with the kernel method. We assume that the differential use of habitats inside individuals’
home ranges, as measured by the UD estimates, reflects the general suitability of habitat for bears. Specifically, we used log-transformed UD values as the response variable in a linear regression.

The kernel calculations used for estimating the UD values induce a correlation between the deviations in neighbouring grid cells, i.e. values of neighbouring cells are likely to be more similar than expected at random (Lennon 1999). Therefore, we randomly sampled the UD estimates taking only one of each sixteen cells. This produced an average distance of approximately 4000 m between the nearest sample locations, so that points in the sampled data could be considered independent for the purpose of our analysis (because the smoothing parameter used in kernel estimates was 1500 m). The resulting number of grid cells with a UD value in each sample in the analysis was 300 for the north and 470 for the south. This sampling was replicated 1000 times for both study areas, and stepwise model selection using AIC as the selection criterion was used to identify the best model for each case. The selected models and variables were recorded for calculating the model selection and variable selection frequencies (Burnham & Anderson 1998). Parameters for the full model used in stepwise selection were selected based on our earlier analysis of home ranges. The final model was selected based on the model selection frequency and coefficients were then estimated using the full data set.

Because the UD values were log-transformed and we did not use any correction term to scale the predictions to correspond to original UD values, our interpretation for predicted UD values (UD') is an index of the use describing the suitability. For the purpose of evaluating the model we classified the landscape by taking the predicted UD' values for the cells within known 99% home ranges, sorting them and dividing them into 10% quantiles. These classes ranked cells from those with low predicted values (1) to those with high predicted values (10). Thus, the highest habitat suitability rank corresponded to the highest 10% of the utilisation density inside bear home ranges (i.e. 10% core of the home range). Note that the lowest rank also included all the predicted values that were smaller than predicted UD values inside the home ranges.

We calculated the area-adjusted frequencies of hunter-killed bears falling into each suitability rank class (the frequency of locations of killed bears within the class divided by the total area of that class inside the region used for harvest). We evaluated the predictive performance of the model by comparing these area-adjusted frequencies within each suitability class by the corresponding rank of that class using Spearman-rank correlation ($r_s$) (Boyce et al. 2002). A model with good predictive performance would have strong positive correlation, as more area-adjusted locations would continually fall within suitability classes with higher ranks (Boyce et al. 2002).

3. Results

3.1. Home range selection

The two study areas were analysed separately because they differed in their habitat composition and the level of human influence. Both $H_t$ and $R_t$ were much lower in female home ranges than on random ranges (Table 1). Also the habitat composition of home ranges differed from that of random ranges in both study areas (south: $F_1, 265 = 2.23, p = 0.03$, north: $F_8, 154 = 2.38, p = 0.02$). Univariate tests indicated that forests were preferred in the home ranges in the southern area ($F_1 = 13.291, p = 0.0003$, Fig. 1 A). In the northern area there was more semi-open land in home ranges than in random ranges ($F_1 = 9.654, p = 0.0022$, Fig. 1 B), whereas in the south the situation was the opposite ($F_1 = 5.057, p = 0.025$, Fig. 1 A).

| Table 1. Mean total human influence ($H_t$) and total relative human influence ($R_t$) on female brown bear home ranges and random ranges in Sweden. Note that the human influence in general was much lower in the northern study area. |
| --- | --- | --- |
| Home ranges | Random ranges |
| Southern study area | | |
| $H_t$ | 284.4 | 745.6 * |
| $R_t$ | 835.5 | 1759.3 ** |
| Northern study area | | |
| $H_t$ | 2.4 | 44.6 *** |
| $R_t$ | 46.6 | 798.6 *** |

***=*p<0.001; **=*p<0.01; *=p<0.05
Based on the above results we reclassified the categorical variable “habitat type” into 4 classes: $F$ = forests, $SO$ = semi-open land, $A$ = agricultural land, barren terrain, permanent snow and urban areas (that are likely to be avoided), and, $W$ = wetlands and open water (natural factors that can occur inside home ranges but are not favoured) (Fig. 2 A). Together with the habitat type of the focal cell ($\text{Hab}$) two neighbourhood measures of habitat were included in the model selection as independent variables: the amounts of forest and semi-open land in 24 neighbouring cells ($F_{24}$ and $SO_{24}$ respectively).

To avoid strong multicollinearity between the explanatory variables, the amount of other habitat types in the neighbouring cells was not considered. Also the relative human influence in the 24 neighbouring cells ($R_{24}$) was included in the analysis together with the relative human influence in the focal cell ($R_{i}$). The full model used as a basis for step wise selection was

$$\ln(UD) = \text{Hab}_{i} + R_{i} + F_{24} + SO_{24} + R_{24} : F_{24} + SO_{24} : R_{24}.$$  

The selected model after each of the 1000 replicates was recorded and the model selection frequencies were used for selecting the model for assigning suitable areas for bears. Because the most frequently selected models were different for the two study areas, we further examined the four most selected models based on combined data from both study areas (Table 2).

All the variables turned out to be highly significant in all of these selected models. The coefficients were very similar for all four candidate models (Table 2), as were the resulting habitat suitability maps. Thus, following the principle of parsimony, we used the simplest model (C1, Table 2) and calculated the predicted UD values (UD') over Scandinavia (Fig. 2C) based on the full data set using the fitted equation

$$UD' = \exp(-7.17 - 0.0026\text{Hab}_{i} - 0.268\text{Hab}_{i} + 0.0173\text{Hab}_{i} + 0.0411F_{24} + 0.0305SO_{24} - 0.292R_{24}).$$  

(Eqn 3)

Predicted values were then divided into 10 suitability rank classes based on the predicted values of the grid cells in known bear home ranges. We evaluated the performance of the habitat model with an independent data set of 706 hunter-killed bears (Fig. 3) by calculating the Spearman-rank correlation ($r$) between the area-adjusted frequencies...
Figure 2. The distribution of (A) four combined habitat classes used in the habitat model, (B) the human influence ($H$) in Scandinavia, and the visualisation of the final habitat assessment for brown bears (C). In panel A the open polygons show the two study areas, $F$=forests, SO=semi-open habitats, $W$=wetlands and open water, and $A$=agricultural and urban areas, barren land and permanent snow cover. In panel C the light areas represent predicted suitability ranks 5 or higher corresponding to the habitats inside 50% core of the bear home ranges, the dark areas represent the lowest suitability rank that also includes habitats not found in bear home ranges, arrows demonstrate areas with high suitability but not yet occupied by bears.
Table 2. The four best candidate models based on model selection frequency describing the habitat use of female brown bears in Sweden, with coefficients estimated with full data set. $H_{ab}$ = habitat type of the focal cell (see text for habitat classification); $F_{24}$ = amount of forest in the 24 neighbouring cells, $SO_{24}$ = amount of semi-open land in the 24 neighbouring cells, $R_{24}$ = relative human influence in the 24 neighbouring cells.

<table>
<thead>
<tr>
<th></th>
<th>Intercept</th>
<th>$SO_{24}$</th>
<th>$A_{24}$</th>
<th>$W_{24}$</th>
<th>$F_{24}$</th>
<th>$SO_{24}$</th>
<th>$R_{24}$</th>
<th>$F_{24} \times R_{24}$</th>
<th>$SO_{24} \times R_{24}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>-7.170</td>
<td>-0.0026</td>
<td>-0.268</td>
<td>0.0173</td>
<td>0.0411</td>
<td>0.0305</td>
<td>-0.292</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>C2</td>
<td>-7.177</td>
<td>-0.0025</td>
<td>-0.265</td>
<td>0.0161</td>
<td>0.0415</td>
<td>0.0308</td>
<td>-0.229</td>
<td>-0.003</td>
<td>-0.004</td>
</tr>
<tr>
<td>C3</td>
<td>-7.171</td>
<td>-0.0025</td>
<td>-0.267</td>
<td>0.0169</td>
<td>0.0412</td>
<td>0.0305</td>
<td>-0.279</td>
<td>-0.001</td>
<td>-</td>
</tr>
<tr>
<td>C4</td>
<td>-7.171</td>
<td>-0.0026</td>
<td>-0.268</td>
<td>0.0173</td>
<td>0.0411</td>
<td>0.0306</td>
<td>-0.285</td>
<td>-</td>
<td>-0.002</td>
</tr>
</tbody>
</table>

The highest suitability rank corresponded to the highest 10% of the UD inside female home ranges. Bear home ranges also are likely to contain habitats that are not important for establishing a home range. For example, if we consider that the highest 50% of the UD (50% home range core) equals to habitat actually needed for a bear to establish a home range, the total area covered by the corresponding predicted suitability ranks (5 or higher) in entire Scandinavia is 117,585 $km^2$. Apparently, bears already occupy most of this available suitable habitat, except for an isolated area in southern Sweden that is separated from the occupied area by a dispersal barrier formed by large lakes and high human influence. Also a large suitable area in south-eastern Norway is still unoccupied (Fig. 2C). This was the last area of hunter-killed bears within suitability classes. The model evaluation showed that there were successively more evaluation points in the higher value suitability classes, demonstrating a significant high positive correlation ($r = 0.98$, $P < 0.001$, Fig. 4), which indicates good predictive capacity of the model. This was evident even though bears close to human settlement (areas with higher $H_i$ and $R_i$) may be more likely to be shot than bears in remote areas of good habitat and females with accompanying offspring were protected from harvest.
Figure 4. Area-adjusted frequency of suitability classes for locations of hunter-killed brown bears in Sweden. Spearman-rank correlation between the area-adjusted frequencies and suitability ranks ($r_s=0.98$, $P<0.001$) indicates that the model predicted locations of hunter-killed bears well.

4. Discussion

The brown bear population in Scandinavia is increasing and expanding its distribution, which makes the management and conservation of bears challenging (Swenson et al. 1998a). Brown bears are a protected species in Europe, but conflicts with humans are likely to increase with the expanding population. Information about large-scale habitat use by brown bears is important for both conservation and preventing conflicts. Our results indicate that, although the distribution of suitable areas for bear in Scandinavia largely follows the distribution of forests, it is essentially restricted by relative human density.

Brown bears need large areas of habitat with a sufficient availability of resources, such as food and escape cover, to satisfy all lifetime requirements (Swenson et al. 2000). Unfortunately only very general level habitat variables were available for predicting the habitat suitability for the entire area of interest. We were concerned whether such coarse habitat types were able to predict the relevant features of the landscape for bears. However, the fact that female home ranges clearly were not randomly distributed over the landscape in relation to these variables indicated that they can be used as surrogates describing the fine scale resources needed by bears. Furthermore, the home ranges both in the north and the south were situated in areas with much lower human influence than in the surroundings. This was found even though the levels of human influence were very different in the two study areas. This suggests that human influence is experienced relative to the surroundings in this expanding population.

Home ranges were largely composed of forests and home ranges in the south were composed of more forest than expected from random. In the north forests were not preferred, which is probably due to their occurrence lower in the mountains and closer to human settlements than the subalpine semi-open land. In the southern area forests and semi-open areas were equally human associated. The results concerning semi-open habitat were somewhat obscure. In addition to association with human activities, also the vegetation in semi-open habitat is likely to be different between the study areas. This was not captured by the available habitat categories. However, our results show that bears are flexible in their habitat requirements (Linnell et al. 2000) and that human influence seems to restrict the use of habitats, which is similar to results from North-America (Waller & Mace 1997, Mace et al. 1999, McLellan & Hovey 2001, Gibeau et al. 2002, Apps et al. 2004, 2006).

At the Scandinavian scale our study areas with home ranges were situated in areas with very little urban and agricultural land, which explains the finding that the avoidance of those habitats was not unequivocal. Nevertheless, the human settlements were clearly avoided, based on the human influence index that we developed. This is in accordance with the idea that habitat selection is difficult to detect in generally suitable composition of habitats with small variation (Orians & Wittenberger 1991, Åberg et al. 2000).

Utilization distribution (UD) is a probability density function that quantifies the relative use of space by an individual (Silverman 1986, White & Garrott 1990, Kernohan et al. 2001). Although the UD has been used in many ecological studies, it has not been commonly used to relate space use to resource attributes (Marzluff et al. 2004, Neatherlin & Marzluff 2004). We used kernel calculations to determine individual UDs from radiolocation data. The proportional occurrence of habitat types within

occupied by bears in Norways, before they went extinct as a reproducing species in this country in 1980s (Swenson et al. 1995).
A home range was then calculated by weighting the amount of habitat (and the value of $H_i$ and $R_i$) with the corresponding UD values and weighted proportions were used in a compositional analysis. This is a simple way of incorporating UD into widely used compositional analysis (Manly et al. 1993) instead of assuming uniform use of resources inside home range boundaries.

We also used UD to build the habitat model by relating the UD values from known female home ranges to habitat and human variables using a multiple regression. A similar approach was termed resource utilization function (RUF) by Marzluff et al. (2004). As a result of the kernel method, the UD estimates for neighbouring cells are autocorrelated. We ensured that our model selection was not biased due to this spatial autocorrelation by randomly sampling the 99% kernel home range estimates.

To maximize the utility of the model we limited the number of the landscape-scale habitat variables entering the model selection to those that were biologically meaningful based on a prior analysis of habitat selection. Considering that brown bears are generalist species adapted to a wide range of conditions, we did not expect to find one distinct habitat model for them. Furthermore, the variables remaining in the selected model were coherent with the general observation that, although bears have adapted to a wide range of different environmental conditions, they are mainly found in forested areas with generally low human density (Linnell et al. 2000, Swenson et al. 2000). We build the model based on the UD values of adult females show higher site fidelity than males or dispersing individuals, because we were interested in areas that are suitable for population establishment. Reproductive females are also the important sex for population dynamics (Knight & Eberhardt 1985). Although sexual difference in bear habitat selection has been detected in many areas (Blanchard & Knight 1991, McLoughlin et al. 2002), the model performance was well confirmed by the distribution of hunter-killed bears of all ages and both sexes (except cubs and females with a litter that were protected from the harvest). Reproductive females may be more sensitive to human disturbance and select for more secure areas for raising their cubs (Gibeau et al. 2002), which may explain some of the hunter-killed bears still falling into areas with lower predicted suitability.

Even though we were conservative using only the information about the differential use of habitats within home ranges and relative human influences, a potential problem with our model is that the data are from an expanding population (Swenson et al. 1998b). It is unknown whether the lowly ranked unoccupied areas are really unsuitable or whether the population will eventually spread into these areas if the population continues to expand its range. However, all of our results were consistent in supporting the habitat suitability model. Thus, we expect that the suitable, but yet unoccupied habitats shown in Fig. 2 C have the potential to be occupied by brown bears as the population increases. The habitat model enables reliable assessment and visualisation of the potentially suitable areas for the bear population in Scandinavia forming a basis for identification of priority areas for the conservation and for implementation of specific management strategies for this expanding population. We estimated that about 120,000 km$^2$ of suitable habitat occurs in Scandinavia. However, although the areas with good quality habitat are fairly continuous, more information about bear movements and dispersal is needed to assess whether all suitable areas are accessible for bears.

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Research, Wageningen, Netherlands.
Kernel-based home range method for data with irregular sampling intervals

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Kernel-based home range method for data with irregular sampling intervals

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ABSTRACT

Studies of habitat selection and movements often use radio-tracking data for defining animal home ranges. Home ranges (HR) can be approximated by a utilization density distribution (UD) that instead of assuming uniform use of areas within HR boundary provides a probabilistic measure of animal space use. In reality, radio-tracking data contain periods of frequent autocorrelated observations interspersed with temporally more independent observations. Using such temporally irregular data directly may result in biased UD estimates, because areas that have been sampled intensively receive too much weight. The problem of autocorrelation has been tackled by resampling data with an appropriate time interval. However, resampling may cause a large reduction in the data set size along with a loss of information. Evidently, biased UD estimates or reduction in data may prejudice the results on animal habitat selection and movement. We introduce a new method for estimating UDs with temporally irregular data. The proposed method, called the time kernel, accounts for temporal aggregation of observations and gives less weight to temporally autocorrelated observations. A further extension of the method accounts also for spatially aggregated observations with relatively low weights given to observations that are both temporally and spatially aggregated. We test the behaviour of the time kernel method and its spatiotemporal version using simulated data. In addition, the method is applied to a data set of brown bear locations.

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1. Introduction

Defining the size, shape and pattern of utilization of an animal's home range is important for studying habitat selection and spacing of individuals. A home range can be defined as an area with a defined probability of occurrence of an animal during a specified time period (Harris et al., 1990; White and Garrott, 1990; Robertson et al., 1998; Kenward et al., 2001a). Home ranges are often estimated from data obtained with radio-tracking techniques (Harris et al., 1990; White and Garrott, 1990; Otis and White, 1999, Kernohan et al., 2001a). Many methods have been developed to define the area used by an animal from such point location data (Dixon and Chapman, 1980; Anderson, 1982; Worth, 1989; Larkin and Halkin, 1994; Seaman and Powell, 1996; Lawson and Rodgers, 1997; Robertson et al., 1998; Kenward et al., 2001). Home range methods have been reviewed by several authors, who have often expressed concern about adequate sample size and autocorrelation of locations (Anderson, 1982; Worth, 1987; Harris et al., 1990; White and Garrott, 1990; Larkin and Halkin, 1994; Lawson and Rodgers, 1997; Robertson et al., 1998; Kenward, 2001, Kenward et al., 2001; Kernohan et al., 2001a).
Radio tracking can be continuous or discontinuous with constant or variable time intervals between observations. Thus, techniques are needed that account for the temporal sequence of observations (Larkin and Halkin, 1994; Robertson et al., 1998).

Home range methods are based on either densities of locations or link distance between locations. Methods, such as probabilistic circles or ellipses, the kernel method and the harmonic mean method, are based on the assumption that aggregation of locations provides information about differential use of space within the home range (Dixon and Chapman, 1980; Anderson, 1982; Worton, 1989; Kernohan et al., 2001a). The minimum convex polygon (MCP) is an example of link distance methods that assume uniform use of space within the range enclosed by the outermost locations (White and Garrott, 1990; Kenward, 2001; Kernohan et al., 2001a).

Kernel contours have frequently been used in habitat selection studies (Mace et al., 1996; Seaman and Powell, 1996; Tufto et al., 1996; Mace and Walker, 1997; Weller and Mace, 1997; Kernohan et al., 1996; Kernohan et al., 1998; Kenward et al., 2001; Marzluff et al., 2001; McLoughlin et al., 2002; Lynn et al., 2003). This is done assuming that an animal uniformly uses the area inside a contour enclosing a certain proportion (e.g., 95%) of the total probability density of the locations. For clarity, here we call such a home range estimate a “flat kernel”, because the original probability density is replaced by a flat distribution, and thus not all information about differential home range use is retained. However, animals are unlikely to use their home range in a uniform manner and consequently, probabilistic methods can be more useful in habitat related studies than the MCP method or flat kernel (Worton, 1987; Harris et al., 1990; Seaman and Powell, 1996; Marzluff et al., 2001, 2004).

Especially in spatially heterogeneous environments it may be important to understand the internal structure of the home range (Kernohan et al., 2001a). The probability distribution that maps an individual’s relative use of space has been termed the utilization distribution (UD). Marzluff et al. (2003) suggested that the use of UD directly would enhance studies of animal movements, species interactions and resource selection. The kernel method actually provides an estimate for the UD depicting the probability of an animal occurring at each location within its home range (Worton, 1987, 1989; Kernohan et al., 2001a; Marzluff et al., 2001, 2004).

The kernel method implicitly assumes statistical independence among the observations (Harris et al., 1990). The problem of temporal autocorrelation has so far been overcome by resampling the data with an appropriate time interval (Swihart and Slade, 1985; Harris et al., 1990; Rooney et al., 1998; Kenward, 2001). It is not straightforward to translate data into statistically independent observations while still retaining an adequate sample size without loss of information. Attempts to achieve statistically independent data by resampling have often resulted in severe reduction in the data and consequently significant underestimation of the range size and rates of movement (Rooney et al., 1998; Kernohan et al., 2001a; Dahle and Svenson, 2003a). At the same time, many authors emphasize that relatively many locations are needed for any home range or UD estimates to be reliable (Harris et al., 1990; White and Garrott, 1990; Arthur and Schwartz, 1999; Girard et al., 2001). When data provide unbiased temporal coverage of the animal’s movements during the study period, the issue of autocorrelation is not necessarily relevant (Cliff and White, 1999; Marzluff et al., 2001). However, if the data contain periods of frequent observations with temporally more isolated and independent observations, UD estimates are likely to become biased.

Problems with temporal autocorrelation can be prevented by using a sound tracking protocol, collecting locations with regular time intervals over a long time period (Robertson et al., 1998; Rooney et al., 1998). However, in practice, bursts of data separated by gaps with no observations are often collected. We suggest a new kernel-based method for estimating UDs with data that results from uneven sampling. The method, hereafter called the “time kernel”, allows the user to decide the temporal scale at which aggregated locations are weighted less in relation to temporally discrete locations. A further development of the time kernel method uses information on both temporal and spatial autocorrelation of observations when weights are calculated. Essentially, an observation gets a relatively low weight only if it is both spatially close to and temporally aggregated with other observations.

Below, we describe the new methods and test them with the help of simulated data. By using simulated data, we gain improved understanding of the potential advantages of the techniques, because the true UD is available for comparisons. We also investigate the time kernel method and the loss of data due to resampling with real radio location data collected for brown bears (Ursus arctos).

2. Methods

2.1. Time kernel calculations

The time kernel (TK) method considers both the spatial and temporal aggregation of observations. The idea is to calculate the UD by the standard kernel method (Worton, 1989, 1995), but by giving less relative weight to temporally close and thus autocorrelated observations that might otherwise bias the UD estimate. Animal observations, i = 1, . . . , n, are described by two spatial coordinates xi and yi, and by the time the observation was made, ti. We first define a function, D(t), which describes the temporal density of observations (Fig. 1A) When a 1-D Gaussian density kernel is used, D(t) is defined by:

\[ D(t) = \sum_{i=1}^{n} \exp \left( -\frac{(t - t_i^2)}{2h_i^2} \right). \] (1)

The temporal smoothing parameter, hi, is analogous to the spatial smoothing parameter used in traditional fixed and adaptive kernel methods (Worton, 1989, 1995). With a small value of hi, the fine detail of the data are used and each observation is considered independently, whereas with a larger value the role of individual observations is decreased and temporally close locations are considered as dependent on each other (Fig. 1A).

Next we use D(t) to get a weight, wi, for each data point, i, under the assumption that a comparatively high value for
Fig. 1 – The calculation of weights for observations, which are shown by vertical lines at the bottom of panels: (A) the smoothed temporal distribution of locations $D(t)$ is calculated using the smoothing parameter values $h_t=0.2$ and $2$. (B) The corresponding relative weights ($w_i/w_i^\text{max}$) of individual observations.

$D(t)$ indicates high temporal autocorrelation, which should be translated into a comparatively low $w_i$. The UD estimate is eventually normalized to unity and thus only relative weights are of significance. Thus, we calculate weights $w_i$ as:

$$w_i = \frac{1}{D(t)}$$

(2)

Fig. 1 demonstrates the process of obtaining weights. Where locations are temporally aggregated, $D(t)$ receives high relative values. When $h_t$ is small, $D(t)$ peaks are more narrow, but with large values of $h_t$, the curve is smoother with fewer peaks (Fig. 1A). With large $h_t$, more observations are considered temporally dependent and consequently there are more observations that receive relatively low weights, whereas with small $h_t$, most observations are considered independent and gain a relative weight of 1 (Fig. 1B).

Following the determination of observation weights, the calculation of the actual spatial kernel home range follows the procedure of the traditional kernel method (Worton, 1987, 1989), but with each radiolocation weighted by $w_i$. When using a normal distribution for smoothing, the spatial kernel is thus defined as:

$$K(x, y) = \frac{1}{2\pi h_s^2} \sum_{i=1}^{n} w_i \exp \left( -\frac{(x-x_i)^2 + (y-y_i)^2}{2h_s^2} \right)$$

(3)

Parameter $h_s$ controls the degree of spatial smoothing in the calculation of the kernel estimate (Worton, 1989, 1995). Biologically, $h_s$ controls for uncertainty in the estimation of the radiolocations and in the perceptual range of an animal. In order to compare individual home ranges, $h_s$ should be the same for all individuals (Kernohan et al., 2003).

In some cases, taking into account only the temporal density of observations in weights calculations may not be sufficient. For example, if animals perform fast long-distance movements to the location of an important resource, using only the temporal density on obtaining time kernel weights may underestimate the value of this resource. To avoid this, weights can be calculated using a spatiotemporal variant of the time kernel (TK STW) by replacing $D(t)$ with $D(t, x, y)$:

$$D(t, x, y) = \sum_{i=1}^{n} \exp \left( -\frac{(t-t_i)^2}{2h_t^2} \right) \exp \left( -\frac{(x-x_i)^2 + (y-y_i)^2}{2h_s^2} \right)$$

(4)

Eq. (4) combines the time kernel with the ordinary spatial kernel in the calculation of weights for observations. The logic is that usually temporally close observations are autocorrelated and should be devalued to avoid an artefactual high-density aggregate in the UD. However, occasionally a fast long-distance movement might occur between the temporally close observations. Correlation structure of such movement can be defined in relation to the spatial kernel that is used in home range calculations. If the spatial kernels for two observations do not overlap, there seems to be little reason to devalue the observations due to temporal autocorrelation—both give information of the preferred locations at different parts of the home range. Consequently, in the spatiotemporal calculation of weights, both temporal and spatial kernel components are multiplied. Heuristically, highest UD values are given to areas where the animal repeatedly returns to after being elsewhere for a while. Observations at such a location are spatially close but they have zero temporal autocorrelation, and therefore a high-density area is generated into the UD. For example, with brown bears, having data with 10 sequential observations 1 h apart at approximately the same location tells little more than that an observation sequence just happened to be recorded when the animal was crossing the location. In contrast, if the animal returns to the same spot 10 times with a week between, there is a strong signal of the location really being preferred by the animal.

The selection of the values for $h_s$ and $h_t$ is necessarily species-dependent and somewhat subjective. Methods based on least squares cross-validation (LSCV) have been suggested for selecting the optimum value for $h_s$ (Worton, 1989; Seaman and Powell, 1996; Kerward, 2001; Kernohan et al., 2001a). The selection of $h_s$ should also take into account the biology of
the species (Kernohan et al., 2001a) and the accuracy of the measurement of spatial locations. The value of \( h_0 \) should be based on the movement rate of the animal. Temporal smoothing can be regarded as comparable to time to independence (TTI), the time needed between observations in order for them to be independent from each other (Swihart and Slade, 1985; Swihart et al., 1988; Kernohan et al., 2001a). Techniques suggested for defining TTI can also be used for adjusting the value of \( h_0 \) (Swihart and Slade, 1985; Swihart et al., 1988; Rooney et al., 1998). As \( h_0 \) describes the standard deviation (Eqs. (1) and (4)), TTI can be thought to approximate \( 2h_0 \).

Since all observations do not receive equal weight in time kernel calculations, effective data size, \( N_{\text{eff}} \), is usually smaller than the original data size. Effective data size can be calculated by summing the weights:

\[
N_{\text{eff}} = \sum_{i=1}^{N} \frac{u_i}{v_{\text{max}}} \tag{5}
\]

where \( u_{\text{max}} \) is the highest individual weight obtained for any observation.

Note that for any data there is a minimum effective number of observations, \( N_{\text{min}} \), which can be found by varying \( h_0 \). With low \( h_0 \), all observations are essentially independent and \( N_{\text{eff}} = N \). Increasing \( h_0 \) starts recognizing dependency between observations, causing non-independent observations to receive less weight. Consequently, \( N_{\text{eff}} \) decreases down to some point \( N_{\text{min}} \). We call the \( h_0 \) corresponding to the minimum effective number of observations \( h_0(N_{\text{min}}) \). When \( h_0 \) is further increased from \( h_0(N_{\text{min}}) \), all observations become apparently correlated to a high degree, and thus they get essentially same relative weights following which \( N_{\text{eff}} \) increases back to \( N \). Thus, using \( h_0 \) values larger than \( h_0(N_{\text{min}}) \) is not meaningful.

\( N_{\text{min}} \) can be used for investigating the temporal correlation structure of the data; if \( N_{\text{min}} < N \), then the data contains periods of high temporal autocorrelation at some time scale and the home range estimate may be correspondingly biased unless this is taken into account in the calculations. If \( N_{\text{min}} = N \), the data are very evenly sampled and partial temporal autocorrelation is not an issue.

2.2. Testing time kernel method with simulated data

Testing the time kernel method was done according to the following scheme: (i) generate a true UD for a hypothetical species based on a habitat quality-biased correlated random walk. (ii) Sample movement paths of individuals in the landscapes depicting the radiolocation data. (iii) Generate UD estimates based on the sampled simulated data using different methods, including the ordinary kernel and the time kernel, and calculate the deviation from the true UD.

For the tests, we chose a landscape structure that is simple enough to allow the replication of these results but complex enough to include some common features of real home ranges (Fig. 2). The landscape we use is bimodal, allowing infrequent moves of the individual between the two high-quality core habitats. Habitat is divided into three classes with respect to quality, which results in uneven habitat use within the home range. Because best habitat occurs in a ring rather than in a filled circle (Fig. 2), the true UD is more difficult to approximate using kernels than what may be apparent on the surface.

Movement paths of individuals were generated by a correlated random walk. The length of each movement is taken from an uniform distribution \( L = [0, L_{\text{max}}] \). The turning angle 

\[ \phi = \text{erg} \] 

around 0 with a standard deviation of the angle being \( \sigma \). Habitat quality has the following importance in the simulation. First, a movement is proposed by the random walk: if the movement would occur to habitat of the same or higher quality, then the proposed move is always accepted. If the move would go to habitat of lower quality, the move is accepted with probability \( p_{\text{accept}} = q/L_{\text{max}} \), where \( q \) is the lower quality and \( L_{\text{max}} \) the higher quality. Note that this condition prevents the random walk moving out into cells with \( q = 0 \). Following a discarded move event, the correlated random walk is interrupted for the following move and the next turning angle is picked from a uniform distribution \([0, 2\pi]\).

As a further complication, our hypothetical animal has two movement modes, a slow and less directed one (e.g., foraging) and a faster and more directed one (escape, long-distance movement, etc.). Parameters for the foraging mode are \( L_{\text{max}} = 3.0 \) for the maximum step length and \( \phi = \pi/6 \) for the turning angle parameter. Parameters for the movement mode have triple speed and more directed movement with \( L_{\text{max}} = 9.0 \) and \( \phi = \pi/18 \), respectively. After a move in the foraging mode, the individual switches to the movement mode with a probability of 0.1. Transition from movement to foraging happens with probability 0.5.

Simulated individual starts its movements from the centre of the landscape, but the first 1000 movements are ignored to remove any dependence of results on the initial location of the individual. Simulated movement was continued as many steps as was needed to sample a given number (we used 800) of hypothetical observations. Movement paths were sampled using random sampling interspersed with bursts of intense sampling. Observations were taken with random intervals with from 1 to 100 time units between. An observation was extended to a sequence of 2-20 sequential observations (taken with identical intervals of 1) with the probability of 0.2. We did not include a sampling scheme with a uni-
form interval between samplings because with such data the time kernel would have been identical to the normal kernel method.

We compared home range estimates generated using (i) the ordinary kernel method, (ii) the kernel with data resampling on an interval for temporal autocorrelation between points (resampled kernel), (iii) the time kernel (TK) and (iv) the time kernel with spatiotemporal calculation of weights (TK STW). UD estimates generated using different methods were compared with respect to the overlap of the estimated and true UD (true obtained from the converged distribution of the random walk obtained from a 10 million step random walk). This was done by calculating the difference in the discrete probability distribution as:

$$d(T, E) = \frac{\sum \sum (E_{xy} - T_{xy})}{2},$$

where $E$ is the estimated home range matrix and $T$ the matrix for true UD and summation is over the $x$, $y$-coordinates of the matrices (discrete version of the Heidel’s volume of intersection (Ishida, et al., 2001b)). If the two spatial probability distributions are completely non-overlapping, $d(T, E)$ equals one.

When comparing home range computation methods, data sets with different effective numbers of observations were produced by setting $h_t = 1.5, 2.25, \ldots$. Each $h_t$ resulted in a different number of effective observations, $N_{eff}$ (Eq. (3)), for the time kernel estimate. For each $h_t$, we generated 200 independent observation set replicates. Importantly, the resampling interval for the resampled kernel method was for each data set adjusted so as to give a number of observations identical to that obtained using the time kernel ($N_{eff}$).

The spatial smoothing parameter $h_t$ would normally be determined from prior knowledge on the spatial accuracy of observations, behaviour of the animal and on the desired spatial resolution of the home range estimate. For our hypothetical case, we set $h_t = 1.5, 2.25, \ldots$. Each $h_0$ resulted in a different number of effective observations, $N_{eff}$ (Eq. (3)), for the time kernel estimate. For each $h_t$, we generated 200 independent observation set replicates. Importantly, the resampling interval for the resampled kernel method was for each data set adjusted so as to give a number of observations identical to that obtained using the time kernel ($N_{eff}$).

For computational purposes, it is practical to use discrete space instead of the full continuous distributions underlying the kernel methods. We discretized the bear home ranges into a grid with a 1000 m × 1000 m cell size, which corresponds to the grain of a habitat map available for the region. Dimensions of the matrix used for each home range were determined by the minimum and maximum coordinates of the bear, buffered all around by a margin of 2.5 times the value of $h_t$. This ensured that tail probabilities extending outside the borders of the matrix were sufficiently small to be negligible ($< 1\%$ of total probability). The contour enclosing 95% of the total UD was used for calculating kernel and time kernel home range area estimates.

3. Results

3.1. Simulated data

Fig 3 shows the performance of different home range computation methods. With simulated data, $N_{min} = 80$ (at $N_{min} = 44$) even though $N = 400$, which indicates significant irregular temporal aggregation of observations. With very small $h_t$, the performance of the TK is very similar to that of the ordinary kernel. The performance improves with increasing $h_t$ (decreasing $N_{eff}$), and the best performance is achieved with $N_{eff} = 210$ ($h_0 = 320$). With any given $N_{eff}$, especially with low values, the TK performs better than the resampled kernel. The performance of the resampled kernel deteriorates rapidly with an increasing resampling interval (corresponds to a decreasing $N_{eff}$), whereas the performance of the TK declines only to the point $N_{min}$. The performance of the resampled kernel may even be worse than that of the ordinary kernel, because it is highly sensitive to selecting a too large resampling interval.

The TK STW performs best of the proposed methods. This method takes points as correlated only if they are close both in terms of space (as determined by Eq. (4)). If two points are temporally close (as determined by the choice of $h_t$) but spatially clearly distinct (as determined by the choice of $h_0$), then the locations are taken as essentially independent. Consequently, the TK STW is less sensitive than the TK to the choice of $h_t$. 

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3.2. Brown bear data

Exploring the bear data with the help of $N_{min}$ exposed severe temporal irregularity (mean $N_{min}$ of 19 ± 1 compared to mean $N$ of 95 ± 11). However, with $h_s = 2$ the comparison of the $N_{eff}$ values for standard TK (mean 28 ± 1) with those of TK STW (mean 51 ± 4) revealed that although many observations are temporally close, they are spatially separate at the time scale used. Fig. 4 demonstrates differences between home range layouts produced with different methods. The shapes of the MCP ranges (B and C) differ markedly from those of kernel-based methods and information about the use of space inside the home range is lost. Although the profiles of the ordinary kernel and TK ranges do not differ as noticeably, the spatial arrangement of the probabilities of occurrence is somewhat different. In the ordinary kernel using all observations, emphasis is given to the large area in the middle of the home range (A). When temporal aggregation of observations is taken into account in the TK estimate, the relative importance of this area decreases and areas in the left of the home range increase in their importance (D). Most importantly, the ordinary kernel with data resampling leaves many observations outside the home range estimate (D).

Resampling of data resulted in almost 70% reduction in data points (from mean 95 ± 11 to mean of 27 ± 1). The smallest sample size after resampling was 12, which hardly is adequate for reliable home range estimation (Harris et al., 1990; White and Garrott, 1990; Arthur and Schwartz, 1999; Girard et al., 2002). This loss of information is evident in Fig. 4, where the time kernel UD estimates (Fig. 4E and F) include areas absent from the resampled kernel estimate (Fig. 4D).

In general, kernel ranges estimated from resampled data were much smaller than TK ranges with corresponding temporal smoothing, which is evident from a comparison of home range areas (Table 1). Areas estimated from resampled...
data were smaller than those estimated using other home range methods (Table 1). Resampling may exclude remote observations by chance, which can affect range sizes significantly. MCP home ranges were in general considerably larger than any of the kernel-based ranges. This is because MCPs may include large unused areas between the outermost locations. Areas calculated with the TK and TK STW methods using different values for \( h \) seemed to be consistent using this data.

### 4. Discussion

Home range estimates are often used for studying animal use of space. Valuable information about habitat use within the home range can be lost if only information about home range borders is used, as is done by MCPs and flat kernels. Using the UD directly, instead of a uniform probability distribution within a given probability contour, can improve our understanding of the animal’s use of space. This also evades the problem of having to choose the proportion of the UD that is used for the contour calculation. Ideally, the data for estimating animal UD should comprise a large collection of observations by chance, which can affect range sizes significantly. MCP home ranges were in general considerably larger than any of the kernel-based ranges. This is because MCPs may include large unused areas between the outermost locations. Areas calculated with the TK and TK STW methods using different values for \( h \) seemed to be consistent using this data.

### Table 1

<table>
<thead>
<tr>
<th>HR method</th>
<th>Area ± S.E. (( \text{km}^2 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>100% MCP</td>
<td>977 ± 192</td>
</tr>
<tr>
<td>Kernel</td>
<td>415 ± 29</td>
</tr>
<tr>
<td>100% MCP with resampling</td>
<td>838 ± 170</td>
</tr>
<tr>
<td>Kernel with resampling</td>
<td>356 ± 19</td>
</tr>
<tr>
<td>TK ( h = 2 )</td>
<td>416 ± 29</td>
</tr>
<tr>
<td>TK ( h = 0.2 )</td>
<td>418 ± 29</td>
</tr>
<tr>
<td>TK STW ( h = 2 )</td>
<td>412 ± 29</td>
</tr>
<tr>
<td>TK STW ( h = 0.2 )</td>
<td>435 ± 30</td>
</tr>
<tr>
<td>TK STW ( h = 1 )</td>
<td>440 ± 30</td>
</tr>
<tr>
<td>TK STW ( h = 1 )</td>
<td>449 ± 30</td>
</tr>
</tbody>
</table>

* Note that \( h(N_{\text{min}}) \) was different for each individual (mean \( h(N_{\text{min}}) \) was 12 ± 3 and minimum \( h(N_{\text{min}}) \) was 2.5 days).

Selection of \( h \) should be based on the movement rate of the animal. For example, if an animal is likely to cover most of its range within short time period, the value of \( h \) should be set small. With small \( h \), most of the observations are considered independent and given equal weights. Estimates of TTI and \( h(N_{\text{min}}) \) provide guidelines for deciding the value of \( h \). Although the optimal value for \( h \) is likely to be smaller than \( h(N_{\text{min}}) \), direct use of \( h(N_{\text{min}}) \) in time kernel calculations gave better results with our simulated data than did the ordinary kernel with resampling with any time interval (Fig. 3). Whether to use temporal or spatiotemporal weights in time kernel calculations depends on both the behaviour of the animal and the intended purpose of the UD estimates. For example, if an animal is likely to spend most of its time around one place (say next site) but exhibits fast long distance visits to the location of some important resource, using standard weighting may underestimate the value of this resource. On the other hand, some animals may pay short visits to resource poor edges of their home ranges just to check surrounding individuals.

On the downside, the time kernel method shares some disadvantages with other kernel-based methods. A degree of subjectivity cannot be avoided in selecting values for \( h \) and \( h \). However, techniques suggested for selecting the value for spatial smoothing are also valid for the time kernel estimator (Worton, 1987, 1989, 1995; Seaman and Powell, 1996; Kenward, 2001; Kernohan et al., 2001a). Likewise, methods of defining TTI can be used for selecting an appropriate value of \( h \) (Swihart and Slade, 1985; Rooney et al., 1998; Otis and White, 1999; Kernohan et al., 2001a). It is an implicit assumption by those advocating resampling that estimates with resampled data will describe the home range more accurately (Rooney et al., 1998). However, information can be lost because of resampling and using intensive observation procedures instead can lead to improved UD estimates (Rooney et al., 1998; Otis and White, 1999; Kernohan et al., 2001a).

The time kernel (TK) method and its spatiotemporal extension (TK STW) allow the user to decide to which extent bursts of frequent observations are taken into account in the estimation of a UD without losing any information through resampling.

A long enough study period and a sampling procedure covering different behaviours of the animal are relevant for home range studies (Worton, 1987; Robertson et al., 1998; Rooney et al., 1998; Otis and White, 1999; Kernohan et al., 2001a). Especially in heterogeneous environment and in case of animals with complex behaviour it is important to have temporally unbiased data. Even if tracking protocol originally had been regular problems in detectability of species could have resulted in temporally irregular data for different individuals. If data are suspected to be irregular, we propose investigating the temporal sequence of the radiolocation data with help of TK method. The first step is to define \( N_{\text{min}} \) by varying the values of \( h \) in the standard TK calculations with a chosen \( h \). If \( N_{\text{min}} \neq N \), data contains periods of high temporal autocorrelation that have potential to bias the UD estimates. In this case, the next step would be to identify a reasonable temporal scale \( (h) \) to work with.
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Bayesian estimation of habitat weighted kernel home ranges

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- Submitted
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Summary

1. Understanding the use of space by animals is essential for the conservation and management of wildlife and their habitats. The elementary measure of the space use is home range, that can be used e.g. for determining habitat preferences, carrying capacities, management boundaries and vulnerability to extinction.

2. Home range is often estimated from location data with kernel methods that produce an estimate of the utilization density distribution—the probability of the individual occurring at each location within the landscape. Kernel methods have been criticized for overestimating the area used by the animal, because kernels often spread to unfavourable habitats close to actual animal observations.

3. We developed a method for estimating kernel home ranges while accounting for habitat boundaries. Essentially, we calculate a kernel home range and modify the kernel by a multiplier for each habitat type. These multipliers reflect the fact that some habitats are preferred whereas others may be avoided. The width of the kernel and the habitat multipliers are estimated simultaneously using a computationally efficient implementation of Bayesian estimation. Because we account for the temporal structure of observations in the estimation, the proposed method can also be used with data consisting of temporally irregular observations.

4. We demonstrate the method with analysis of radio-location data on brown bears (Ursus arctos). For example, we found that bear home ranges had more plausible shapes and were smaller when habitat multipliers were used in the estimation, because the kernel tails spread less to habitats with none or very few observations.

5. Synthesis and applications. Good quality description of animal home ranges can give vital insights into important ecological processes. The proposed method improves current kernel estimation by including Bayesian estimation of habitat preferences and by providing better estimates of home range sizes even with relatively small sample sizes. Because no additional information to animal locations and habitat type distribution is needed, the method is applicable to a wide range of studies.

Keywords: Bayesian analysis, Habitat selection, Home range, Kernel, Movements, Telemetry data, Utilization density distribution

1. Introduction

Space use by an animal is often described by its home range; an area with defined probability of occurrence of an animal during a specific time period (Powell 2000, Kernohan et al. 2001). Information about home ranges forms a basis for many ecological analyses. Home range estimates are widely used in the analysis of animal movements, habitat selection, individual interactions and survival (Powell 2000, Kernohan et al. 2001). Thus, good estimates of home ranges can provide vital insight into many basic topics in animal ecology. Of the various methods developed for estimating home ranges from telemetry data (described and reviewed e.g. by (Dixon & Chapman 1980, Anderson 1982, Worton 1989, Larkin & Halkin 1994, Seaman & Powell 1996, Lawson & Rodgers 1997, Robertson et al. 1998, Kenward et al. 2001)) kernel density estimators are widely viewed as most reliable,
because they allow multiple centres of activity and provide estimates of the utilization density distribution (UD) that describes the probability of an animal being in any part of its home range (Powell 2000, Kernohan et al. 2001).

A critical component in calculation of kernel home range is the value of the kernel width (also called the smoothing parameter or the bandwidth) (Silverman 1986, Worton 1989, 1995, Seaman & Powell 1996, Seaman et al. 1999, Blundell et al. 2001, Kernohan et al. 2001, Hemson et al. 2005). However, kernel estimation has been criticized for the lack of objective way of determining suitable smoothing. Selecting too wide kernel width spreads the estimate and conceals details of the internal structure of the home ranges, whereas narrow kernel width results in unrealistic peaks and leads to a discontinuous estimate. Methods used currently for selecting the kernel width are the reference smoothing factor and least squares cross validation (LSCV)(Silverman 1986, Worton 1989). Both have been criticized either for over or under smoothing (Worton 1995, Seaman & Powell 1996, Seaman et al. 1999, Powell 2000) and neither one provides any measure of uncertainty (Kernohan et al. 2001). LSCV can also be biased by large number of observations that are spatially identical or close to each other (Silverman 1986).

Thus, kernels using LSCV may lead to poor estimates in case of site fidelity or intensive use of core areas (Hemson et al. 2005). Also irregular sampling can cause such temporal and spatial aggregates in data that may bias the kernel estimation (Katajisto & Moilanen 2006). Finally, kernel estimates often overestimate the home range sizes (Seaman et al. 1999), because being continuous they often spread to unused habitats adjacent to actual animal observations, which occur in good habitat.

We developed a novel likelihood-based Bayesian approach for estimating kernel home range that deals with the problems presented above. The principle idea is that the kernel is modified by a multiplier for each habitat type. The kernel width and habitat multipliers are estimated simultaneously using Bayesian estimation and their uncertainty is incorporated into the final home range estimate. The temporal sequence of the data is taken into account so that aggregated observations are given less weight in estimation.

Following the general idea of constructing habitat weighted kernel home range we explain the details of the likelihood calculations and of how temporally aggregated data is handled. Finally we describe the full Bayesian estimation of the kernel width and habitat multipliers together with construction of the Bayesian UD. We demonstrate the advantages of the proposed method by estimating Bayesian home ranges and posterior parameter distributions for a set of Scandinavian brown bears (Ursus arctos) and by comparing the home range sizes estimated with and without habitat multipliers.

2. Methods

2.1. Constructing a habitat weighted kernel home range

We first describe how a kernel home range (utilization density distribution, UD) with effects of habitat type is constructed. Assume a landscape grid of dimensions \(X \times Y\). Assume there is a data set \(O\) of \(N\) observations taken at locations \((x_i, y_i), i = 1, \ldots, N\) within the landscape for a specific individual. The UD estimate is constructed in three stages. (i) A two-dimensional normal distribution kernel (Silverman 1986, Worton 1989) is placed around each observation location and these kernels are summed over the landscape grid. (ii) The summed kernel value at each grid cell is multiplied by a habitat specific multiplier that reflects the habitat preferences of the animal. (iii) To get the final UD estimate, the UD is standardized over the grid to sum to 1. How the kernel width and habitat multipliers should be estimated from the data is essential for the construction of the UD estimate. We present a likelihood-based Bayesian approach to this estimation problem. Symbols used are summarized in a table in Table S1 in Supplementary Material. An efficient strategy for computations that enables such Bayesian estimation is presented in Appendix S1 in Supplementary Material.

2.2. The likelihood of the data

The vector of estimated parameters, \(\theta\), consist of the kernel width (or smoothing factor), \(\sigma^2\), and a multiplier, \(m(h)\), for each habitat type, \(h = 1, \ldots, H\). Let \(U(O, u, v, \theta)\) be the UD value generated by data at location using parameter set \(\theta\). We assume that the UD estimate has been standardized, where summation is over the landscape grid, and . By definition is then the proportion of time the individual spends at location within the home range,
and it can therefore be interpreted as the unconditional probability of an independent observation being made at . Consequently, the likelihood of the data is

\[ l(O|\theta) = \prod_i U(O_i, x_i, y_i, \theta), \quad (1) \]

where \( i = 1, 2, ..., N \). The likelihood of Eq. 1 is actually maximized when a very narrow kernel is placed around each observation, because each observation is allowed to explain itself. Thus, estimating directly by maximization of Eq. 1 is not suitable for the purpose of UD estimation and we need to use jackknife estimate for the likelihood of data. The observations are one by one left out from the construction of the UD and the value of the UD at the position of the missing observation is used as a criterion for estimating. As these values are small, we use log-likelihoods for which the expression becomes

\[ l(O|\theta) = \sum_i \log(\theta_i) = \sum_i \log[U(O - |i\rangle, x_i, y_i, \theta)], \quad (2) \]

If the kernel is too narrow (too small kernel width, \( \sigma_i \)), it does not extend to the observation left out in the jackknife, whereas if the kernel is too wide (too large \( \sigma_i \)), the probability mass spreads outside of the true UD area and the likelihood of data goes down. The habitat type multipliers correct for the relative frequency at which observations are made at various habitat types. The amount of data, landscape configuration and positions of observations determine how wide posterior distributions are obtained for parameters in Bayesian estimation.

### 2.3. Handling temporally aggregated data

Up to this point it has been assumed that all observations are evenly distributed over time. However, this frequently is not the case – data sets may consist of periods of more frequent sampling with longer intervals between (Katajisto & Moilanen 2006). For example, ten observations taken within few seconds at essentially the same location, should really only count as one observation. If not taken into account, irregular sampling may hamper parameter estimation in three ways: (i) the value of UD in areas with temporally clustered observations is overestimated, (ii) \( \sigma_i \) may be underestimated if temporally close observations are allowed to fully explain each other during the estimation, and (iii) likelihood calculations are biased if observations in temporal clusters are given the same importance as more independent observations. However, even though a sequence of temporally clustered observations should not be treated as fully independent, they do contain more information than just one observation. Therefore, we include into the estimation a mechanism for handling temporally irregular data. This method follows the lines of (Katajisto & Moilanen 2006).

Observations are given weights according to their temporal density

\[ D(t) = \sum_{i=1}^{N} \Phi(\sigma_i, t - t_i), \]

where \( t_i \) is the time of observation \( i \) and \( \Phi() \) is one dimensional normal distribution kernel with width \( \sigma_i \) (standard deviation of the kernel). The more temporally aggregated the observations the higher values \( D(t) \) receives. Following the principle that comparatively high value for \( D(t) \) should be translated into a comparatively low weight, we calculate the temporal weights \( w_i \) as

\[ w_i = \frac{D_{\text{min}}}{D(t_i)}, \quad (3) \]

where \( D_{\text{min}} \) is the smallest value obtained by \( D(t) \) for any observation. Thus, the least autocorrelated observation (as determined by \( \sigma_i \)) receives a weight \( w_i = 1 \), and more temporally clustered observations get weights <1.

The temporal scale of independence, \( \sigma_i \), can be set either based on time of independence (TTI) or the minimum effective number of observations, \( N_{\text{min}} \). TTI can be based on prior knowledge of the species or estimated with various methods (Swihart & Slade 1985, Rooney et al. 1998, Kernohan et al. 2001). As describes the standard deviation, one can then set . A less heuristic criterion is to calculate the effective number of observations,

\[ N_{\text{eff}} = \sum_{i=1}^{N} w_i, \]

with different values of \( \sigma_i \), and use \( \sigma_i \), at which \( N_{\text{eff}} \) gets a minimum \( N_{\text{min}} \) (Katajisto & Moilanen 2006). With even sampling \( N_{\text{min}} \approx N \), but with irregular sampling \( N_{\text{min}} \ll N \).

The temporal weights for observations, \( w_i \), modify UD estimation at three points. First, when placing the spatial kernel around an individual observation location, the kernel is made to sum to \( w_i \) not to 1. Thus, individual observation belonging to
a temporal cluster contributes less to the construction of the UD than temporally more independent observation. Consequently, UD is not biased towards a sequence of temporally close observations. However, if the animal repeatedly returns to the same location (having been elsewhere meanwhile), the site gets a high UD value. Second, temporal weights determine the degree at which a pair of observations is allowed to explain each other in the parameter estimation. Assume that two observations, \( a \) and \( b \), are temporally autocorrelated at level \( \rho(a,b) = \exp\left(-\frac{(t_a-t_b)^2}{2\sigma^2}\right) \). Without taking this into account the spatial kernel of observation \( a \) would have contribution \( K_a(x_a,y_a) \) at the location \( (x_a,y_a) \). We modify this contribution so that the influence of \( a \) to location \( (x_b,y_b) \) becomes \([1 - \rho(a,b)]K_a(x_a,y_a)\) and temporal autocorrelation decreases the pairwise explanatory power. Otherwise a narrow kernel around an autocorrelated observation would automatically explain the other nearby autocorrelated observations with high likelihood. Finally, log-likelihoods are weighted so that temporally dependent observations influence the likelihood of data less than independent observations as \( L_i = w_i \log(l_i) \).

### 2.4. Bayesian estimation of parameters

Parameter estimation was done using the metropolis algorithm, that can be viewed as a stochastic version of a stepwise mode-finding algorithm, always accepting steps that increase the probability density but only sometimes accepting downward steps (Gelman et al. 2004). Such Bayesian estimation requires significant computation. However, if we discretize the possible values allowed for the kernel width some of the calculations need to be done only once, which speeds up the likelihood calculations and enables the Bayesian estimation process. Details of the efficient strategy for computations are explained in Appendix B.

Our jump distribution was as follows. In each iteration of the algorithm each parameter (\( \sigma \), and habitat multipliers \( m(h) \), for each habitat type \( h \)) was modified with a probability of \( 2/(1 + H - 1) \), meaning that on average two parameters were modified simultaneously. For \( \sigma \), the jump was \( \pm 1 \) on its level, with equal probability of 0.5 for both directions of the jump. For habitat multipliers a jump meant multiplication with a uniformly distributed random deviate \( r \in [0.9,1.1] \). Thus, the jump distributions satisfy the requirement of the metropolis algorithm of being symmetric. Uninformative priors were used for all parameters.

The metropolis algorithm was run 100000 iterations with the first 10000 disregarded as a burn-in period. For calculation of temporal weights we varied \( \sigma \), and used the value that minimized \( N_{eff} \). The starting point of estimation was determined as follows. The level of smoothing \( \sigma \), was set to 20 (out of 100) corresponding to four cells. If this \( \sigma \) produced zero likelihood (meaning the kernel was too narrow to explain the data), the level was iteratively increased until a positive likelihood of the data was reached. The initial value for each \( m(h) \) was calculated as follows. Let the density of observations in habitat type \( h \) be \( d_h = a_h / a \), where \( a_h \) is the area in the landscape being of type \( h \) and \( a \) is the number of observations in habitat type \( h \). The multiplier for the habitat type having highest \( d_h \) (\( d_{max} \)) was fixed to 1. Other habitat types were left as free parameters, and they got initial values \( m(h) = \max(0.01, d_h / d_{max}) \), where \( d_{max} \) is the highest density of observations over all habitat types. Overall, the starting point of estimation should have negligible effect on the estimation as regions of the parameter space having high likelihood are attained already during the burn-in period.

The outcome of the Bayesian estimation is a list of parameter combinations with associated likelihoods. Posterior distributions for all parameters were produced together with the Bayesian estimate of the home range itself. Each parameter combination \( \theta_n \) has a likelihood \( l(\theta_n) \) and for each parameter set there corresponds a standardized UD estimate matrix \( U_n \) with dimensions \( X \times Y \). The Bayesian estimate of the home range is a likelihood-weighted sum of individual UDs, \( \sum_n l(\theta_n) U_n / \sum_n l(\theta_n) \), where summations should be understood as matrix summations over all parameter sets \( n \) evaluated during the Bayesian estimation (excluding the burn-in period).

### 3. Application to brown bear data

#### 3.1. Telemetry data and comparisons

We used real radio-tracking data for 27 adult individual brown bears (\textit{Ursus arctos}) from central Sweden to demonstrate the Bayesian estimation and the effect of using habitat multipliers on home range layout. Data were collected with irregular sampling interval for various purposes by the Scandinavian
Brown Bear Research Project and individual sample sizes varied between 35 – 636 radiolocations. We exemplify the posterior distributions of the kernel width and habitat multipliers with sample individuals and summarize posteriors over all bears used in the analysis. To investigate the effect of habitat multipliers we compare pairwise home range sizes and the effective areas of different habitat types inside home ranges estimated with and without habitat multipliers using Bayesian approach. Because the potential bias due to temporal aggregates in the data has been shown elsewhere (Katajisto & Moilanen 2006), we don not concentrate on that but account for the temporal sequence in all home range estimations.

For estimates with habitat multipliers we used the Pan European Land Cover Monitoring (PELCOM) habitat data and information about human distribution. Habitat types used in the analysis were: forest (F), human influenced forest (HIF), semi-open habitat (SO), urban and agricultural land (U), barren terrain (B), swamps (S) and open water (W). We used 1100m grid cell size in all the calculation according to the habitat data. Habitat type forest was fixed to value 1 as it had the highest density of observations for all individuals. A landscape with a 50-cell buffer from the outermost observations of the individual was used for each bear. Estimates without habitat multipliers were produced by feeding in a uniform landscape structure. For the comparison of the home ranges sizes the home range boundaries were defined as the 99% cumulative UD contour.

3.2. Results and conclusions

Uncertainty in the kernel width estimation is indicated by the dispersion of the posterior distributions that varied individually as shown by the example bears and the summary posterior (Fig. 1A). The distribution of the kernel width is likely to be influenced both by the number and the spatial distribution of the radiolocations (Seaman et al. 1999). While the multiplier for forest was fixed to 1, other habitat types tended to receive smaller weights with variable posterior distributions (Fig. 1B – D). The habitat multipliers reflect the habitat preference relative to the availability of different habitats for each individual and information about general preferences can be drawn from the summary posteriors. For example, even though some individuals have high multiplier values for human influenced forest, the posterior summarized over all bears is concentrated very close to zero (Fig. 1B), whereas dispersion of the summary posterior for semi-open habitat indicates that individual variation is so large that little can be said about the overall preference based solely on habitat multipliers (Fig. 1C). When interpreting results one should recognize that the estimates of kernel width and habitat multipliers are not independent from each other. The actual Bayesian home range estimate reflects the uncertainty illustrated by the posterior dispersion, because different parameter combinations are weighted based on their likelihood.

The use of habitat multipliers resulted in smaller estimated home range sizes (Table 1). Estimates

| Table 1. Home range sizes and effective areas of habitat types inside 99% cumulative UD estimated with and without habitat multipliers using the Bayesian approach. Comparisons are made with Student's t-Test (df = 25). In calculations with habitat multipliers type 'forest' was fixed to 1. |
|---------------------------------------------------------------|-----------------|-----------------|-----------------|-----------------|
| Mean area, km² (± SE)                                         | With habitat multiplier | Without habitat multiplier | Paired comparison | Mean difference (95% CI) | t   | p   |
| Total area                                                   | 991 (± 155)        | 1055 (± 162)    | 63.7 (15.5 – 111.9) | 2.72 | 0.0116 |
| F                                                           | 736 (± 103)        | 716 (± 98)      | -20.2 (-40.2 - 0.21) | -2.08 | 0.0477 |
| HIF                                                         | 14 (± 13)          | 34 (± 17)       | 20.0 (-3.6 - 43.5)  | 1.74 | 0.0935 |
| SO                                                          | 188 (± 51)         | 205 (± 51)      | 16.8 (0.3 – 33.4)   | 2.09 | 0.0467 |
| B                                                           | 3 (± 8)            | 67 (± 15)       | 67.0 (36.7 – 97.3)  | 4.55 | 0.0001 |
| S                                                           | 0 (± 0)            | 1 (± 0.5)       | 0.9 (-0.2 - 2.1)    | 1.7  | 0.101  |
| W                                                           | 5 (± 2)            | 21 (± 5)        | 16 (5.2 – 27.7)     | 3    | 0.0059 |
| U                                                           | 5 (± 3)            | 10 (± 5)        | 5.9 (0.4 – 11.4)    | 2.2  | 0.0373 |

F = forest, HIF = human influenced forest, SO = semi-open habitat, B = barren terrain, S = swamps, W = open water, U = urban and agricultural land
Habitat weighted home range

accounting for habitat type spread less into unused habitats such as barren terrain, agricultural and urban land, semi-open habitat and water bodies as evaluated by the effective areas of habitats (Table 1). Instead, the UD concentrated more in preferred forest, whereas human influenced forest and swamp were similarly represented within both estimates (Table 1). Consequently, using habitat multipliers resulted in more realistic home range estimates that follow the distribution of different habitat types on the landscape, which is best illustrated by the example layouts (Fig. 2). For example, the arrows in Fig. 2 for bear #2 show how the estimate with habitat multipliers does not spread over the large water bodies as the more roundish estimate without habitat multipliers. Similarly the estimate for bear #4 goes around human influenced areas (urban or agricultural land and human influenced forest). Also, the UD around distant individual radiolocations is not concentrated circularly around the observations, as in the estimates without habitat multipliers, but instead follows the preferred habitat close to the observation (Fig. 2 arrows for bear #4).

4. Discussion

Kernel methods are widely used for estimating animal home ranges, because they provide estimates of utilization density distribution (UD) and deal with multiple centres of activity. However, despite the sensitivity of kernel estimation to the degree of smoothing, objective method for selecting the kernel width that would also provide an estimate of uncertainty has been lacking. Currently used LSCV based kernel width selection may also be biased because of the artificial clustering of observations due to temporally irregular data collection. Moreover, although home range is likely to be
HABITAT WEIGHTED HOME RANGE

affected by the distribution of important resources or conspecifics (Mitchell & Powell 2004, Horne & Garton 2006), most methods for estimating home ranges ignore the fact that animals live in heterogeneous landscapes. Consequently, current kernel estimates spread unrealistically to unfavourable habitats and thus tend to overestimate the home range sizes. As home range estimates form a basis for many investigations of animal movements and habitat use, home range models with better fit are likely to enhance our understanding of factors affecting animal space use and eventually the planning of management or conservation practises.

The proposed Bayesian approach improves kernel home range estimation by incorporating uncertainty of the parameter values into the construction of the actual home range (or UD). At the same time it handles temporally dependent observations by giving them less weight in the calculations. This

Figure 2. Home range layouts estimated with (left) and without (right) habitat multipliers using the Bayesian approach shown for two example individuals of Scandinavian brown bears. The original radiolocation data and individual landscapes, that the home range estimates with habitat multipliers follow, are shown in the middle. The posterior distributions for the habitat multipliers as well as for the kernel width estimated with habitat multipliers for both bears can be seen in Fig 1. Arrows point out locations with differences described in the text.
method utilizes the information about the habitat preferences in the location data providing more realistic home range estimates that do not spread to unfavourable habitats, thus also providing better estimates of the home range sizes. The resulting posterior distributions for habitat multipliers also give information about the habitat preferences of the animal. However, one should be careful in interpreting habitat multipliers as their estimation is not independent from the estimation of the kernel width.

Other home range methods capable of detecting habitat boundaries include model-supervised kernel smoothing (MSKS) (Matthiopoulos 2003a) and movement based mechanistic home range models (Lewis et al. 1997, Moorcroft et al. 1999, Mitchell & Powell 2004). However, unlike the MSKS, the proposed Bayesian approach does not require any auxiliary information about an animal’s use of space in addition to animal locations and habitat distribution. Moreover, in contrast to data demanding mechanistic models, the Bayesian method should work with relatively little data, because habitat multipliers prevent estimates from spreading too much, even though the kernel width tends to grow with decreasing number of observations. The only crucial data requirement, as for any home range estimation method, is that the observations cover the behaviour of the animal with reasonable resolution (e.g. daily migration between feeding and nesting site).

A relevant extension of the proposed approach includes fitting a regression model inside the Bayesian estimation process. As the distribution of animals on a landscape may not be solely a function of landscape structure but also behaviour (Moorcroft et al. 1999, Mitchell & Powell 2004), this would allow e.g. incorporating movement restrictions in form of distance from the home range centre (Matthiopoulos 2003b) or competition in form of distance to surrounding individuals as suggested by (Lewis et al. 1997, Moorcroft et al. 1999).

Acknowledgments

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References


Appendix S1

An efficient strategy for computation of Bayesian home range

The construction of a kernel home range with effects of habitat type requires significant computation. For a parameter set one in principle needs to (i) place kernels of the given width \( (\sigma_s) \) around each observation, (ii) multiply the UD matrix with the habitat multipliers for each grid cell and (iii) standardize the UD estimate. Furthermore, when using the jackknife likelihood calculation, this procedure needs to be replicated once for each observation.

Placing of variable-width kernels around observations is by far the slowest part of the calculations. However, unlimited precision is not needed for biologically relevant estimation of \( \sigma_s \). We discretized possible values of \( \sigma_s \) to 100 different levels, starting from 0.25 cell size and doubling every five levels resulting in a range of \( \sigma_s \in [0.25, \sim 250000] \) divided logarithmically into 100 levels. A kernel estimate without habitat multipliers \( (m(h)=1 \text{ for all } h) \) can be calculated once for each level of \( \sigma_s \). Then, the habitat weighted estimate of the UD can be obtained simply by multiplying this precomputed matrix by habitat multipliers for each cell. Furthermore, instead of the full UD estimate only likelihoods at observation locations are required for the likelihood calculation. Computations proceed as follows. First, the weighted jackknife likelihood of data is

\[
L(O|\theta) = \sum_{i=1}^{s} -w_i \log(U(O - |i|, x_i, y_i, \theta)).
\]

This includes the weighted contribution of all other observations, \( q \), at the location of observation \( i \),

\[
U(O - |i|, x_i, y_i, \theta) = \frac{\sum_{q\in(O-i)} w_q K_q(x_q, y_q)}{\sum_{q\in(O-i)} w_q},
\]

where \( K() \) is the normalized kernel value of observation \( q \) at location \( (x_q, y_q) \). The key is how \( K_q(x_q, y_q) \) is calculated:

\[
K_q(x_q, y_q) = \frac{m(h(x_q, y_q))|1 - \rho(i, q)|\Phi(x_q - x_i, y_q - y_i, \sigma_i)}{\sum_{v=1}^{r} \sum_{u=1}^{r} m(h(u, v))\Phi(x_v - x_i, y_v - y_i, \sigma_i)}.
\]

Here the nominator is the contribution of the kernel around observation \( q \) to the location of observation \( i \) at \( (x_i, y_i) \), corrected for temporal autocorrelation and multiplied by the habitat multiplier for the location. Of this, quantity \( |1 - \rho(i, q)|\Phi(x_q - x_i, y_q - y_i, \sigma_i) \) does not depend on the habitat multipliers and it can be precomputed and stored once for every combination of \( i, q \) and \( \sigma_i \). The denominator is the habitat weighted sum of the kernel around observation \( q \) over the entire landscape, and it can be simplified as

\[
\sum_{v=1}^{r} \sum_{u=1}^{r} m(h(u, v))\Phi(x_v - x_i, y_v - y_i, \sigma_i) = \sum_{v=1}^{r} m(h)\sum_{u=1}^{r} \left\{ \Phi(x_v - x_i, y_v - y_i, \sigma_i), \text{ if } h(u, v) = h \right\}.
\]
of which the latter double sum can be computed and stored once for each level of \( \sigma_s \). Thus, the denominator reduces to a point product between two short vectors.

Simplification of computations in this manner resulted in a speedup of 4-6 orders of magnitude for the data sets we used. The price paid for this is (i) the extra memory needed for precomputed matrices and (ii) the discretization of \( \sigma_s \). Neither of these is a serious limitation; data sets of some thousands of observations can still be analyzed on a desktop PC and the accuracy obtained for the distribution of \( \sigma_s \) is quite enough to capture biologically significant effects of distance.

**Table S1**

A table of explanations for symbols used in the main text and Appendix S1

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>( i )</td>
<td>index for observation</td>
</tr>
<tr>
<td>( N )</td>
<td>number of observations in data, ( i = 1, 2, ..., N )</td>
</tr>
<tr>
<td>( (x_i, y_i) )</td>
<td>spatial coordinates of observation ( i )</td>
</tr>
<tr>
<td>( w_i )</td>
<td>temporal weight of observation ( i )</td>
</tr>
<tr>
<td>( t_i )</td>
<td>time of observation ( i )</td>
</tr>
<tr>
<td>( X, Y )</td>
<td>dimensions of the study area (in grid cells)</td>
</tr>
<tr>
<td>( h )</td>
<td>index for habitat type</td>
</tr>
<tr>
<td>( H )</td>
<td>number of habitat types in analysis, ( h = 1, 2, ..., H )</td>
</tr>
<tr>
<td>( h(x, y) )</td>
<td>habitat type at location ( (x, y) )</td>
</tr>
<tr>
<td>( m(h) )</td>
<td>habitat preference multiplier for habitat type ( h )</td>
</tr>
<tr>
<td>( \theta )</td>
<td>set of parameters estimated simultaneously</td>
</tr>
<tr>
<td>( O )</td>
<td>set of observations, ( O = {1, 2, ..., N} )</td>
</tr>
<tr>
<td>( U(O, x, y, \theta) )</td>
<td>UD value generated at location ( (x, y) ) by set of observations ( O ) and parameter vector ( \theta )</td>
</tr>
<tr>
<td>( \sigma_s )</td>
<td>kernel width of the spatial kernel (SD of bivariate normal distribution)</td>
</tr>
<tr>
<td>( \sigma_t )</td>
<td>width of the temporal kernel, used in correction of temporal dependency of observations and in the calculation of temporal weights</td>
</tr>
<tr>
<td>( \Phi(d_x, d_y, \sigma_s) )</td>
<td>contribution of a two-dimensional kernel ( K_q(x, y) ) build around observation ( q ) to a location ( (x, y) ), where distance between observation and location is described by ( d_x = x - x_q ) and ( d_y = y - y_q )</td>
</tr>
</tbody>
</table>
The role of harvest induced infanticide in the reproductive biology of the brown bear
(Ursus arctos)

Jonna Katajisto, Otso Ovaskainen & Jon Swenson

- Submitted
The role of sexually selected infanticide in the reproductive biology of the brown bear (*Ursus arctos*)

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**Abstract**

Sexually selected infanticide (SSI) means that a male kills the young of a female to shorten her time to oestrus and to gain a mating opportunity. Harvesting males may provoke SSI by disturbing their social organization. This is probably the case in Scandinavian brown bear (*Ursus arctos*) populations, where cub survival decreased after harvesting adult males from the area. Quantification of the effect that removal of adult males exerts on cub survival and reproduction is essential for the harvest management of bears. We estimate the likelihood of losing an entire litter separately during and after the mating season and examine whether removing adult males from the vicinity of a female has an effect on the survival of the litter. We construct an individual-based model that follows the yearly reproductive cycle of females and estimate the model parameters with Bayesian approach using a time series of the reproductive status recorded for 73 females during the years 1986 – 2004 in Scandinavia. Our results indicate that, although removal of males increases individual cub mortality, it does not have a major effect on the mortality of entire litters, possibly because females manage to protect part of their litter. Consequently, cub mortality provoked by harvesting adult males does not inevitably shorten the time until the female’s next oestrus and is not necessarily compensated by a shorter litter interval. These results are essential for the modelling of effects of harvest-induced SSI in bears under different harvest schemes.

**Keywords:** Bayesian analysis, Brown bear, Scandinavia, Sexually selected infanticide, Survival, *Ursus arctos*

1. Introduction

The effects of harvest on population dynamics depend partly on the interaction between hunter selectivity and the mating system of the target species (Greene & Umbanhoward 1998). In polygynous species the reproductive potential of a population is not often limited by the number of males, and hence the strategy of selectively harvesting males has been considered to increase the sustainable yield (Swenson et al. 1997, Sæther et al. 2004). Male-biased harvesting is widespread in the management of ungulate game species, and also common in other large mammals with long parental care, where females with accompanying offspring are protected from harvest and adult males are taken as trophies (McLoughlin et al. 2005). However, excessive male-biased harvest may have disadvantageous consequences for population size when the removal rate of males is so high that some of the females remain unfertilized (Milner-Gulland et al. 2003, Whitman et al. 2004), or when the mean age of males decreases causing reduction in the reproductive success of females that would preferably mate with older males (McLoughlin et al. 2005, Bellemain et al. 2006b).

Harvest of adult males may also disturb the social structure of the population and cause male replacements, which can be detrimental for the survival of cubs (Whitman et al. 2004). One particular mechanism is sexually selected infanticide (SSI), which means that a male kills the young of a female to gain a mating opportunity (Hrdy 1979, Hrdy & Hausfater 1984, Packer & Pusey 1984). Infanticide is classified as SSI if the perpetrator is
not the father of the young it kills, if killing of the young shortens the time to the female’s next oestrus, and if the perpetrator has a high probability of siring the female’s next litter (Hrdy & Hausfater 1984). These three requirements have been documented in brown bears (Ursus arctos) in Scandinavia (Bellemain et al. 2006a), and the occurrence of SSI or counter-strategies related to it has been documented also in other brown bear populations (Wielgus & Bunnell 1995, Swenson et al. 1997, 2000, 2001).

Brown bears are solitary carnivores with large overlapping home ranges. Female bears are induced ovulators that have their oestrous periods during a mating season from late spring to early summer (Craighead et al. 1995). During this season both sexes increase their range size and females may mate with several males as well as males with several females (Craighead et al. 1995, Dahle & Swenson 2003c). Such promiscuous mating behaviour of females may have evolved in part to confuse paternity and avoid SSI (Hrdy 1979, Wolff & Macdonald 2004, McLellan 2005). In Scandinavia the female usually keeps the litter with her over the next wintering period and separates from the cubs during the following spring (Swenson et al. 2001, Dahle & Swenson 2003a). The litter typically consists of 1-3 and occasionally of 4 cubs. Females that are accompanied by a litter are not receptive to males (Dahle & Swenson 2003a), which leads to a minimum interval of two years between successful litters, when at least one of the cubs survives until the family break up. In order to gain a mating opportunity with a female, an infanticidal male would have to kill all cubs in her litter. If a female loses her litter during the mating season, she can become receptive within a short time and give birth to a new litter in the following year. Thus, SSI not only affects the survival of cubs, but it also alters a female’s reproductive cycle.

Humans are responsible for most adult brown bear mortality both in harvested and non-harvested populations (McLellan et al. 1999, Schwartz et al. 2005). Especially large males are a popular trophy in some areas, which skews human-caused mortality towards males (Miller et al. 2003). As one male can inseminate several females, hunting of males has been considered unimportant for bear population dynamics. The potential effects of male-biased harvest have been recognized only recently, and the consequences of disturbance in the social system rarely have been considered (Swenson et al. 1997). As results of studies regarding harvest of males and SSI remain equivocal, it is important to better understand the consequences of harvesting males for the successful management and conservation of bears (Swenson 2003, McLellan 2005).

There are two opposing views of how male-biased harvest can affect the survival of cubs through SSI (McLellan 2005). First, it has been suggested that, because males are prone to kill cubs, removing a large male from the population should generally increase the survival of cubs and thus have a positive effect on population growth rate (Miller 1990, Miller et al. 2003). The opposing view is that removing a large male can increase the likelihood of a new male entering the area and killing the cubs that he has not sired, which would decrease the population growth rate (Swenson et al. 1997, 2001, Swenson 2003). Reproduction also may be lowered indirectly due to SSI, because females may use suboptimal habitats in order to avoid infanticidal males (Wielgus & Bunnell 1994, 2000, Wielgus et al. 2001, Ben-David et al. 2004).

Whether SSI occurs in bear populations, especially in North America, is a controversial subject (Wielgus et al. 2001, Miller et al. 2003, McLellan 2005). The controversy concerning the opposing effects of harvesting adult males has persisted partly because it is difficult to observe infanticide and to identify the perpetrator in nature. Furthermore, because bears are seasonal breeders, SSI is expected to occur only during the mating season, and hence the traditional analysis of SSI requires data with a sufficiently high temporal resolution. Consequently, most studies on SSI have been based on comparisons of annual vital rates between harvested and non-harvested populations (Swenson et al. 1997, Miller et al. 2003, McLellan 2005). As the vital rates are likely to depend on a large variety of factors (McLellan 2005), population-level comparisons have only a limited power to disentangle the mechanisms related specifically to SSI, and the use of individual-based models has been suggested as a more effective approach (Boyce et al. 2001).

In this paper we study the role of SSI and harvest of adult males in the reproductive biology of the brown bears by using individual based approach. There exist very few direct observations of SSI. However, because in case of SSI female should lose the entire litter during the mating season, we can approach the question by quantifying the likelihood of litter loss separately for the mating season, and by examining whether removing adult males (by harvest or otherwise) from the vicinity of a female has an effect on the survival of the litter. Because the length of the mating season may vary due to
induced ovulation, our census-type data does not allow for direct estimation of these parameters. Therefore, we constructed an individual-based model that follows the yearly reproductive cycle of females, and use the data to estimate the parameters of the model through a Bayesian approach.

2. Material and methods

2.1. Study areas

We used data collected by Scandinavian Brown Bear Research Project from two study areas located in northern Sweden (67°N, 18°E) and in central Sweden and south-eastern Norway (61°N, 18°E) (Swensson et al. 1998, 2003c, Dahle & Swensson 2003b). Boreal coniferous forests dominate both study areas, although lakes and bogs cover large areas especially in the south and mountains with sub alpine habitats cover part of the northern area. Both study areas are sparsely populated by humans.

The two study areas differ in their levels of bear harvest. Legal harvest of approximately 5% of the population is allowed during a restricted season in autumn within both study areas throughout the study period, but large areas of the northern area are covered by three national parks in which harvest is prohibited. However, poaching may have been intensive in the northern population, although less on the study area than on its surroundings (Swensson et al. 2001). Females with a litter are protected from harvest in both populations.

2.2. Brown bear data

Radio-marked bears were located biweekly or weekly from an aircraft or from the ground using receivers and handheld or aircraft-mounted antennas during their entire active period from April to October (Dahle & Swensson 2003b, 2003c). The reproductive state of radio-tracked females, i.e. the number and age of cubs following the female, was systematically monitored from an aircraft or the ground after females emerged from their winter dens. Females were also observed in order to count cubs after the mating season and before entering the den in the autumn, and occasionally otherwise during the tracking. In the study populations the mating season normally takes place from the beginning of May to the beginning of July (Dahle & Swensson 2003c). The data that we use is a time series of the reproductive status recorded for 28 females (59 litters of which 4 were known to be lost) in the northern and 45 females (120 litters of which 34 were known to be lost) in the southern study area during the years 1986 – 2004. The time of the first reproduction was known for 15 and 27 females in the northern and southern study areas, respectively.

The location, age and sex of the bear are known for all legally killed bears. For radio-tracked individuals, also other types of mortality are known. As each female in the data set was radio-marked, we have information about their home ranges. Thus we could estimate which of the males that had died potentially interacted with a given female. During the study period 26 adult males (≥3 yr) died in the northern study area and 247 in the southern area, of which 25 in north and 72 in south were estimated to have died in the vicinity of at least one female in the analysis. We determined that an adult male died (because of harvest or other reasons) in the vicinity of the female if the site of death or the centre of the male’s home range during the year the male died was within 40 km of the centre of the female’s home range. We estimated the centre of an individual’s home range as the arithmetic mean of the observed locations after iteratively removing 5% of the outermost observations. In case of females, we used locations over the entire period the female was mature. As males move over larger areas and as their ranges may be affected by the presence of other males, we calculated the centre of a male’s home range (in case of radio-tracked males) separately for each year of data. Using the same method Bellemain et al. (2006b) found out that 95% of all known reproductive couples of bears in Scandinavia were located within 40 km from each other, thus interactions related to SSI are unlikely to occur over larger distances. Both female and male bears become mature at age of three in both study areas, although bears in the south tend to start reproduction earlier than those in the north (Swensson et al. 2001, Zedrosser et al. 2006).

2.3. The models

We modelled females and the fates of their litters using a stochastic, individual-based model that follows the yearly reproductive cycle of the females (Figure 1). The model accounts only for whether or not the female had a litter, not the number of cubs in the litter. We divided the active period into two intervals, the first from den emergence until the end of the mating season, and the second continuing
Bear harvest and SSI

until the autumn. We modelled the reproductive state of a female \(i\) at three instances during a year \(t\): just after den emergence in the spring \((A_i^t)\), during the mating season just before the mating takes or would take place \((B_i^t)\), after mating season before denning in the autumn \((C_i^t)\). We denoted the state of a female by the age of the cubs, so that for \(y = 0\) \(A_i^t, B_i^t, C_i^t = y\) refers to a female having cubs that are \(y\) years old at year \(t\). A female with no cubs was denoted by \(A_i^t, B_i^t, C_i^t = -1\). We assumed that cubs separated latest when they are two years old, so that \(A_i^t \leq 2\), and \(B_i^t, C_i^t \leq 1\).

We first considered a basic model, in which we analyzed the survival of the litters without reference to the male population. We then extended the model to account for males by assuming that the likelihood of SSI (i.e. probability of losing a litter during the mating season) depends on the occurrence of male mortality in the vicinity of the female. In the basic model (model A) we assumed that a female may lose her litter either during (with probability \(p\)) or after (with probability \(q\)) the mating season. We modelled these processes separately for cubs-of-the-year \((p_0, q_0)\) and for yearlings \((p_1, q_1)\). Cubbs in the southern study area are often separated as yearlings (Dahle & Swenson 2003a). We were unable to distinguish the separation of yearlings from their mortality, and thus \(p_1\) and \(q_1\) relate also to the probability of separating the litter.

Our main emphasis was in the probability \(p_0\), as the most likely cause of losing the entire litter of cubs-of-the-year during the mating season is SSI. Moreover, losing a litter during the mating season can affect the reproductive cycle of the female. As the female’s age or experience may affect her reproductive success, we modelled the probability \(p_0\) of losing a litter during the mating season separately for primiparous females \((p_{0f})\) having their first litter and multiparous females \((p_{0s})\) having their subsequent litters. We assumed that a female may mate only if she is not accompanied by cubs during the mating season \((B_i^t = -1)\) (Dahle & Swenson 2003a). We denoted the probability of successful mating by \(f\), meaning that the female will give birth to a new litter in the beginning of the following year.

In model B, we examined whether adult male mortality due to harvesting or other causes had an effect on SSI. To do so, we allowed the probability \(p_0\) of losing the entire litter during the mating season to depend on whether any males died in the vicinity of the female \(\Delta t\) years ago at year \(t - \Delta t\). If any males died, we set \(m_{\Delta t} = 1\), otherwise we set \(m_{\Delta t} = 0\). We modelled the relation between male mortality and the probability of losing the cubs during the mating season as 

\[ p_0 = \logit^{-1}(a + b' m_{\Delta t}) \]

where \(x \in \{f, s\}\) indicates whether the female was primiparous or multiparous. We were especially interested in \(b\), the effect of removing males. The primary cause of death of adult bears was harvest, which occurs in the autumn, and thus the effect of removing adult males can be seen the following year at the earliest. We did not consider multiple time lags simultaneously, but separately considered the effect of a fixed time lag \(1 \leq \Delta t \leq 3\). Previous stud-

**Figure 1.** A schematic description of the model that follows the yearly cycles of Scandinavian brown bear females and their litters. The boxes on top show the state variables related to the females and the harvest. The white boxes depict the states for which we have data, the shaded box illustrates the missing information that we deduced indirectly using Bayesian approach (Appendix A). The proportions in the time line do not represent absolute times and the arrows point to periods of varying length rather than exact points in time.
ies in Scandinavia have shown time lags within this interval (Swenson et al. 1997, Swenson et al. 2001).

To summarize, model A had a total of 6 free parameters \((p_0, p_1, q_0, q_1, f)\), and model B had a total of 8 free parameters \((a^I, a^I', b^I, b^I', p_1, q_0, q_1, f)\). We did not include the number of the cubs in these models, as our main interest was in the occurrence of SSI, in which case the entire litter is lost. We however analyzed the fates of individual cubs using a separate approach.

### 2.4. Parameter estimation

We estimated the parameters of the above described models using a Bayesian approach. The data consisted of visual observations of the states \(A_i\) and \(C_i\) for each female bear. Although most females were observed also on the beginning of July in the end of usual mating season, reliable observations of the intermediate state \(B_i\) were not always available, because the length of the mating season may vary individually due to induced ovulation. However, the value of \(B_i\) can often be deduced from the existing data. To start with, if \(A_i = C_i\), we also must have \(B_i = A_i\). But, if \(A_i \geq 0\) and \(C_i = -1\), the female may have lost the litter either during or after the mating season. As we assumed that a female may mate only if she does not have a litter, we must have \(B_i = -1\) if the female has cubs in the subsequent year \((A_i^{t+1} = 0)\). If the female does not have cubs in the subsequent year, there are two possibilities \((B_i = A_i\) or \(B_i = -1\)), in which case we considered the state \(B_i\) as missing data, for which we estimate a posterior distribution together with the actual model parameters. Few observations about female states \(A_i\) and \(C_i\) were missing, in which case we treated them as parameters to be estimated.

The posterior distribution of the parameter vector (including the missing data) was calculated using Gibbs sampling, the technical details of which are described in Appendix A. We assumed an uninformative (flat) prior for the probabilities \(p_0, p_1, p_1, q_0, q_1,\) and \(f\) in the range \([0, 1]\). The natural range of the parameters \(a^I, a^I', b^I\) and \(b^I\) is \((-\infty, \infty)\), but we restricted the range to \([-5, 5]\), in which we assumed a uniform prior. The restriction of the range was done for technical reasons, and was biologically justified, as values within the restricted range already cover unrealistically strong negative and positive effects of adult male mortality.

### 2.5. Mortality of individual cubs

In case of SSI, the male attempts to kill the entire litter, and the death of individual cubs is thus highly correlated. To see whether individual mortality rates could lead to the death of an entire litter without being SSI involved, we excluded all cases where the entire litter was lost, and used the actual counts of cubs-of-the-year to estimate the probability \(v\), that an individual cub from a litter of size \(n\) would die during the summer independently from the fate of the other cubs. The mortality of individual cubs was not divided into two seasons, because the exact time of death was not always known. We omitted cases with uncertain information about the number of cubs. We again used Bayesian inference (see Appendix B for details), and calculated the posterior distribution for \(v\) separately for litters with \(n = 2, 3, 4\) cubs.

### 3. Results

#### 3.1. Seasonal litter loss and mating success

In the southern population for primiparous females the probability of losing the entire litter was higher during the mating season than after it, whereas these probabilities were equal in case of multiparous females (Table 1, Figure 2). In the northern population the probabilities of losing the first litter during or after the mating season did not differ, but the probability of losing a subsequent litter was higher after the mating season (Table 1, Figure 2). In both study areas the probability of losing a litter during the mating season was higher for primiparous females than for multiparous females, although the result was only marginally significant in the northern area (Table 1, Figure 2). A comparison between the two study areas (Table 2) showed that the probability of losing all the cubs-of-the-year during the mating season was higher in the south than in north, but there was no difference after the mating season.

The probability of losing or separating from a litter with yearlings was similar during and after the mating season in both study areas. As expected, the probabilities of separating from yearlings were much higher in south than in north, because many yearlings were kept for another year in the north. The probability of a successful mating was high in both areas (Table 1, Figure 2).
3.2. Effect of the mortality of adult males

In the north, primiparous females lost their entire litter of cubs-of-the-year during the mating season more often if a male had died in the area 3 years earlier (Figure 3, Table 1), but there was no such difference for multiparous females. In contrast, if a male had died in the area the previous year, the mortality of cubs-of-the-year seemed to be reduced for primiparous females and increased for multiparous females, the difference between the two female types being statistically significant (Table 1). The removal of adult males had generally no effects in the southern study area, though there was a weak trend for a decreased probability of losing the litter during the mating season with time lags of 2 and 3 years for primiparous females and for an increased probability with time lags of 1 and 2 years for multiparous females. There were probably in general fewer males per female in the northern than in the southern study population (Dahle & Swenson 2003c). We note that the results for the northern study area must be interpreted with caution, as the litters of the females were not fully independent from each other with respect to the distribution of males, which may lead to overestimation of the significance levels.

Table 1. Statistics of the posterior distributions estimated separately for southern and northern brown bear populations in Scandinavia. \( P(x>y) \) indicates the probability that \( x>y \). We note that \( P(x\leq y)=1-P(x>y) \). The results for which \( P(x>y)>0.95 \) or \( P(x<y)>0.95 \) (which correspond to \( p<0.05 \) in classical statistics) are shown in bold.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Study Area</th>
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<tr>
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<td>Southern</td>
<td>Northern</td>
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<td>Model A</td>
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<tr>
<td>( P(p_0^f &gt; p_0^s) )</td>
<td>0.977</td>
<td>0.927</td>
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<tr>
<td>( P(p_0^f &gt; q_0) )</td>
<td>0.992</td>
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<td>( P(p_0^f &gt; q_s) )</td>
<td>0.724</td>
<td>0.022</td>
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<td>( P(p_1 &gt; q_1) )</td>
<td>0.472</td>
<td>0.880</td>
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<td>Model B</td>
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<tr>
<td>( P(b_1^f &gt; 0) )</td>
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<td>0.079</td>
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<td>( P(b_0^f &gt; 0) )</td>
<td>0.221</td>
<td>0.564</td>
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<td>( P(b_1^f &gt; 0) )</td>
<td>0.116</td>
<td>0.997</td>
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<td>( P(b_0^f &gt; 0) )</td>
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<td>( P(b_1^f &gt; b_0^f) )</td>
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<td>( P(b_0^f &gt; b_1^f) )</td>
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<td>( P(b_0^f &gt; b_0^f) )</td>
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<td>0.974</td>
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<tr>
<td>Cub mortality</td>
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<tr>
<td>( P(v_3 &gt; v_3) )</td>
<td>0.031</td>
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<td>( P(v_3 &gt; v_4) )</td>
<td>0.000</td>
<td>0.001</td>
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<tr>
<td>( P(v_3 &gt; v_4) )</td>
<td>0.005</td>
<td>0.013</td>
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4. Discussion

Our results indicate that especially primiparous female bears have a high risk of losing their entire litter, the risk being much higher than what would be expected from the mortality rate of individual cubs. In addition to SSI, possible explanations for these higher losses of cubs include inexperience or poor condition of the mother and human disturbance around the winter den site. However, neither of these is likely to play a major role in our results, as we excluded from the analyses the litters that were known to be lost in the winter den, and as maternal conditions have not been observed to affect cub mortality in Scandinavia (Swenson et al. 1997, 2001). The role of SSI is emphasized also by the fact that the litter mortality of primiparous females was most common during the mating season. Thus, lost may bias these estimates downwards. However, the mean mortality estimates for the litter sizes of 2, 3 and 4 were small (0.05, 0.12 and 0.39 in the southern study area, and 0.06, 0.10 and 0.40 in the northern area), and thus the probability of losing the entire litter due to cubs dying independently from each other (0.003, 0.002 and 0.023 in south, and 0.004, 0.001 and 0.026 in north for litters of 2, 3 and 4 cubs respectively) was very unlikely compared to $p_o$ and $q_o$, although higher for the few litters with four cubs.

### 3.3. Mortality of individual cubs

In litters where at least some of the cubs survived, mortality of individual cubs was similar in both study areas (Table 2, Figure 4). Cubs in larger litters had higher mortality (Table 1, Figure 4). We note that excluding the cases where the entire litter was lost may bias these estimates downwards. However, the mean mortality estimates for the litter sizes of 2, 3 and 4 were small (0.05, 0.12 and 0.39 in the southern study area, and 0.06, 0.10 and 0.40 in the northern area), and thus the probability of losing the entire litter due to cubs dying independently from each other (0.003, 0.002 and 0.023 in south, and 0.004, 0.001 and 0.026 in north for litters of 2, 3 and 4 cubs respectively) was very unlikely compared to $p_o$ and $q_o$, although higher for the few litters with four cubs.
females that reproduce first time and have little experience in avoiding infanticidal males had higher litter mortality during the mating season than females with second or subsequent litters.

Female brown bears have counter-strategies to avoid SSI, such as multi-male mating and use of suboptimal habitats, together with different movement and activity patterns from males (Wielgus & Bunnell 1994, 1995, 2000, Swenson 2003, Benda-David et al. 2004, Bellemain et al. 2006a). Our results suggest that the ability of the female to avoid SSI increases with the female's experience. The other factor increasing SSI in case of primiparous females is that males are not likely to kill infants of the females that they have copulated with (Hrdy & Hausfater 1984, McLellan 2005, Bellemain et al. 2006a). A primiparous female has been ready to breed only during the previous year, so it is possible that fewer males in the area have mated with her than with multiparous females, which males may have been monitoring more intensively. If so, more of the males would benefit from killing the litter of a primiparous female.

We aimed at testing two opposing hypotheses of how harvesting males could affect the survival of cubs through SSI. In the northern study area our results for primiparous females actually give little support for both seemingly contrasting hypotheses. First, in line with the hypothesis that the removal of males could directly reduce cub mortality, the loss of litters with cubs-of-the-year seemed to be reduced the year following the removal of a male. Second, in line with the hypothesis that removal of males increases the likelihood of SSI due to disturbance in the social system, the loss of litters with cubs-of-the-year was increased 3 years after the death of a male. In contrast to earlier studies (Swenson et al. 1997, 2001), we found practically no effect of adult male mortality on the litter loss in the southern study area. The difference may be explained by the fact that we concentrated on the mortality of entire litters (i.e. successful SSI), whereas the earlier studies considered the loss of individual cubs. In addition, the earlier studies were done in the levels of subpopulations or reproductive areas rather than individuals and they did not consider the status of the females (primiparous vs. multiparous) or seasonality explicitly (the times before and after the mating season). As the harvest rate is higher in the southern study population (Swenson et al. 1997), the higher mortality of litters during the mating season in the south is in line with the hypothesis that in the long-term probability of SSI increases with male removal.

It is difficult to disentangle the alternative hypotheses, partly because the effects of the different time lags are not causally independent from each other. To illustrate, if the death of an infanticidal male in year $t$ decreases the litter loss in year $t+1$, there will be fewer females to mate during year $t+1$. Thus there will be fewer litters with cubs-of-the-year in year $t+2$, and hence more females willing to mate, resulting in a high number of litters in year $t+3$. The low availability of females willing to mate in year $t+3$ may increase the likelihood of SSI in year $t+3$, even without any direct causal link to the disturbance of the social system due to the death of the male in year $t$. In addition, although the method we used for determining which of the adult males interact with a certain female was biologically justified (Bellemain et al. 2006a), the estimates are uncertain because bear ranges vary in area and shape, and males of different age or size may contribute differently to reproduction (Bellemain et al. 2006b). Also sex ratio and density of surrounding individuals may affect the occurrence of SSI (McLellan 2005).

In Scandinavia, the mean litter interval in the southern study population is 1.6 years, which is significantly smaller than the interval of 2.6 years in the northern study population (Swenson et al. 2001). However, times between successful litters do not differ significantly between the study areas (Swenson et al. 2001). The difference is largely explained by the higher mortality of litters with cubs-of-the-year in the south during the mating season. Additionally, cubs are more often separated as yearlings in the southern population. Quantification and timing of the mortality of entire litters are essential for modelling bear population dynamics, as losing a litter in the breeding season shortens the female’s time to oestrus and a lost litter can be partially compensated for by a new litter in the subsequent year. The probabilistic modelling approach used here enabled estimating the litter mortality separately for mating season even from temporally coarse census data.

Male-biased harvest has been justified by the argument that harvesting adult males from the vicinity of a female removes potentially infanticidal males and can thus improve the survival of her litter (see review by Miller (1990)). We found no significant support for this argument. Furthermore, removing adult males from female reproductive areas in Scandinavia has previously been associated with increased cub mortality, possibly due to social disturbance caused by SSI (Swenson et al. 1997, 2001). Here we observed the same in the north with
a time lag of 3 years, and in the comparison between
the north and the south in the sense that breeding
season litter mortality is in general much higher in
the more heavily harvested southern population. It
is important to separate the mortality of entire litters
from the mortality of individual cubs. Our results
indicate that although removal of males increases
cub mortality (Swenson et al. 1997, 2001, Swenson
2003), it does not have a major effect on entire litter
mortality. The cost associated with SSI due to
harvesting adult males seems to be primarily higher
cub mortality in litters with partial cub loss. This
also means that anti-infanticidal strategies of
females are relatively successful, as they manage to
protect part of their litter. Cub mortality provoked
by harvesting adult males does not inevitably shorten
the time until the female’s next oestrus, hence cub
mortality is not necessarily compensated by a shorter
litter interval. These results are important for
management, as they allow one to assess the effects
of harvest induced SSI on the growth rate of bear
populations.

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appropriate ethical committees in both countries.

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Appendix A

Bayesian estimation of the model parameters

Here we describe how the parameters of the models A and B were estimated using Bayesian inference through Markov Chain Monte Carlo (MCMC) methods (Gelman et al. 2004). We used Gibbs sampling, in which each parameter is updated in turn conditional on the current values of the other parameters. In order to do so, we derive the so called full-conditional distributions, which describe the posterior density of each parameter conditional on the values of the other parameters values. We ran the MCMCs for 1,000 iterations, of which the first 100 were dropped out as burn in. The programming was performed with Mathematica (Wolfram Research Inc 2004).

Model A

In case of model A, the model parameters are \( p^0_i \), \( p_i^0 \), \( p_f \), \( q_0 \), \( q_f \), and \( f \). In addition, all values of \( B^i_t \) and some of \( A^i_t \) and \( C^i_t \) were missing, and they were treated as parameters to be estimated.

Full-conditional distributions of the model parameters

All model parameters represent probabilities associated to Bernoulli random variables, i.e. events (death of litter or successful mating) that may or may not have happened. Denoting by \( n \) the number of trials and by \( m \) the number of successes, the posterior density for such a parameter is given by Beta\((m+1, n-m+1)\), where we have assumed the uniform prior Beta\((1,1)\) (Gelman et al. 2004). In case of \( p^0_i \), \( n \) is the total number of cases in the data for which a primiparous female has cubs-of-the-year in the spring \( (A_t^i = 0) \). Of these, \( m \) is the number of
cases in which the litter was lost during the mating season ($B'_i = -1$). In case of $p_a$, $n$ and $m$ the same calculation is done for multiparous females. In case of $p_a$, the values of $n$ and $m$ are calculated for yearlings ($A'_i = 1$), not accounting for whether the female is primiparous or multiparous. In case of $q$, $n$ is the total number of cases with a female having cubs-of-the-year in the mating season ($B'_i = 0$). Of these, $m$ is the number of cases in which the litter was lost before wintering ($C'_i = -1$). In case of $q$, the same calculation is done for yearlings ($B'_i = 1$). In case of $f$, $n$ is the number of cases with a female having a possibility to mate ($B'_i = -1$), and $m$ is the number of cases in which cubs-of-the-year were found in the spring ($A'^{a1} = 0$).

**Full-conditional distributions of the missing data $B'_i$**

As noted in the text, the values of the missing data (the $B'_i$) can sometimes be deduced deterministically from the other data. If $A'_i = C'_i$, we must have $B'_i = A'_i$. If $A'_i \geq 0$ and $A'^{a1} = 0$, we must have $B'_i = -1$. The uncertain case is $A'_i \geq 0$, $C'_i = -1$, and $A'^{a1} = -1$, as we may either have $B'_i = A'_i$ or $B'_i = -1$. For example, let us consider the case of cubs-of-the-year ($A'_i = 0$). The likelihood of the chain $A'_i = 0$, $B'_i = 0$, $C'_i = -1$, $A'^{a1} = -1$ is $(1-q_0) q_2$, whereas the likelihood of the chain $A'_i = 0$, $B'_i = -1$, $C'_i = -1$, $A'^{a1} = -1$ is $p_f (1-f)$. Hence the full-conditional probabilities are $P(B'_i = A'_i) = z_1/s$ and $P(B'_i = -1) = z_2/s$, where $z_1 = (1-q_0) q_2$, $z_2 = q_0 (1-f)$, $y \in [0,1]$ according to the age of the cubs, and $s = z_1 + z_2$.

**Full-conditional distributions of the missing data $A'_i$**

The value of $A'_i$ is uncertain only if $B'^{a1} = A'_i = -1$. In this case, the likelihood of the chain $B'^{a1} = -1$, $C'^{a1} = -1$, $A'_i = -1$, $B'_i = -1$ is $(1-f)$, whereas the likelihood of the chain $B'^{a1} = -1$, $C'^{a1} = -1$, $A'_i = 0$, $B'_i = -1$ is $f p_0$. The full-conditional probabilities follow as in the case of $B'_i$.

**Full-conditional distributions of the missing data $C'_i$**

There is never uncertainty about the value of $C'_i$. If $B'_i = -1$, we always have $C'_i = -1$. If $B'_i = 0$, $A'^{a1} = -1$ implies $C'_i = -1$ and $A'^{a1} = 1$ implies $C'_i = 0$. The case of yearlings follows the same logic. Thus missing values of $C'_i$ are updated purely deterministically.

**Model B**

In case of model B the parameters $p_{a1}$ and $p_{a2}$ are replaced by the parameters $a'$, $b'$, $a'$, and $b'$. Given the parameters $ax$, $bx$, where $x \in \{f, s\}$, the probability of litter loss is given by $p_{a1} = \logit^{-1}(a' + b' m_n)$. We assumed a uniform prior in $[-5.5]*[-5.5]$, in which case the full-conditional distribution for the parameter pair $(a', b')$ is in this range proportional to $(p_{a1})^{a1}(1-p_{a1})^{a2}$, where $n$ and $m$ are the number of trials and number of successful trials as explained above. We sampled from this distribution using the discrete grid approximation (Gelman et al. 2004) using step size 0.2 in both directions.

All of the other parameters were updated as in case of model A.

**Appendix B**

**Bayesian estimation of the mortality of individual cubs**

We estimated the probability of death of individual cubs-of-the-year using Bayesian inference. Denoting by $n$ the total number of cubs in the data belonging to a given litter size and by $m$ the number of cubs that died (Table B.1.), the posterior density for the death probability is given by Beta($m+1, n-m+1$), where we have assumed the uniform prior Beta(1,1) (Gelman et al. 2004).

**Table B.1. The raw data from which mortality of individual cubs was estimated. The entries are in the form $n (m)$, where $n$ is the total number of cubs-of-the-year, and $m$ the number of cubs that died.**

<table>
<thead>
<tr>
<th>LITTER SIZE</th>
<th>SOUTH</th>
<th>NORTH</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>77 (3)</td>
<td>48 (2)</td>
</tr>
<tr>
<td>3</td>
<td>112 (14)</td>
<td>74 (7)</td>
</tr>
<tr>
<td>4</td>
<td>10 (6)</td>
<td>5 (3)</td>
</tr>
</tbody>
</table>
Effects of targeted harvesting on Scandinavian brown bears

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- Manuscript
Effects of targeted harvesting on Scandinavian brown bears

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ABSTRACT

The population of brown bears in Scandinavia is growing and it is expected that hunting will be increased in the future to limit the population growth and conflicts between humans and bears. We investigate the effects of different hunting policies on the predicted population growth rate of the bears. Scenarios investigated comprise random hunting, hunting biased towards large or young individuals and allowing harvest of females with cubs. For this purpose we constructed an individual-based model that included details of bear behaviour, such as sexually selected infanticide (SSI). Reproduction and mortality sub-models were parameterized using Bayesian estimation and a large data set of bear life-histories compiled by the Scandinavian Brown Bear Research Project over a period of 19 years. We found that elevated harvest of 10% is unlikely to endanger the population, but allowing harvest of females with cubs has a small negative effect on the population growth rate. Increasingly popular trophy harvest of males has a positive influence on the population growth rate, because males are able to mate with multiple females a year. However, long-term effects of intensive trophy harvest should be considered cautiously, as it lowers the average age of adult males and results in heavily skewed population structure, which may eventually influence the reproductive success of females. Some effects of increased hunting will according to our model manifest themselves only after a time-delay, which indicates that a gradual increase in hunting combined with monitoring of population growth would be a conservative and safe strategy to increase bear harvest in Scandinavia.

1. Introduction

After a population bottleneck in the early 1900’s the brown bear (Ursus arctos) population in Sweden and Norway has increased both in numbers and range due to successful conservation (Swenson et al. 1994, Swenson et al. 1995, Swenson et al. 1998b). As a consequence, conservative harvesting of bears was initiated in 1943. Since then the population has been increasing and expanding its range while being harvested (Swenson et al. 1998b). Population growth has been fast, Sæther et al. (1998) estimated an annual population growth rate of up to 16%. Growing concerns about threats that the increasing bear population causes to humans and livestock have raised the pressure for controlling the population by increasing the harvest. Indeed, properly planned, hunting is an important tool for bear management (Boyce et al. 2001). However, if the harvest is to be substantially increased from the present level, it is important to evaluate the impacts of different harvest schemes.

In reality, the size of the individual and whether or not a litter accompanies it are the only cues that can be used in selective hunting. Also, age or sex-specific behaviour, such as mobility or caution, may influence the rate at which the hunters detect different types of individuals, independent of their relative occurrence in the population. Consequently, harvest could be skewed either towards large or small individuals or towards individuals exhibiting a
behaviour that makes them vulnerable. Additionally, the harvest of females accompanied by a litter can be restricted, as is presently the case in Sweden.

Scandinavian brown bears show high demographic variance among individuals (Sæther et al. 1998). Likewise, the behaviour of individuals may influence their susceptibility to being killed and thus the response of the population to different types of harvest. For example, trophy harvest of large males may have side effects via decreased survival of cubs due to sexually selected infanticide (SSI) (Swenson et al. 1997, 2001a, Swenson 2003). Factors such as SSI should be taken into account in the planning of future harvesting practices.

We constructed a stochastic individual-based simulation model that includes demographic uncertainty to test different realistic bear harvest strategies. An individual-based approach was chosen, because it enabled including individual differences that are important for both to model the demographic stochasticity appropriately and to include realistic behavioural rules related to SSI (Wiegand et al. 1998, Grimm 1999). Such structure also enabled targeting the harvest to different individuals in an intuitive way.

The Swedish bear population is currently hunted approximately at a 5% rate, and reducing the harvest is very unlikely. Therefore we compared different ways of increasing the harvest level. Our aim was to use population viability analysis (PVA) simulation techniques to quantify the effects of different harvest scenarios on the expected population growth rate. We did not investigate predicted extinction rates because based on present population data extinction of the brown bear population in Sweden seems very unlikely. Bayesian inference was used to estimate parameter distributions used in the simulations from life-history data of total 296 radio-marked bears from southern Sweden.

2. Material and methods

2.1. Essential features of bear biology and harvesting

Brown bears are solitary carnivores with large overlapping home ranges. Both female and male bears become mature at age of three in Scandinavia (Swenson et al. 2001b, Zedrosser et al. 2006). Female bears have induced ovulation and have their oestrous period during the mating season from late spring to early summer (Craighead et al. 1995, Dahle and Swenson 2003c). During this season both sexes increase their range of movements and females may mate with several males as well as males with several females (Craighead et al. 1995, Dahle and Swenson 2003c, Bellemain et al. 2006a). In Scandinavia the female keeps the litter with her over the next wintering period and usually separates from the cubs during the following spring (Swenson et al. 2001b, Dahle and Swenson 2003a). The litter typically consists of one to three and occasionally of four cubs. Females that are accompanied by a litter are not receptive to males (Dahle and Swenson 2003a), which leads to a minimum interval of two years between successful litters.

If a female loses her entire litter early in the mating season she may become receptive and give birth to a new litter the following year. Thus, an infanticidal male benefits a mating opportunity by killing a litter following a female that he has not mated with previously (and thus can not be the father of the cubs). This is called sexually selected infanticide (SSI) (Hrdy and Hausfater 1984). Infanticide is classified as SSI if the perpetrator is not the father of the young it kills, if killing of the young shortens the time to the female’s next oestrus, and if the perpetrator has a high probability of siring the female’s next litter. These three requirements have been documented in brown bears (Ursus arctos) in Scandinavia (Bellemain et al. 2006a).

Harvest in the study area occurs during a restricted season from 21st of August until 15th of October. The total harvest is currently limited by a quota set by the authorities for each of the ten counties where bear hunting is allowed. All hunters must within 24 hours report bears that are killed or wounded. When the quota is met, the season is closed with a 24-hour notice. Females that are accompanied by a litter are protected from hunting. Hunters report the location, sex and weight of the killed bear. Hair samples and premolar tooth are sent for further DNA analysis and age determination (Matson et al. 1993).

2.2. Bear data

We used information collected during 1986-2004 from 296 radio-tracked bears in south-central Sweden (61°N, 18°E) for parameterising the simulation model. Bears were radio-marked early in the spring using helicopters (Arnemo et al. 2006).
Those equipped with radio collars were located biweekly or weekly from an aircraft or from the ground using receivers and handheld or aircraft-mounted antennas during their entire active period from April to October (Dahle and Swenson 2003b, 2003c). Most of the female bears were followed throughout their entire lives, and their reproductive state (i.e. the number and age of cubs) was systematically monitored each spring after bears emerged from their winter dens. Time series collected for 45 females with a total of 120 litters were used in the estimation of the parameters related to reproduction (Katajisto et al. 2006). Age-specific natural mortality rates were estimated based on the known natural deaths of radio-tracked individuals belonging to each sex-age group.

2.3. The simulation model

2.3.1. General description

We built an individual-based simulation model to investigate the effects of different realistic harvesting scenarios on the population dynamics of the bear. Our main interest is in population level statistics, which include the annual population growth rate, stable age-sex structure and litter interval. These emerge from the mortality and reproduction rates of the individuals. Along with the change in population growth rate, the aim was to gain information about the relative importance of individuals belonging to different age and sex classes. We also explored the effects of allowing the harvesting of females with a dependent litter. Our aim was not to estimate the absolute population growth rate but rather the changes in it due to changes in the harvesting. The model was implemented in C/C++.

2.3.2. Model variables

The basic unit in the model is the individual. The model follows the yearly cycle of individuals that are independent from their mother. Individuals are characterised by age, sex, life-stage and reproductive status. Life-stage of an individual can be either cub, yearling, juvenile, or adult. Both females and males can mate first time at the age of three years. The reproductive status of a breeding female can be either primiparous (reproducing for the first time), multiparous (female has reproduced earlier) or senescent (27 years or older (Schwartz et al. 2004)). Females give birth to male and female cubs with equal probability.

Mortality rates and probability of first reproduction depend on the sex and age, or life-stage, of the individual (Table 1). Mortality of cubs of the year is modelled in two steps. First, the probability that the entire litter dies depends on the reproductive status of the mother, with the probability of losing the first litter being higher than the probability of losing later litters. Second, mortality of individual cubs (given that the entire litter was not lost) depends on the number of cubs in the litter. Litter size depends on the reproductive status of the female, it being smaller for primiparous and senescent females.

We assumed no density-dependence in reproduction or mortality rates. This is because we have no real data about the form of density-dependence as the population has been expanding and hunting is keeping densities below the carrying capacity of the landscape for bears. Space was not modelled explicitly, but the probability of SSI is modelled so that the death of adult males influences only a limited number of females (Katajisto et al. 2006).

2.3.3. Process and sequence of events

The model proceeds in annual time steps. Individual processes are modelled probabilistically in the following order: birth, separation of cubs and spring litter loss, SSI, mating, late separation of cubs and litter loss, other natural mortality, harvest, aging and maturation. A schematic description of the model is presented in Fig. 1 and summary information about parameter distributions for processes is given in Tables 1 and 2.

Birth

Females that mated successfully previous spring give birth to a litter with one to four cubs, with the probability of different sizes of litters \( (l_n) \) depending on the reproductive state of the female \( (x = f, s) \) \( f \) primiparous and \( s \) multiparous females). Following (Schwartz et al. 2004), the reproduction of older females is lowered so that the litter-size distribution of senescent females follows that of the primiparous and females stop their reproduction at age of 30 years. Females give birth to male and female cubs with equal probability.

SSI and separation of the litter

A mother separates from the litter of yearlings with a certain probability \( (p_i) \). All two-year-old cubs
become independent. SSI is modelled so that the probability of losing an entire litter with cubs of the year depends on whether any adult males have died close to female two years earlier (Katajisto et al. 2006). Because the hunting season occurs in the autumn and the mating season is in the spring, there is time lag of two years before harvesting-induced SSI has an effect (Swenson et al. 1997, Swenson et al. 2001b).

Mating
If a mature female is not accompanied by a litter, it may mate successfully. The probability of first successful mating \( (f) \) depends on the age of the female \( (a = 3,4,5) \). Earliest mating occurs at age three, and the probability increases until the age of five, after which it stays at a constant high level. Note that cubs are born in the beginning of the following year, so that female has her first litter as four year old as earliest. We assumed that male abundance had no effect on female mating success. Male bears are known to visit many females during the mating season (Dahle and Swenson 2003c, Schwartz et al. 2003), and thus an extremely skewed sex ratio would be needed before female mating would fail due to the lack of male bears.

![Figure 1. Diagram describing the population processes and the yearly sequence of events in the simulation model.](image)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Median (95% HPDI)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Family breakup</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_1 )</td>
<td>0.716 (0.616 - 0.811)</td>
<td>probability of separating from yearlings before mating</td>
</tr>
<tr>
<td>( q_1 )</td>
<td>0.730 (0.515 - 0.885)</td>
<td>probability of separating yearlings after mating season</td>
</tr>
<tr>
<td><strong>Litter loss</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( a_0^f )</td>
<td>-0.371 (-1.400 - 0.600)</td>
<td>intercept of the SSI model for primiparous females</td>
</tr>
<tr>
<td>( b_0^f )</td>
<td>-0.700 (-2.200 - 0.800)</td>
<td>effect of removing males in the SSI model for primiparous females</td>
</tr>
<tr>
<td>( a_0^s )</td>
<td>-1.796 (-2.800 - -1.000)</td>
<td>intercept of the SSI model for multiparous females</td>
</tr>
<tr>
<td>( b_0^s )</td>
<td>0.455 (0.600 - 1.600)</td>
<td>effect of removing males in the SSI model for multiparous females</td>
</tr>
<tr>
<td>( q_0 )</td>
<td>0.164 (0.103 - 0.238)</td>
<td>probability of losing a litter with cubs of the year after mating season</td>
</tr>
<tr>
<td><strong>Mating</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f )</td>
<td>0.910 (0.851 - 0.956)</td>
<td>probability of a successful mating</td>
</tr>
</tbody>
</table>

Table 1. Explanation of the parameters for brown bears in south-central Sweden in the reproduction sub-model of (Katajisto et al. 2006), organised under the respective process in the main model. The multivariate median and 95% HPDI describe the posterior distribution from which the parameter values were drawn in the simulations. (SpatialMedian function in Mathematica (Wolfram Research Inc.), which minimises the summed Euclidean distance between the median point and the data, was used for the multivariate median.)
**Late separation of cubs and litter loss**
A mother may separate from her yearlings or lose her entire litter of cubs of the year also after the mating season \( (q_t) \).

**Other natural mortality**
The mortality of cubs of the year in the litters not experiencing entire litter loss \( (m^c) \) depends on the litter size \( (n = 2, 3, 4) \), because cubs in larger litters have higher mortality (Katajisto et al. 2006). The mortality rates \( (m^c_i) \) of other individuals depend on their sex \( (s) \) and life-stage \( (a) \).

**Aging and maturation**
Individuals and litters age one year and the life-stage of the individual may change; cubs become yearlings, yearlings become juveniles (2-3 years old) and juveniles become adult (4 year olds and older).

---

| Table 2. Explanation of the parameters for brown bears in south-central Sweden that were used in the simulation model outside the reproduction sub model organised according to the related demographic process. Median values and 95% HPDI (highest probability density intervals) describe the posterior distribution from which the parameter values were drawn in the simulations. |
|---|---|---|
| Parameter | Median (95% HPDI) | Description |
| **Birth** | | |
| \( l_1^f \) | 0.243 (0.103-0.440) | probability of litter size 1 at first reproduction |
| \( l_2^f \) | 0.586 (0.389-0.768) | probability of litter size 2 at first reproduction |
| \( l_3^f \) | 0.114 (0.027-0.282) | probability of litter size 3 at first reproduction |
| \( l_4^f \) | 0.029 (0.001-0.146) | probability of litter size 4 at first reproduction |
| \( l_1^s \) | 0.117 (0.066-0.188) | probability of litter size 1 at later reproduction |
| \( l_2^s \) | 0.379 (0.292-0.470) | probability of litter size 2 at later reproduction |
| \( l_3^s \) | 0.435 (0.344-0.530) | probability of litter size 3 at later reproduction |
| \( l_4^s \) | 0.063 (0.027-0.118) | probability of litter size 4 at later reproduction |
| **Mating** | | |
| \( f_3 \) | 0.451 (0.283-0.626) | probability of first successful mating as a 3-year-old |
| \( f_4^f \) | 0.731 (0.501-0.897) | probability of first successful mating as a 4-year-old (given that did mate as 3-year-old) |
| \( f_5^f \) | 0.871 (0.478-0.995) | probability of first successful mating as a 5-year-old (given that did mate as 3-year-old) |
| **Natural mortality** | | |
| \( m^0_2 \) | 0.045 (0.014-0.104) | probability of an individual cub dying in a litter with 2 cubs, excluding total litter loss |
| \( m^0_3 \) | 0.115 (0.067-0.178) | probability of an individual cub dying in a litter with 3 cubs, excluding total litter loss |
| \( m^0_4 \) | 0.385 (0.184-0.617) | probability of an individual cub dying in a litter with 4 cubs, excluding total litter loss |
| \( m^1_f \) | 0.117 (0.068-0.184) | probability of a female yearling dying |
| \( m^1_j \) | 0.016 (0.004-0.044) | probability of a juvenile female (2-3 year old) dying |
| \( m^a_j \) | 0.011 (0.004-0.025) | probability of an adult female (4 years or older) dying |
| \( m^m_1 \) | 0.017 (0.004-0.046) | probability of a male yearling dying |
| \( m^m_j \) | 0.023 (0.009-0.047) | probability of a juvenile male (2-3 year old) dying |
| \( m^a_j \) | 0.018 (0.008-0.033) | probability of an adult male (4 years or older) dying |
2.3.4. Initialization and input

We started simulations with 600 individuals (50 female and male cubs, 50 female and male yearlings, 100 female and male juveniles, 100 adult females and males). In the beginning of the simulation run the cubs and yearlings were assigned randomly to 50 adult females. The age of the juveniles was assigned with equal probability of 2 or 3 years. The adult females and males were assigned an age based on a random number between 4 and 35 years.

For each harvest scenario, the model was run with 1000 parameter sets that were randomly drawn from the posterior parameter distributions of the model parameters (Tables 1 and 2). For each parameter set, to minimise the effect of initial population, the model was first run using the basic harvest scheme (See 2.5.2. and Fig. 2) until the proportions of different individuals in the population stabilised and the population size reached ceiling of 10000 individuals, which was considered high enough to remove any drastic effects of stochastic events. Extra individuals exceeding the population ceiling were removed randomly in the beginning of each year in order to limit the computation time required for analyses. After the initial transient, we changed the harvest parameters and ran the model 65 years during which the model output was recorded.

2.3.5. Model output

The stochastic growth rate was estimated as geometric mean of the amount by which the population grew each year (Caswell 2001). We also recorded the distribution of different types of individuals at the end of the year (before aging). After the change in the harvest parameters, we calculated the average annual population growth rate of the first 5 years to investigate the short-term effect on the population growth rate. The population was then allowed to stabilize again during one bear generation (for certainty we used 15 years, as the average generation length in bears has been estimated to be 10 years (Harris and Allendorf 1989, Tallmon et al. 2004) and the average annual growth rate for the following 50 years was calculated to explore the long-term consequences of the harvest strategy in question.

The long-term effects are of consequence when starting a new hunting policy. The short-term effects are of interest for monitoring after the implementation of a new hunting policy. If long-term effects are large but short-term effects small, then it should be understood that the real impact of the hunting policy is likely to become visible only after a significant time delay. A delay in observing changes to population dynamics is inevitable, because the “old” population structure is inherited from the basic hunting regime to the time of the new policy, and it takes time for the new population structure to change and stabilize.

2.4. Parameter estimation

2.4.1. Reproduction sub-model

We have previously constructed an individual-based model that followed the fate of females and their litters and estimated the posterior distribution of the reproductive parameters and SSI from records of female reproduction histories (Table 1). We modelled the relation between male mortality and the probability of SSI as \[ p_i = \log^{-1}(a \cdot b^3m_2) \]
where \( x \in \{f, s\} \) indicate whether the female is primiparous or multiparous, and \( m_2 = 1 \) whether adult males had died within 40km from the centre of the female’s home range two years earlier and otherwise \( m_2 = 0 \). Parameters \( a \) and \( b \) were estimated using Bayesian inference through Markov Chain Monte Carlo (MCMC) methods and Gibbs sampling (Gelman et al. 2004). The details of this model and its parameter estimation are given in (Katajisto et al. 2006). The reproductive process in the present model has identical structure. Parameter values for the simulations were randomly drawn from the joint posterior parameter distribution (the posterior density of each parameter is conditional on the on the values of all other parameters).

2.4.2. Life-stage specific probabilities of death

Because the mortality of individual cubs does not influence the reproductive cycle of females, the mortality of cubs excluding entire litter loss was estimated separately from the reproduction model. We used counts of cubs of the year to estimate the probability \( m^n \), that an individual cub from a litter of size \( n \) would die independently from the fate of the other cubs in the litter. We used Bayesian inference and calculated the posterior distribution for \( m^n \) separately for litters litters with \( n = 2, 3, 4 \) cubes (Table 2). The posterior parameter distributions for other sex- and life-stage dependent probabilities
of dying for other reasons than harvest were estimated based on radio-tracked individuals (Table 2). Mortality probabilities were estimated separately for females and males according to the categories yearlings, juveniles or adult.

All mortality parameters represent probabilities associated to Bernoulli random variables, i.e. an individual either dies or does not. Denoting \( n \) as the total number of individuals alive belonging to a certain group defined by sex and life-stage and \( m \) as the number of individuals of that group that had been observed to die, the posterior density for the probability of death is given by Beta\((m+1, n-m+1)\), where we have assumed the uniform prior Beta(1,1) (Gelman et al. 2004).

### 2.4.3. Litter size distribution and probabilities of first successful mating

Bayesian inference also was used in the estimation of the posterior probability distribution of giving birth to litters \( I_n \), with \( n = 1,2,3,4 \) cubs separately for primiparous \((x = f)\) and multiparous \((x = s)\) females. This was done using the Dirichlet distribution, which is the multivariate generalisation of the beta distribution that is used in Bayesian estimation of parameters of a discrete probability distribution (Cohen 1988). We had information about the litter size of 114 litters of multiparous females and 20 litters of primiparous females. The litter size distribution in the data for multiparous females was \( (1,2,4,0,46,6) \) and \( \beta^+ = (5,13,2,0) \) for primiparous females. Assuming a uniform prior \((1,1,1,1)\) represented by Dir\((\alpha)\), the posterior for multiparous females is Dir\((\alpha + \beta^+)\) and for primiparous females Dir\((\alpha + \beta^-)\).

Posterior distributions for the probabilities of first successful mating \( f_a \) at age of \( a = 3,4,5 \) were estimated from radio-marked females following the same logic as in the calculation of death probabilities. If the number of females that reproduce for the first time at a certain age is denoted by \( n \) and the total number of radio marked females of the same age (that have not reproduced yet) is denoted by \( m \), the posterior density for the probability of first reproduction at that age is given by Beta\((m+1, n-m+1)\), where we again assumed the uniform prior Beta(1,1) (Gelman et al. 2004).

### 2.5. Simulation experiments

#### 2.5.1. Process versus parameter uncertainty

We examined to which extent the variability in the predicted annual population growth rate was due to parameter uncertainty compared to variation due to the stochastic demographic process. We drew 1000 random parameter sets from the parameter posterior distributions and ran the model for 50 years after transient (keeping population size around 10000 individuals as described above) with each set. We calculated the average annual growth rate and 95% confidence intervals over all 50,000 years in order to estimate the variation in the growth rate caused by both the stochastic process and the parameter uncertainty. For comparison we fixed the model parameters to their medians (Tables 1 and 2) and ran the model for the same total amount of years to attain the variation solely due to stochasticity of the model. The harvest during these runs followed the present harvest scheme (see 2.5.2.).

#### 2.5.2. Effects of harvesting

We evaluated harvest scenarios that were built in such a way that they could realistically be accomplished. The sex of the individuals is difficult for hunters to ascertain visually, except in the case of a female with a litter. However, a hunter can evaluate the size of the individual. Realistically, harvest could be skewed (either intentionally or accidentally) towards large individuals that are likely to be adult males, or towards smaller individuals that are likely to be independent yearlings or juveniles of both sexes. Consequently, we considered three different main scenarios while keeping the overall harvest rate constant (Fig. 2):

(i) Random (R): where individuals of different age and sex were harvested with equal rate

(ii) Trophy (T): where the harvest is biased towards large individuals, so that adult males amounted to 50% of the total kill and all other groups were harvested with equal rate

(iii) Young (Y): where harvest was biased towards young individuals so that yearlings and juveniles of both sexes together amounted to 65% of the total catch while all other groups were harvested with equal rate.
These scenarios were further varied by allowing the harvest of females with cubs (A scenario), which is currently not allowed (NA scenario). Cubs of the year are harvested in none of the scenarios, because they are an unlikely target for the legal harvesting. Because the mortality of orphaned cubs has not been estimated we replicated the random A scenario with two different assumptions: (i) that all orphaned cubs of the year die, and (ii) that all orphaned cubs of the year survive. This extra mortality of cubs was not counted into the total harvest catch. Because females with cubs occasionally are harvested by accident, we allowed 0.5% harvest rate of females with cubs also in NA scenarios. To summarize, total 11 variants of the three main harvest scenarios were compared to present harvest regime (Table 3, Fig. 2).

Although male-biased harvest has been reported for many north-American bear populations (Wielgus and Bunnell 2000, Miller et al. 2003, Schwartz et al. 2003), hunters in Scandinavia have so far shown little selection and harvest has been apparently random, except that hunting of females with a litter has been prohibited (Fujita 2000). Consequently, we used random harvest of 5% of the population as the basis for our simulations, but we also had females and their litters protected.

Based on the population estimates made in 1994 and 2005 (Swenson et al. 1995, Kindberg and...
asymptote. With 10000 individuals, the 95% confidence interval of the estimated annual population growth rate was from 1.073 to 1.120 when parameters were drawn randomly for each of the 1000 replicate simulations (Fig 3). As the growth rates in Fig. 3 already include the effects of approximately 5% of hunting mortality, this result implies a yearly population growth rate in the absence of hunting from 1.123 to 1.170, with a median of 1.146. When variation due to parameter uncertainty was removed by keeping the parameter values constant at their medians, the 95% confidence interval was from 1.069 to 1.094 (Fig 3).

Even though the population size in simulations was quite high (10000), stochastic variation was relatively large, and with a population size realistic to Scandinavia (3000 – 3500 individuals) the stochastic process is likely to dominate the parameter uncertainty in the model. This result also reflects the rather large amount of data used in model parameter estimation, which resulted in relatively narrow 95% HPDIs for most parameters.

3.2. Effects of harvesting

The stable age distribution of the population in the end of the year with the present level of random harvest (R5 NA) included 16% cubs of the year, 13% yearlings, 20% juveniles and 51% adult individuals. The overall sex ratio was even; for yearlings and juveniles the ratio of females to males was 0.9, whereas there were 1.1 adult females per each adult male. Sex ratio of young individuals is less than unity because of the relatively high estimated natural mortality of yearling females. The average age of adult females was 9.9 years and of adult males 9.0 years. The average age of all females was 5.8 years and that of males was 5.0 years. The average age of harvested males based on harvest reports from the area (5.1) was close to that from the simulations, but the average age of reported killed females was lower (4.9). Interestingly this difference seemed to be mainly due to a large proportion of (12%) female yearlings in the reported harvest, compared to that of 8% predicted by simulations. (Note that because cubs of the year and females with cubs are not harvested, the life-stage distribution of the population does not correspond exactly to that of the harvest.)

Allowing the harvest of females with cubs reduced the population growth rate by approximately one percent unit in the short-term (P(R5 NA > R5 A) = 0.998) and little more in the long-term (P(R5 NA > R5 A) = 0.999), assuming that orphaned cubs would die (Fig. 4). When we assumed that all orphaned cubs survive, there was no significant reduction in the population growth rate in the short-term (P(R5 NA > R5 A) = 0.597), but in the long-term allowing harvest of females still reduced the population growth rate with approximately 0.7% (P(R5 NA > R5 A) = 0.999, Fig. 4). Releasing the harvest of females with cubs resulted in a sex ratio of 0.9 females to 1 male for all independent age groups.

Weighting large males in the harvest increased the population’s long-term growth rate (Fig. 5A). As expected, this trophy harvest resulted in a female biased overall sex ratio of 1.2 females to 1 male. Moreover, there were 1.8 adult females per each adult male in the stable sex-age distribution, and the mean age of adult males was decreased to 6.7 years.

Targeting harvest to young individuals did not result in significant changes in the population growth rate (Fig. 5A). The sex ratios were unchanged compared to random harvest, with exception of adult individuals having an even sex ratio. The average age of females as well as males was increased to 6.2 and 5.8 years respectively, and that
of adult females and males was increased to 10.7 and 10.1 years respectively.

When the total kill was increased from 5 to 10%, all harvest scenarios showed significant short- and long-term reductions in the population growth rate, as expected (Figs 4, 5B). However, for trophy harvest (T10 NA and T10 A), the long-term reduction was only little more than 1% (Fig 5B). Higher harvest rates resulted in an unstable population structure when skewed towards young individuals, which was indicated by the variance in long-term change (Fig 5B). When harvest of females with cubs was allowed, 3% of the simulations resulted in growth rate smaller than 1 in the long-term. And in 1% of simulations with harvest biased towards young individuals, the population growth rate was below 1.

4. Discussion

Harvesting different types of individuals from the population is likely to have different consequences both to the population growth rate and the structure of the population, which may eventually contribute to the pattern of expansion of the population. Scandinavian population has been harvested over 60 years, but the previous analysis of the population viability (Sæther et al. 1998) did not consider harvest mortality separately from the natural mortality. And effects of harvesting that targets different types of individuals has not been analysed previously.

The population growth rates for many bear populations have been shown to be sensitive to changes in the survival of reproducing females and young individuals (Boyce 1995, Sæther et al. 1998, Wiegand et al. 1998). As a result, females followed by a litter have often been protected from harvest, as is the case also in Scandinavia. There was no significant short-term effect of releasing the harvest of females with cubs if the orphaned cubs were assumed to survive, but there was a significant long-term reduction of approximately 0.7%. This effect is not very large, partially because increased mortality for females with cubs results in a lowered mortality for females without cubs. If the orphaned cubs die, both the short and long-term reductions in the annual population growth rate are predicted to be larger and significant. We have earlier observed that if the mother dies late in the year, which is the case in the harvest, the cubs have chance to survive (Swenson et al. 1998a).

Skewing harvest towards young individuals did not have any significant effect on the population growth rate. However, because natural mortality of female yearlings was already relatively high (Table 2), increased harvest mortality might create an unstable population structure in the long run. The age structure of the reported hunted bears suggests that yearling females may also be especially vulnerable for harvest. Females do not disperse as far distances as males and consequently the density of related females can be locally high (Støen et al. 2005a, 2005b), this could explain elevated mortality of yearling females, even though overall density of bears would not be close to carrying capacity because of harvest. On the other hand, if harvest is
concentrated in these areas with high density of females, inexperienced yearlings would be the likely catch.

As expected for a species where a male can inseminate several females, male-biased hunting did not decrease the annual population growth rate. It is likely that there would exist a minimum ratio of males to females that must be present to assure successful breeding by all available females (McLoughlin et al. 2005), but in reality this ratio might be relatively low for the bear, because the home range of a male bear in Scandinavia can cover several female ranges and both sexes roam to mate (Dahle and Swenson 2003b, 2003c). Also, a sizable fraction of the adult females of the population would be with cubs, which means that the ratio of females available for mating to mature male is smaller than the actually ratio of adult females to male. Nevertheless, with trophy hunting the age structure of the male population was biased towards young individuals, which might have negative effects on reproduction as females tend to select for older males (Bellemain et al. 2006b), which was not taken into account here. We modelled successful SSI that could be directly related to the harvest of males (Katajisto et al. 2006). However, SSI does not necessarily result in the loss of the complete litter, and it could additionally increase the mortality of individual cubs (Swenson et al. 1997, 2001a), which also was not accounted for in our model. Consequently, the long-term effects of male-biased harvest should be interpreted with caution, but overall it seems likely that harvesting more males than females would result in an increase in the population growth rate.

Which harvest strategy should be used ultimately depends on the management goals. Obviously, the present level of harvest has not been negative for the preservation of the species, as the bear population has continued growing and expanding (Swenson et al. 1994, Swenson et al. 1995, Sæther et al. 1998). Indeed, the reproductive rate of the Scandinavian population is high compared to those of the North-American populations (Schwartz et al. 2003). The current official goal of 1000 bears in Sweden has already been exceeded and the present population estimate is around 2550 bears (Kindberg and Swenson 2006). Consequently, the likely future goal of management is to maintain a level population size. Based on our results, if the harvest rate is kept at the present level, the population will continue growing rapidly. Even twice the current harvest rate can be sustained according to our simulations. This applies when there is no major change in the distribution of suitable habitat for bears and as long as density dependent reduction in survival or reproduction is small. Increasing the population growth rate by male-biased harvest does not seem like a reasonable choice for harvest given such a management goal. As shown by the differences between the short- and long-term change, some effects of increased hunting will manifest themselves only after a time-delay. This emphasises the importance of reliable monitoring of the population size for adaptive harvest management following changes in the harvesting policy.

The conservative strategy would be to maintain random harvest while gradually increasing the harvest rate. The protection of females with cubs seems advantageous for the safety of the population, as it ascertains that a fraction of the reproductive females always is protected. On the other hand, there seems to be large individual variation in lifetime fitness of females in terms of litter production (Swenson et al. unpublished data). High individual reproductive output is due to a short inter-birth interval, because some females tend to wean their litter as yearlings whereas others keep the litter until it is two years old. We assumed that this variation is due to factors that are not heritable. However, if female offspring of a mother with a short litter interval also are likely to separate their cubs as yearlings, and female offspring of a mother with a longer litter interval likewise keep their litters longer, the consequences of protecting females with cubs could be qualitatively different. To illustrate, a female with 2-year litter interval belongs to the harvested population on average every second year, whereas a female with 3-year litter interval is vulnerable to harvest only every third year. Consequently, when females with cubs are protected, the harvest is actually biased towards females that are good (= fast) reproducers. In the long run this could change the reproductive parameters of the population. However releasing the harvest of females with cubs in a population with females with long litter intervals is likely to have a stronger negative effect, because with slower reproduction every reproductive female is relatively more important for population growth.

In summary, Scandinavian brown bear population seems to be quite robust for changes in the harvest policy, and the harvest rate can be gradually increased without endangering the population.
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