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Reproductive patterns and human-influenced behavior in brown bears. Implications for the conservation of large carnivores.

Reproduksjonsmønster og menneskeskapt atferdsendring hos brunbjørn. Konsekvenser for bevaringen av store rovdyr.

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Department of Ecology and Natural Resource Management
Philosophiae Doctor (PhD) Thesis 2010:01

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Contents

Abstract

Monitoring the status of wildlife populations and understanding the effects of human activities on wildlife is central for wildlife conservation. Both goals are especially challenging for rare, secretive large carnivores. The objectives of this thesis, which includes 7 papers and manuscripts, were 1) to improve a method to monitor brown bear (*Ursus arctos*) populations based on counting females with cubs-of-the-year, including a study on reproductive patterns, and 2) to explore some effects of human activities on the behavior of large carnivores, using brown bears as a model species. Six of the studies were descriptive, based on empirical data, and the main findings in relation to the aforementioned objectives are the following:

1) Regarding females with cubs, the study improved distance-based criteria to distinguish family groups, and highlighted the need for cautious interpretation of population trends based on counting females with cubs. In addition, the results showing the existence of a spatiotemporal reproductive pattern for Scandinavian female bears suggested that interactions among individuals and behavior in solitary carnivores may play a larger role in their population dynamics than what has been traditionally assumed.

2) Bears showed a fine-scale behavioral response, both on a seasonal and daily basis, to human activities, which resembled the sensitive responses of prey to their predators. Bears appeared to rely on cover and distance to human settlements to avoid encounters with people, and altered their movement patterns when the bear hunting seasons started. Finally, the last manuscript unites demographic and behavioral perspectives of human persecution on large carnivores to discuss that such persecution is likely influencing not only them, but the apex, regulatory role that large carnivores can play in the ecosystems.

The importance of behavioral responses and single individuals should be taken into account for conservation-oriented management of large carnivores, which should not only be based on demographic sustainability. The results also stressed carnivores' need for cover and areas with low accessibility for humans. Results from the papers and synopsis led me to propose that large carnivores should not be systematically hunted.

Sammendrag

Bestandsovervåking og forståelsen av de påvirkningene den menneskelige aktiviteten har på viltbestander er sentrale i bevaringen av viltarter. Begge mål er spesielt utfordrende for sky og sjeldne store rovdyr. Målene for denne oppgaven som inneholder sju arbeider var: 1) å forbedre en overvåkningsmetode for brunbjørnbestander (Ursus arctos) basert på telling av binner med årsunger, som også inkluderer en studie av reproduksjonsmønster, og 2) å undersøke noen av påvirkningene menneskelig aktivitet har på store rovdyrs atferd med brunbjørn som en modellart. Seks av arbeidene er deskriptive basert på empiriske data og hovedresultatene i henhold til de nevnte målene er:

1) Med hensyn til binner med unger forbedret studien de distansebaserte kriteriene for å skille familiegrupper, og trekker frem nødvendigheten av en varsom tolkning av bestandstrender basert på tellinger av binner med årsunger. I tillegg, resultatene som viser forekomsten av et spatiotemporalt reproduksjonsmønster hos skandinaviske binner antyder at gjensidig påvirkning mellom individer og atferd blant solitære rovdyr kan spille en større rolle i deres bestandsdynamikk enn det man tidligere har antatt.

2) Bjørnene viste en finskala tilpassning i atferd, både på sesong- og døgnbasis, overfor menneskelig aktivitet, som likner på den atferd byttedyr har overfor rovdyr. Bjørner ser ut til å bruke skjul og avstand til bebyggelse for å unngå møte med folk, og endrer deres bevegelsesmønster når jaktsesongen startet. Det siste manuskriptet forener demografiske og atferdsmessige perspektiver på menneskelig forfølgelse av store rovdyr og diskuterer at slik forfølgelse trolig påvirker ikke bare rovdyrene, men også den regulerende rollen som topp-predator de store rovdyrene bør ha i et økosystem.

Viktigheten av atferdmessig respons og enkeltindivider bør tas hensyn til i bevaringsorientert forvaltning av store rovdyr og ikke bare være basert på demografisk bærekraftighet. Resultatene viser betydningen av at rovdyr trenger skjul og områder som er lite tilgjengelig for mennesker. Resultatene av disse arbeidene har fått meg til å foreslå at store rovdyr bør ikke jaktes systematisk.

Resumen

El seguimiento del estado poblacional y la evaluación de los efectos de las actividades humanas sobre la fauna son esenciales para su conservación. Ambas metas son un reto especial trabajando con grandes carnívoros, en su condición de animales elusivos y escasos. Los objetivos de esta tesis, que incluye siete artículos y manuscritos, fueron 1) mejorar un método de seguimiento de poblaciones de oso pardo (*Ursus arctos*) basado en el conteo de osas con crías, incluyendo un estudio sobre patrones de reproducción, y 2) explorar algunos efectos de actividades humanas sobre el comportamiento de los grandes carnívoros, con los osos como especie modelo. Seis de los trabajos fueron descriptivos, basados en datos empíricos, y sus resultados esenciales, en relación con los objetivos expuestos, son los siguientes:

1) En relación a las osas con crías, el estudio mejoró los criterios basados en distancias entre observaciones para distinguir grupos familiares, y resaltó la necesidad de interpretar con cautela tendencias de la población basadas en el conteo de osas con crías. Además, los resultados mostraron la existencia de un patrón espacial y temporal de la reproducción, sugiriendo que las interacciones entre individuos y el comportamiento en carnívoros solitarios pueden jugar un papel más importante en las dinámicas poblacionales de lo que se viene suponiendo.

2) Los osos mostraron una respuesta comportamental concreta a las actividades humanas, tanto a escala estacional como diaria, que recuerda a las sensibles respuestas de las presas respecto a sus predadores. Parece que los osos utilizan la cobertura de la vegetación y la distancia a asentamientos humanos como medios para evitar encuentros con gente, y modifican sus patrones de movimiento cuando comienza la temporada de caza. El último manuscrito liga perspectivas demográficas y de comportamiento de la persecución humana sobre los grandes carnívoros, discutiendo que ésta afecta no sólo a los carnívoros, sino probablemente también al papel regulador que ellos pueden desempeñar en los ecosistemas.

La importancia de las respuestas de comportamiento y el valor de cada individuo deberían ser tenidos en cuenta por un modelo de gestión de los carnívoros con enfoque conservacionista; la gestión no debería basarse sólo en términos de sostenibilidad demográfica. Los resultados también resaltaron la necesidad de áreas con buena cobertura y reducida accesibilidad para la gente. A partir de los diferentes trabajos aquí incluidos, así como de la discusión de la tesis, propongo que los grandes carnívoros no deberían ser objeto de caza.

List of papers

I. Ordiz, A., Rodríguez, C., Naves, J., Fernández, A., Huber, D., Kazcensky, P., Mertens, A., Mertzanis, Y., Mustoni, A., Palazón, S., Quenette, P.Y., Rauer, G., Swenson, J.E., 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. Ursus 18(2), 158-167.

II. Ordiz, A., Støen, O-G., Swenson, J.E., Kojola, I., Bischof, R., 2008. Distance-dependent effect of the nearest neighbour: spatiotemporal patterns in brown bear reproduction. Ecology 89(12), 3317-3335.

III. Fernández-Gil, A., Ordiz, A., Naves, J., 2010. Are Cantabrian bears recovering? Ursus 21(1), 000-000.

IV. Ordiz, A., Støen, O-G., Delibes, M., Swenson, J.E. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Under review

V. Ordiz, A., Støen, O-G., Langebro, L., Brunberg, S., Swenson, J.E., 2009. A practical method for measuring horizontal cover. Ursus 20(2), 109-113.

VI. Ordiz, A., Støen, O-G., Sæbø, S., Kindberg, J., Delibes, M., Swenson, J.E. Behavioural effects of hunting in a large carnivore. Under review

VII. Bischof, R., Ordiz, A., Swenson, J.E. Saving large carnivores but losing the apex predator. Under review

Synopsis

Placing this study in the frame of Conservation Biology

Some 30 years ago, after the pioneering, far-sighted contributions of some North American field biologists in previous decades, Conservation Biology was born as a multidisciplinary science to address the dynamics and problems of species, communities and ecosystems that were (and increasingly are) perturbed by human activities (Soulé 1985). In this thesis I have approached a few of the broad disciplines that lie within the toolbox of conservation biology, aiming to help preserve large carnivore populations (and not only individuals).

Monitoring, ecology, wildlife biology and management are among those disciplines (Soulé 1985). Monitoring wildlife populations, i.e. gathering information to assess their state and to draw inferences about changes over time (e.g. Yoccoz et al. 2001), and understanding the effects of human activities on wildlife, are central for wildlife conservation. Both goals are especially challenging for elusive, rare, secretive large carnivores, which often inhabit multiple-use landscapes (e.g. Noss et al. 1996). Most adult mortality in large carnivores, even in protected areas, is human-caused (Woodroffe and Ginsberg 1998) and, as a matter of fact, humans have caused large population reductions and extinctions worldwide. Besides demographic effects, large carnivores alter their behavior to reduce encounters with humans, e.g. becoming more nocturnal, avoiding areas with high human activity or hiding in dense vegetation (Boydston et al. 2003, Kolowski and Holekamp 2009). However, the potential consequences of human persecution of large carnivores at behavioral and evolutionary scales, not only for the carnivores, but for the ecosystems where they inhabit, remain quite unstudied.

Major objectives of this thesis

The papers compiled here focused on two issues: **1)** improving a method to monitor brown bear (*Ursus arctos*) populations based on counting females with cubs-of-the-year, including a study on spatiotemporal reproductive patterns, and **2)** exploring effects of human activities on bear behavior. Both paths, initially a bit apart from each other, merged during this study to highlight the importance of both single individuals and behavioral responses. I will argue that behavioral responses to exploitation and disturbance, i.e. to human activities, and the importance of each individual should be taken into account for conservation-oriented management of large carnivores, most especially because management has traditionally lacked attention to behavioral issues (e.g. Caro 2007).

Brown bear, the model species

The objectives of the thesis focused on determined characteristics of brown bears, some of which are quite specific for the species, and relate mainly to objective **1**, whereas other characteristics are shared with other carnivores and relate with objective **2**. There are two main periods of brown bear activity and one of inactivity within the year. The mating season takes place in spring and lasts until early July here in Europe (Dahle and Swenson 2003a, Fernández-Gil et al. 2006). From mid-July to den entry in October is the season of hyperphagia (e.g. Nielsen et al. 2004, Moe et al. 2007). This period, when bears accumulate fat for the winter, is essential for successful hibernation and cub production (Farley and Robbins 1995). From late fall to early spring the bears hibernate (with some exceptions in non-boreal latitudes; e.g. Naves et al. 2001), living from fat reserves. These main periods during the annual cycle were considered in the design of the different studies, because bear movement patterns differ from spring to summer (paper I), intra-specific interactions among bears are more intense in spring (mating season) than later (paper II) and outdoor human activities also differ during the year (e.g. seasonal hunting periods in late summer-fall, which was important for papers IV and VI).

1) Regarding monitoring, one segment of brown bear populations is particularly interesting. Adult females are defined as the critical segment of bear populations, because they are responsible for reproduction and their survival rates are the most important single component of overall population trajectory (e.g. Harris et al. 2007). Implantation of the embryos is delayed (e.g. Spady et al. 2007), and female bears give birth to 1–4 offspring while hibernating in dens during winter (Pasitschniak-Arts 1993). The offspring separate from their mothers when they are 1.4–3.5 years old (McLellan 1994). In Europe, females reproduce every two to three years (e.g. Dahle and Swenson 2003b). Bear females with cubs-of-the-year (hereafter, FWC) constitute the most easily identifiable part of bear populations (e.g. Knight et al. 1995). Thus, some monitoring programs focus on FWC, which was the segment of the population I focused on in papers I-III.

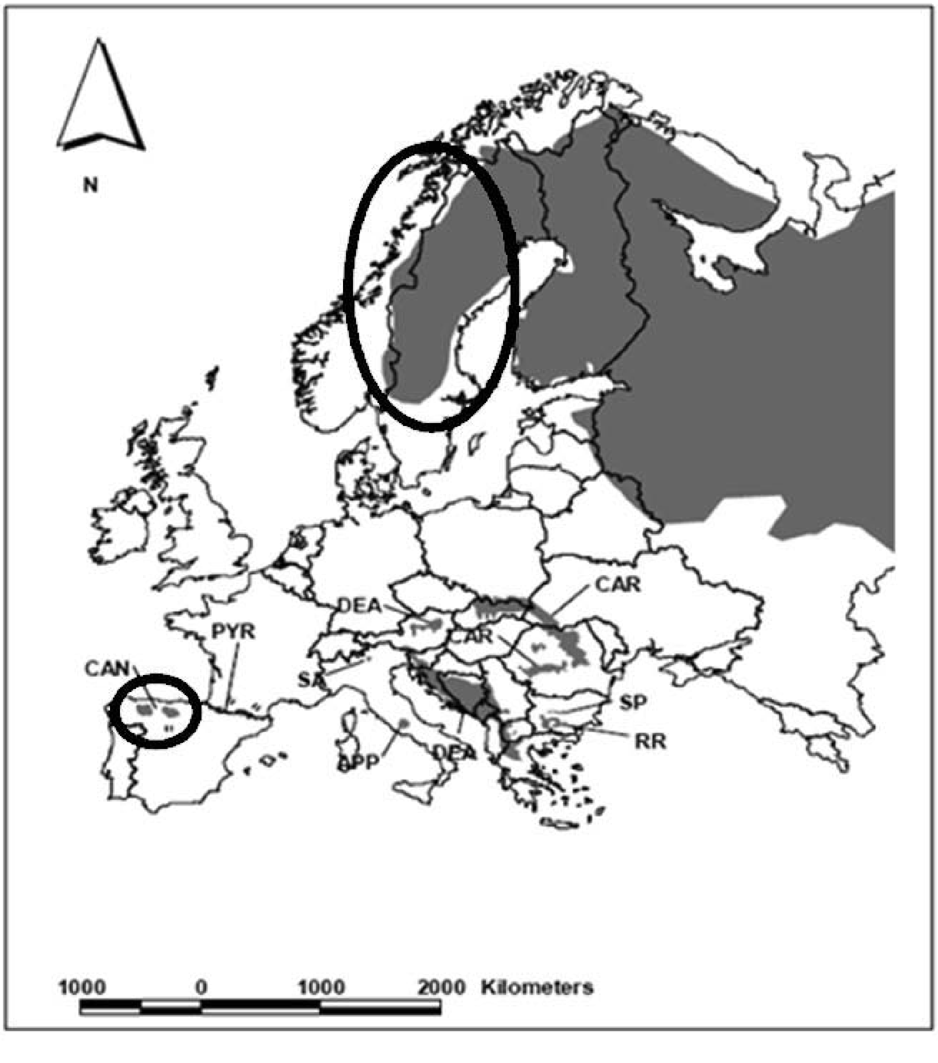
2) Other characteristics of brown bears make them interesting to explore the effects of human activities on large carnivore behavior. Bears are the largest carnivores in Europe and

North America, and, as large carnivores in general, are threatened by human-caused mortality, habitat fragmentation and habitat loss (e.g. Servheen et al. 1999). Brown bears tend to avoid human activity throughout their range (e.g. Mace et al. 1996), which has been documented in Scandinavia (Nellemann et al. 2007) and in the Spanish Cantabrian Mountains (NW Spain; Naves et al. 2001), the two main study areas of this thesis. Whereas in North America bears are primarily diurnal (e.g. Munro et al. 2006), European bears, the same species, show a marked resting period at mid-day and the highest activity levels occur during crepuscular and nocturnal hours (Kaczensky et al. 2006, Moe et al. 2007). The reasons for these differences may be related to the more intensive and long-term persecution of large carnivores in Europe, which has denser human populations and has had them much longer (Woodroffe 2000). Some results of this section of the thesis (papers IV-VII) also apply to other large carnivores.

Study areas, study populations

Most of the research has taken place in Scandinavia and in the Cantabrian Mountains, but we also used data from other European bear populations (Figure 1). Detailed descriptions of the study areas are available in the papers and references therein. The Scandinavian bear population has ~3000 bears with a population growth rate estimated at 4.5 % for 1998-2007 (Kindberg et al. 2009). After centuries of persecution, bears were protected from hunting on state land in Sweden in 1913, hunting became legal again in 1943 and has been managed with annual quotas since 1981 (Swenson et al. 1995). The Scandinavian Brown Bear Research Project (SBBRP) has been studying this population since 1984. More than 550 bears have been radio-collared and tracked for as long as possible, preferably until death, for a variety of research goals. Please look at www.bearproject.info for a further description of the project. On the other hand, the critically endangered Cantabrian brown bear population, one of the most endangered in the world (Servheen et al. 1999), has around a hundred bears in two subpopulations, which together occupy only ~7,500 km^2 (Swenson et al. 2000, Naves et al. 2003). Also from the 1980's, research on Cantabrian bears has focused on annual counting of FWC (see papers I and III), habitat suitability (Naves et al. 2003), long-term diet analyses (Naves et al. 2006) and genetic data (Pérez et al. 2009). This thesis therefore focused on a bear population managed through a hunting regime in the boreal forest of Scandinavia and on an officially protected population on the temperate mountains of south-western Europe (Picture 1). Next, I will present the papers linked to the two objectives of the thesis.

Figure 1 Distribution of brown bears in Europe as of 1999. Two ovals locate the study areas mainly included in this thesis, i.e. the Scandinavian and the Cantabrian bear populations.
CAN = Cantabrian, PYR = Pyrenees, SA = Southern Alps, APP = Appennines, DEA = Dinaric-Eastern-Alps, CAP = Carpathians, RR = Rila-Rhodope Mountains, SP = Stara Planina Mountains. In the north of Europe the bear population ranges from Scandinavia to Easter Russia. This figure has been modified from Linnell et al. 2002



Rationale behind the interest on females with cubs-of-the-year

Counting carnivores is a common duty for wildlife biologists and managers, and it is challenging due to the characteristics just described (e.g. rarity, elusiveness), which justifies focusing monitoring on the most conspicuous segment of the populations. In the case of brown bears, monitoring programs focusing on annual counting of FWC have some advantages. Females are accompanied by cubs for a long time, are more active during daylight hours (Knight et al. 1995), which makes them more detectable, have smaller home ranges (Blanchard and Knight 1991, Dahle and Swenson 2003a) and less home-range overlap compared with other age and sex classes (Mace and Waller 1997, Støen et al. 2005), which helps in distinguishing them. Also, litter sizes are limited and mothers, cubs, or both can have recognizable marks that make them easier to identify (e.g. Schwartz et al. 2003). Beyond the fact that FWC are the easiest part of the population to distinguish and count, the interest of monitoring FWC is based on the following assumptions: A) Trends in this segment of the population are correlated with trends in the population as a whole, which may be true only if demographic parameters (e.g. age distribution of the population, age of first reproduction, reproductive intervals) are reasonably stable during the period of interest (e.g. Eberhardt and Knight 1996, Boyce et al. 2001, papers I and III). B) Annual counts of FWC can be useful to monitor bear populations by providing information regarding minimum population size, population trends, and reproductive success (e.g. Knight and Eberhardt 1985, Wiegand et al. 1998). C) In some areas, such as the Cantabrian Mountains, radio-tracking has not been permitted for a long while and counting FWC (through direct observation and tracking footprints) has been the sole available index to monitor the population since the 1980's (papers I and III and references therein). The method has also been used in North America for the same period (e.g. Schwartz et al. 2002). Criteria used to discriminate among different FWC are based on the spatial and temporal distance among sightings, which we aimed to improve in paper I, and on family group descriptions (Knight et al. 1995). An essential component of this monitoring method is movement behavior.

What is the probability that two observations of a FWC separated by x km and y days belong to the same family group?

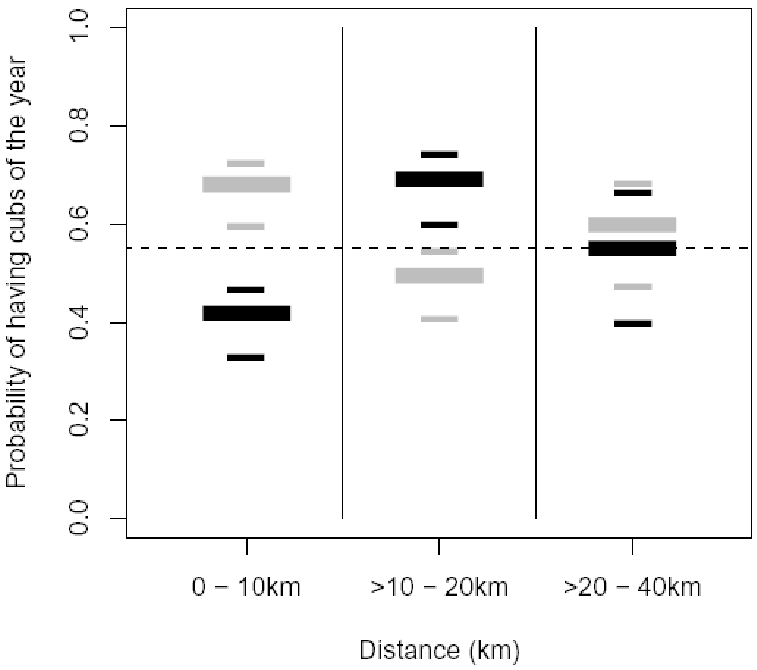
We gathered radio-tracking data from most bear populations in Europe, providing paper I with a pan European scope. Using generalized linear models (GLM, McCullagh and Nelder

1983, Crawley 1993), which have been a tool repeatedly used in my thesis, and non-linear regression fitted to the distances travelled by FWCs within certain time lags separating observations, we obtained a quantitative tool to help assign observations of FWC to different (or the same) family groups. We obtained results specifically applicable for the different European bear populations, depending on their geographical origin (boreal vs. temperate forest). Our distance-based criteria to differentiate unique FWC improved former approaches by statistically relating the distance separating 2 observations of FWC to the temporal lag between them, which had not been considered in previous, pioneering approaches (Blanchard and Knight 1991). However, we also discussed a major limitation of our method. If FWC are living near each other, distance criteria are not enough to distinguish them. Although the process of identification of FWC also accounts for family group descriptions, which facilitates the process, previous research within the SBBRP has found that some female bears have overlapping home ranges, forming assemblages of related females (Støen et al. 2005). This suggested that females living close to each other and potentially breeding the same years would be difficult to distinguish. This background posed the second research question.

Do reproductive females living near each other influence each other's reproduction?

Therefore, in paper II we investigated whether there are spatiotemporal reproductive patterns (e.g. Ims 1990) in brown bear females living near each other. Whereas environmental or internal factors may promote reproductive synchrony, i.e. females giving birth to cubs in the same years, other factors such as competition for limited resources might promote reproductive asynchrony among neighboring females. We used logistic regression to estimate the probability of an adult female having cubs of the year in a given year as a potential function of environmental and intra-specific variables. Indeed, the probability of having cubs was significantly affected by the distance to the nearest neighboring female and whether or not she had cubs, and this was not just an effect of local density. The effect of distance to the nearest neighbor on female reproductive success had been found before in voles (Mappes et al. 1995), but to our knowledge this was the first such finding in a wild population of a large, solitary mammal. Moreover, we found that the pattern changed spatially; at short distances, <10 km between home-range centroids, a female was less likely to have cubs when her nearest neighbor had cubs, whereas the pattern reversed at greater distances between neighboring females (10 to 20 km); then the probability of a female having cubs was higher when its nearest neighbor also had cubs, and the pattern disappeared for distances >20 km (Figure 2). We argued that reproductive suppression was probably caused by resource competition among females living close to each other, apparently in accordance with female-induced reproductive suppression found in many mammal groups (e.g. Digby 1995, Moelhman and Hofer 1997, Wolff et al. 2002). The indication of reproductive suppression in brown bears suggests a mechanism for population regulation in the species, which had been found only in group-living mammals (e.g. Creel and McDonald 1995). Therefore, interactions among individuals and behavior in solitary carnivores may play a larger role than traditionally assumed. Regarding monitoring, the pattern showing that females living close to each other would not tend to have cubs in the same year would facilitate counting unique FWC, reducing the limitation discussed in paper I.

Figure 2 Predicted probability of a female having cubs of the year (large horizontal bars) and associated SE boundaries (small horizontal bars) from the logistic regression model with the effect of distance from the nearest neighboring adult female modeled as a categorical variable (cuts at 10 and 20 km). Predictions for females with nearest neighboring females that have cubs of the year are represented by large black bars, predictions for females with neighbors without cubs of the year are represented by large gray bars. More details in paper 2



Constraints using the trend of FWC as a surrogate of population trends

If a population trend estimate is wrong, which is more likely if it is based on a single index, negative consequences such as relaxing conservation efforts may arise. Paper III highlights the need to pay careful attention to the assumptions under which the FWC index may be a surrogate of population trends. We discussed the major factors limiting the interpretation of an increasing trend of Cantabrian bears published by Palomero et al. (2007), because sampling effort increased during the study period, which was not properly considered, the collection of data was opportunistic, and thus did not meet the requirements of probabilistic analyses to correct field data, and biological explanations for the observed trend of the FWC were not considered. For instance, up to 9 cases of infanticide have been reported in the Cantabrian Mountains after 1996 (Fernández-Gil et al. 2010, paper III). In case the rate of infanticide has been increasing recently (there were no observed events before 1996), the mean interval between consecutive litters would decrease, resulting in increasing observations of FWC even in a stable population. In such scenario, an increasing trend of FWC may be even concealing an actual low recruitment, with some females breeding in consecutive years after losing their litters. Unfortunately, information on parameters that would help clarifying this issue, e.g. age structure of the population, is lacking in the Cantabrian Mountains.

Human "disturbance"; Rationale behind a predator-prey approach

Understanding the interactions between humans and wildlife is a growing topic in conservation biology (Gill et al. 1996, Frid and Dill 2002, Rode et al. 2006). In a humanized biosphere (e.g. Vitousek et al. 1997), human activities not only cause large proportions of wildlife mortality, but also disturb a large variety of animals (Blanc et al. 2006). Evolutionary adaptive behaviors have likely arisen after a long coexistence between predators and prey, and disturbance stimuli could even be analogous to predation risk from an evolutionary perspective (Frid and Dill 2002). Following, I propose that it is possible to apply a predator-prey approach to evaluate the effects of hunting and other human activities on the behavior of large carnivores.

Predation causes mortality, but both predation risk and disturbance potentially affect population dynamics indirectly by forcing individuals to invest in anti-predator behavior (e.g. vigilance) and thus discard more profitable activities (e.g. foraging and resting; Lima 1998, Frid and Dill 2002). Non-lethal, behavioral effects of predation risk are large for many taxa (e.g.

Preisser and Bolnick 2008), can be more important for population dynamics of prey than direct demographic, lethal effects (Creel and Christianson 2008), and can even drive trophic cascades (e.g. Ripple et al. 2001). The importance of non-lethal effects of natural and human predation applies to a large variety of prey populations (e.g. Madsen 1998, Preisser et al. 2007, Stankowich 2008) and predator-prey and predator-avoidance theory may also provide insight into the effects of human activity on wildlife (Frid and Dill 2002).

Such an approach may be useful to study the effects of human activities on large carnivores (Rode et al. 2006). In contrast with the evolutionary arms race between prey and their predator species (Vermeij 1987), there has been little time for co-evolution between large carnivores and modern humans (and most especially with technologically equipped humans). This time has been even shorter in America than in the denser human populated Europe (Swenson et al. 1995, Zedrosser 2006). Thus, whereas prey species evolved anti-predator adaptations under natural predation and in multi-predator systems (e.g. Sih et al. 1998), large carnivores have had less time to adapt to a specific predator, modern humans. Indeed, it is not clear whether (adult) large carnivores that experience virtually no predation, and therefore may have lost anti-predator behavior, and only recently have had to cope with humans, are able to flexibly adjust their behavior to subtle variations in human-derived risk. However, considering that where predation exerts a strong influence on prey demography, individuals often alter their daily behavior (e.g. Berger 1999 and references therein), and that humans induce the highest proportion of adult mortality on large carnivores, it can be expected that hunting results in behavioral effects on large carnivores. Behavioral effects of hunting with demographic consequences have been already shown in prairie dogs *Cynomis ludovicianus* (Pauli and Buskirk 2007). Assessing the nature of the large and increasing alterations that humans cause to trophic interactions requires an understanding of how species' demography and behavior are altered (Searle et al. 2008). Based on these arguments, I suggest that studying the effect of human activities on large carnivore behavior and indirectly on their population dynamics is of interest not only for the carnivores, but for the ecosystems they inhabit and where they potentially play apex roles (e.g. Ale and Whelan 2008).

As described earlier, the Scandinavian brown bear has been managed as a game species for > 60 years, and suffered a previous story of heavy human persecution that almost drove the population to extinction ~80 years ago (Swenson et al. 1995). Legal hunting is the single-most important cause of mortality for brown bears in Sweden; nonhuman-caused mortality accounted only for 13.5% of confirmed deaths of marked animals between 1984 and 2006 (Bischof et al. 2009). Between 1998 and 2008, 102 ± 53 bears (mean ± SD) have been harvested annually in Sweden; 34 ± 16 hunted bears per year in the counties (Dalarna and Gävleborg) considered in this thesis (J. Kindberg, SBBRP, pers. comm.). Even in protected areas, data from 22 intensive studies of large carnivores indicated that 74% of 635 known-cause deaths were directly caused by people, with values as high as 83% for wolves (n= 86) and 89% for brown bears (n= 258; see Woodroffe and Ginsberg 1998). Therefore, a predator-prey approach to studying the influence of humans on large carnivores may well apply for every human-dominated landscape, i.e. the most common scenario worldwide today. We have approached this issue with the Scandinavian bear population as a model study, and at different scales.

What influences the concealment of resting sites?

In paper IV we analyzed the concealment, i.e. horizontal and canopy cover, at resting sites (i.e. beds) of GPS-collared bears at different distances from human settlements, different times of the day, and in relation to seasonal shifts in human activities throughout the non-denning season. Beds are specific sites that bears use only once to rest for several hours a day. Scandinavian brown bears have two daily resting periods, a short one during the night (~3 h) and the most marked during the day (~9 h; Moe et al. 2007), i.e., bears spend much time of their active part of the year at these specific spots. However, whereas activities such as feeding (e.g. diet analyses) or movement (e.g. home-range estimations) are well documented for a large variety of animals, including brown bears, resting-site selection has received much less attention, even though animals devote so much time for resting. The difficulty of finding such specific sites in the field without appropriate methods may explain this lack of attention.

Cover is a key habitat factor (Mysterud and Østbye 1999) for many animal groups, and brown bears are not an exception (e.g. Suring et al. 2006). Thus, we aimed to understand the behavior and requirements of a large carnivore when choosing specific resting sites at a very fine scale and in relation to human-derived risk, taking into account different temporal scales (day vs. night; spring vs. summer-fall) to account for changes throughout the year in both bear phenology and human activities. Again using GLMs, we analyzed the concealment around beds and random sites that we visited in the field in 2007, including a set of intra-specific, environmental and human-related variables. In summer-fall, when the human activity was more common, more scattered and more dangerous (e.g. bear hunting season), bears seemed to avoid potential encounters with people not only by increasing the distance of their beds to human settlements, but by choosing more covered daybeds (the time of the day with human activity outdoors) than in spring. When bears rested near human settlements, they used denser vegetation at daybeds. Interestingly, we also found that cover was greater at beds than at random sites (only 50 m away from the beds), which suggested a very fine-scale habitat selection and highlighted the need of fieldwork to study such specific selection (see discussion of paper IV). Bears were aware of shifts in human activities within very short temporal frames, and responded to the increasing danger posed by humans both on a seasonal and a daily basis, suggesting the evolution of fine-scale anti-predator, "antihuman" behavior in this large carnivore. Linked to this study, paper V was a comparison of methods to measure cover around beds in the most effective way. Thus, we compared devices previously used to measure cover in the field with a new device, the cover cylinder that S. Brunberg (SBBRP field project leader) invented.

Besides demography, does hunting affect the bears behaviorally?

Because legal hunting is the single most important cause of mortality for bears in Sweden, exploring whether this specific activity also influences bear behavior was the next step (paper VI). Using a Bayesian approach (Lunn et al. 2000), we compared the diurnal movement patterns of GPS-collared bears in the first week of hunting with those patterns during the week prior to hunting. We focused on these two weeks to avoid large variation in environmental factors that might confound the results, i.e. daylight length, which changes rapidly at our boreal latitude, and berry availability, the essential food source for bears in the study area at the time the hunting season takes place (Dahle et al. 1998). We also examined relationships between changes in movement patterns and hunting-related mortality of bears. After hunting started, bears moved significantly more during 19% of the day, which corresponded with the hours when 51% of the bears were killed in the first week of bear hunting in 1998-2008 (n= 104 killed bears). The annual bear hunting season occurs during the hyperphagia season, when bears must store fat for the winter. Bears consuming berries are highly constrained by fluctuations in berry availability and by physiological factors (e.g. Welch et al. 1997). Increased movements when hunting starts constitutes a non-lethal effect of hunting that adds to the limitations of a berry-based diet. Future research should extend the study period to the whole hyperphagia season, compare movement patterns after-before hunting starts, and evaluate how behavioral responses to hunting affects bears' condition and forthcoming reproductive success, because there is a strong correlation between the condition of the females in the autumn and subsequent reproductive success (Welch et al. 1997 and references therein). So far, changes in movement patterns could be used as indicators of the extent and severity of human disturbance on carnivores, which may have unforeseen consequences (Kolowski et al. 2007).

Are we saving large carnivores but losing the apex predator?

Finally, paper VII synthesizes demographic (e.g. Bischof et al. 2009) and behavioral perspectives (e.g. papers IV and VI) to discuss that human persecution on large carnivores is likely influencing not only them, but the apex, regulatory role that "big, fierce" carnivores can play in the ecosystems. Top predators facilitate biodiversity and preserving them delivers biodiversity conservation, although such functions may be context-dependent and do not hold for all species and systems (Sergio et al. 2008). Any change in large carnivores' population dynamics and ecology in general is therefore bound to reverberate throughout the food web. The loss of predators, particularly top ones, leads to biodiversity loss (Terborgh et al. 2001), e.g. due to mesopredator release implicated in the decline and extinction of prey species (Crooks and Soule 1999). We argue that human persecution on species that do not have predators of their own may diminish their role in the ecosystems. Humans are a recent, but strong evolutionary force (e.g. Darimont et al. 2009) and have climbed to the top of trophic systems (e.g. Ray et al. 2005). However, this human reign shows a lack of redundancy with, and less competence than, large carnivore functionality (Berger 2005). The overabundance of ungulates in systems where large carnivores have been extirpated or numerically reduced (e.g. Ripple and Beschta 2005) can be a good example of how demoting the role of large carnivores can have strong, negative consequences on ecosystems functionality, which should be taken into account in large carnivore management.

Discussion

The importance of single individuals and behavioral interactions

Some results of this thesis suggest that individual, intraspecific interactions of a population-regulatory nature typically associated with social species apparently play a role in the population dynamics of brown bears (paper II). Some individuals would have a larger role than others in the dynamics of the populations, e.g. because individuals differ in reproductive potential (Caro 1999). This is probably even more important in small populations, and *small* is certainly a common attribute of many populations of large carnivores today. On the other hand, conservation of biodiversity is facilitated by maintaining population densities and distributions of strongly interactive species (i.e. species such as brown bears and wolves whose virtual or effective absence leads to significant changes in some feature of their ecosystems, Soulé et al. 2003) above estimable thresholds for ecological effectiveness (Soulé et al. 2005). The importance of behavioral responses and single individuals at both intra- and inter-specific levels spreads to the interpretation of our results regarding monitoring and effects of human activities.

Monitoring is central to conservation and behavior can be of help (Caro 2007), because ranging patterns, breeding times and breeding locations affect spatial and temporal aspects of population censuses (Caro 1999). Besides the interesting and challenging discussion on the behavioral and physiological mechanisms that may explain the spatiotemporal reproductive pattern that we found in Scandinavian brown bears (paper II), which deserves further research, it seemed that females living close to each other did not tend to have cubs in the same year, thus facilitating monitoring of FWC by reducing the limitation discussed in paper I. Behavioral mechanisms (e.g. reproductive suppression) affecting age at first reproduction, influence population growth rates and therefore population viability analysis (Caro 1998, 1999). Thus, this should be considered for species such as brown bears, given that delayed primiparity has been documented (Støen et al. 2006) and reproductive suppression may also be a explanatory reason for the reproductive pattern we found (paper II). Also, it has been shown that the removal of males in species with sexually-selected infanticide (SSI) can lead to a further reduction in population size (Whitman et al. 2004). SSI has been documented in different populations of brown bears (e.g. Swenson et al. 1997, Fernández-Gil et al. 2010), and may have played a role in the reproductive pattern we observed. Because the home range of a male can include the smaller home ranges of several females, SSI could synchronize reproductions if several females are affected in the same season (paper II). Also, census techniques should account for behavioral factors that affect individual sighting probabilities (e.g. Gaillard et al. 2003) or individual ranging behavior. For instance, we found that reintroduced females travelled larger distances than native ones (paper I), which must be considered both for a) monitoring, because observations further apart from each other would likely be assigned to different FWC, but could be of the same, i.e. an error type I that would lead to an overestimation of FWC; and b) potential reintroductions. Reintroduced bears appear to have a larger exploratory behavior than native ones, i.e. reintroduced bears roam over areas much larger than those originally planned to room them, which has occurred repeatedly in Europe (Apollonio et al. 2003, paper I).

Monitoring FWC; valuable, but insufficient

Although recognizing the usefulness of the FWC index, one must carefully consider its assumptions during the analysis and interpretation of data, because the trend of the population does not necessarily follow the trend of the FWCs (Eberhardt and Knight 1996, paper III). Beyond that, the monitoring system of a critically endangered population should not be based only on one index of counts of adult females and births, which is of great interest, but completely omits essential demographic parameters, e.g. mortality. Unfortunately, this is the case with the current monitoring system of brown bears in the Cantabrian Mountains. I agree with Nichols and Williams (2006), who argued that monitoring should not be a stand-alone activity, but a component of a larger process of conservation-oriented science or management. For example, understanding rates and causes of bear mortality is critical for the species' conservation (e.g. McLellan et al. 1999). Obviously the Cantabrian case should not be an exception, and gathering such information is essential to focus conservation effort. Poison is still a common threat, which caused at least 6 deaths of bears since 2000 in the Cantabrian Mountains (Fernández and Naves, unpublished data), affecting also other species (e.g. wolves, Ordiz 2008). If reducing human-caused mortality was a real objective, the next step would be implementing the best possible methodology to achieve that goal, which in the case of mortality issues clearly point to radio-tracking techniques (e.g. McLellan et al. 1999, Bischof et al. 2009 among many others). Beyond the marking of very few bears (e.g. Clevenger et al. 1992, Naves et al. 2001), radio tracking has never been a technique of common use in the Cantabrian Mountains. Focused monitoring programs would decrease the incidence of deliberate delaying tactics to adopt new strategies, while increasing attention on science and its use in conservation (Nichols and Williams 2006).

Human influence on the behavior of the bears

Despite the growing recognition of the importance of non-lethal, behavioral effects in predator-prey interactions, such effects are rarely considered in conservation or wildlife management, i.e. studies of predation in vertebrate conservation and management usually consider only direct predation (Creel and Christianson 2008). Likewise, management of large carnivores often is based on demographic parameters (e.g. hunting quotas of bears based on population size) or, far worse, on political decisions (e.g. pre-emptive control of wolves to avoid potential attacks to unprotected livestock) with no attention to behavioral implications of killing individuals. In carnivore systems the behavioral side should not be ignored (Brown et al. 1999), which should expand to large carnivore management. At least for highly interacting species, sustainability based on demographic parameters is not enough (Soulé et al. 2005). Because knowledge on behavior has not contributed much to conserve animal populations over the past ~15 years, this gap between behavior and conservation must be linked (Caro 1999, 2007).

For instance, understanding basic behavior and patterns of mortality we can assess the effects of human activities in terms of habitat disturbance (e.g. Caro 2007). We found that bears modified their daily movement patterns when hunting started, which we interpreted as a behavioral effect of hunting occurring during the key hyperphagia season (paper VI). As previously stated, further research is required to see if such disturbance has demographic effects, but it at least highlights that human activities affect large carnivores behavior by increasing the time allocated for vigilance or fleeing and thus reducing the time for feeding or resting. This can leave the animals unable to utilize a spatial or temporal resource to its full potential (e.g. Kitchen et al. 2000). It has been shown that bears perceive human presence as a risk and respond with anti-predator behavior, such as vigilance or displacement, losing time for feeding. Bears cannot forage continuously, but must feed in distinct bouts separated by periods of digestion and defecation, thus night-time foraging alone (when there is no human activity) is unlikely to provide bears the time needed to meet their needs. Large individuals may be sensitive in particular to minor reductions in time spent foraging (Rode et al. 2006). Behavioral responses may affect the demography of animals under disturbance regimes. For instance, prairie dogs subjected to hunting increased alertness eightfold and decreased foraging and resting sharply after shooting started, with dramatic consequences for population-level processes (Pauli and Buskirk 2007). Therefore, hunting may have negative demographic effects beyond the killing of individuals (Loveridge et al. 2007, Packer et al. 2009), including brown bears (e.g. Swenson et al. 1997). Targeted animals may adjust their daily activity patterns to prevent encounters with humans, which may affect the distribution, dispersal patterns, and social organization of hunted species (e.g. Croes et al. 2007). The effects of predation, including hunting, can only be determined by considering both non-lethal and lethal effects (Cresswell 2008). This should be considered in large carnivore management, especially because behavioral effects may be particularly strong in large-bodied and long-lived species (Heithaus et al. 2008).

Additionally, hunting seasons often overlap with important phenological periods, e.g. ungulate hunting during the rut or bird hunting along migratory routes, which can reduce the rate of fattening and next reproduction (Fox and Madsen 1997, Bechet et al. 2004). Hunters aim to kill bears before the quota is filled, causing a large hunting effort in the first week of hunting, a phenomenon also reported elsewhere (e.g. Ruth et al. 2003). Managers should consider reducing disturbance as much as possible, perhaps by reconsidering hunting methods or hunting periods, which would apply for many species under hunting regimes that result in a sudden increase of mortality and disturbance at the beginning of hunting seasons. Also, the particularities of the behavior of targeted species should be taken into account by the hunting management regime. For instance, because the removal of adult males in species with SSI, like brown bears, can lead to reductions in population size, estimations of long-term sustainability of hunting should be sensitive to the breeding system (Caro et al. 2009). Such an approach should likely be considered in the management of bear hunting in Sweden, for instance, given that SSI has been repeatedly documented in this population (e.g. Swenson et al. 1997). The current hunting system based on quotas, although sustainable enough to permit population growth, may imply unforeseen evolutionary consequences.

The need of areas inaccessible to people

Despite the low human density in our area, bears responded to the increasing danger posed by humans both on a seasonal and a daily basis, choosing beds further away and in denser cover when the chance to meet humans was greater (paper IV). These results reinforce the importance of cover for large carnivores to reduce encounters with people, who should be made aware of this behavior to avoid areas with dense vegetation and/or rugged terrain where bears rest. Indeed, areas with low accessibility for humans appear indispensable for the occurrence and survival of large carnivores in human-dominated landscapes (e.g. Naves et al. 2003, Fernández et al. 2006, Nellemann et al. 2007). The less accessible a landscape type is, the more it is used by the bears (Petram et al. 2004). Bear-human interactions may be curtailed by recognizing important sites for the bears (Rode et al. 2001, Naves et al. 2006), and therefore human presence should be minimized in spots with dense cover in the "flat" boreal forest and in rugged areas (e.g. rocky outcrops or steep slopes) elsewhere, e.g. in the Cantabrian Mountains (Naves et al. 2003) or in the Alps (Petram et al. 2004).

However, the shrub layer, i.e. the most important vegetation layer providing cover, is systematically removed in many areas, with arguments such as reducing the probability of fire, increasing pasture for cattle or, surprisingly, promoting conservation of endangered species (Revilla et al. 2001). Unfortunately this also occurs in the Cantabrian Mountains, where shrub formations (e.g. heathers *Erica* spp.) are considered negative for human interests and are eliminated in the name of reasons such as to *improve* habitat for capercaillie *Tetrao urogallus cantabricus*, against calls to preserve the non-forest matrix as a direct source of food, refuge and connectivity between forest patches (Quevedo et al. 2006). Eliminations of cover occur also inside protected areas (e.g. Picture 2). A discussion on the effectiveness of protected areas escapes the intent of this thesis (but see Gaston et al. 2008 for a review), but there is growing evidence that even quiet, non-consumptive recreation in protected areas may not be compatible with the goal of biodiversity protection, especially for carnivores (Reed and Merenlender 2008). Cover has been shown to be a key habitat factor for a large variety of animals including carnivores (e.g. paper IV and references therein), which claims for cover protection.

Let's be realistic, ask for the "impossible": large carnivores should not be hunted

The conservation and management importance of trophic cascade theory is clear nowadays and the key role of predators is a rationale for carnivore conservation (e.g. Hebblewhite et al. 2005). It is also well documented that large carnivores do not only control their prey numerically, but through behavioral effects that can drive trophic cascades (e.g Schmitz et al. 2004, Peckarsky et al. 2008). Unfortunately, this is not often acknowledged by management decisions. We argued (paper VII) that hunting large carnivores can reduce their capacity to play apex roles. Apex predators are rare (Brown et al. 1999) and by definition their abundance is not controlled by other predators, but by factors such as prey availability (e.g. Carbone and Gittleman 2002). In other words, top predators are not evolutionarily meant to be hunted. Hunting large carnivores can reduce numbers that are low per se, plus can induce behavioral responses, such as alteration of habitat use and disruption of social systems, with potential demographic consequences, as described above. Such negative effects can occur even when the overall harvest is not demographically regarded as excessively high (Milner et al. 2007), i.e., when it is still considered sustainable. Demographic parameters have been used to justify the delisting of wolves and brown bears from the US Endangered Species Act, without considering whether these species had recovered to play a normative ecological role (Pyare and Berger 2003). In places where wolf hunting is legal in Europe, it is often carried out without biological understanding of population dynamics (Boitani 2000). Obviously, none of these cases consider that individuals are not all equivalent for the dynamics of their own species (e.g. Coulson et al. 2006), nor attend to their ecological role. Indeed, the recovery of large carnivores may be an important restoration strategy for ecosystems degraded by ungulates (Beschta and Ripple 2009) and, in contrast to delisting ideas, the restoration of large carnivores to their pre-historic status has been suggested in recognition of their key ecological functions (e.g. Donlan et al. 2006).

The issues rose here, based on behavioral, demographic and also evolutionary aspects partially related to papers II, IV, VI and VII, point out that just "sustainability" should not be argued to kill large carnivores. I propose that systematic hunting of large carnivores, e.g. pre-emptive control, must cease. Non-pre emptive control on a case-by-case basis, e.g. when correctly applied prevention measures fail to avoid repeated attacks on livestock, could be an exception.

Stop hunting large carnivores would favor their numerical recovery. Yet, whereas the *carnivore comeback* (Enserink and Vogel 2006) may represent good news in terms of partial numerical and range recovery, thinking big, i.e. at ecological scale, the ultimate goal should be the *apex comeback*. Given the potential reversibility of behavioral traits (Duckworth 2009), large carnivores rid of human persecution might recover (where lost) their capacity to instill fear on their prey (*sensu* Ripple and Beschta 2004), i.e. their capacity to control prey both numerically and behaviorally. This links with the need for large areas with reduced accessibility to humans and their activities, i.e. effectively protected areas. Behaviorally complex animals adjust their use of space to their perception of the distribution of predation risk (e.g. Willems and Hill 2009). For example, Hebblewhite et al. (2005) documented that human activity mediated a trophic cascade driven by wolves, suggesting that human exclusion of large predators may seriously impact ecosystem dynamics, through a depressing effect on habitat use by the predators.

Concluding remarks

Broad-based ecosystem management can increase an ecosystem's value so that it can provide benefits for future generations (e.g. Gerber et al. 2009). This statement should be paramount, leading to a conservation-oriented management of large carnivores, given their role for ecosystem functionality. Management usually lags far behind scientific knowledge, and has a narrow, short term view. However, considering that micro-evolutionary changes may be rapid and occur in time frames comparable to human disturbance and anthropogenic change, concerned managers should realize both the evolutionary and ecological implications of human activities and management actions (Ashley et al. 2003). The involvement of managers in broadening the scope is also essential for improved knowledge of behavioral responses to influence conservation (Caro 2007, McCleery et al. 2007). Conservation biology is a "mission-driven discipline" (Meine et al. 2006) and we keep running out of time. As Leopold (1953) wrote, the last word in ignorance is the man who says of an animal or plant "what good is it?" Half a century later, it is time to see nature as an interconnected whole in which every part, humans included, depends on the smooth functioning of the whole (Freyfogle 2006). In my opinion, the difference between the goals of having some small populations of large carnivores or populations able to play their normative, interacting role defines the line between true conservation and mere convenience.

A personal note

I have presented a few personal opinions in this synopsis. Nonetheless, some are rooted on discussions over the years with my colleagues at bear projects in Spain and Scandinavia, wolf projects in Spain, Portugal, and Italy, wildlife rangers in Asturias and friends, especially CRV.

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Picture 1 Some images of the study areas in the boreal forest of central Sweden (above), and in the Cantabrian Mountains (NW Spain; below). Photos A. Ordiz (2005-2007)

Picture 2 Shrub, i.e. cover, elimination in the most protected corner of the Cantabrian Mountains (see text, page 21). Photo D. Ramos (2009)

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When our feelings in the field are proved by statistics, they become knowledge, he whispered wise...

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It must have been easier for wildlife to be wild before *Homo* discovered the fire, invented the wheel and evolved to *terribilis* to fire and asphalt this planet. For the welfare of matches and wheels, must be... If the conservationists from the late 1800s- early 1900s knew what is going on today, they would turn over to their graves... However, there should be chances for changes! If there is anything of value in this thesis, let it be for living landscapes and their rare, elusive, and most secretive parts, which deserve a much better ecological consideration.

Casi nunca me sentí lejos de casa, aunque últimamente… De mi familia recibo Todo. No lo expresan palabras que no existen; ni hacen falta. De mano, haberme inculcado el disfrute de lo sencillo, de lo tranquilo, de lo intenso, de la naturaleza. Gracias eternas. Gracias también paciente Paula…
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Compilation of papers

Paper I

Distance-based criteria to identify minimum number of brown bear females with cubs in Europe

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Abstract: Counts of females with cubs-of-the-year (FWC) have been used as an index for monitoring brown bear (*Ursus arctos*) populations or estimating a minimum number of adult females in several small and medium-sized populations. Because discriminating among family groups is crucial to this procedure, we sought to improve criteria used to differentiate among FWC using spatial and temporal distances between sightings. We used telemetry data from 11 FWC from southern and central Europe and 15 FWC from Sweden to determine the likelihood that observations were of the same FWC based on the distance moved and elapsed time period. Euclidean distances traveled by each FWC were estimated daily. We then calculated straight-line distances traveled by each FWC using intervals of 1–180 days, or the maximum available. We obtained the maximum values (highest percentiles) of distances over time for each FWC. We considered 2 periods of bear activity: early spring, from first observations after denning until 30 June, and the remaining active season from 1 July until the onset of denning. Native FWC living in the boreal forest of Scandinavia moved farther than those living in the temperate forests of southern and central Europe. Differences among FWC in southern and central Europe may be related to habitat characteristics and to the origin (native or released) of the bears we studied. For example, based on the upper 95% prediction interval of the curve fitted of the 80 percentile in the early spring–June period, 2 observations 30 days apart are unlikely to be of the same individual if >13 km apart for FWC in the boreal forest, >15 km and >7 km, respectively, for released and native FWC in southern and central Europe. Our findings may be useful for biologists and managers to help differentiate FWC and thereby estimate the minimum number of family groups present, particularly in areas with low densities of FWC.

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Key words: brown bear, census, Europe, females with cubs-of-the-year, identification criteria, movements, *Ursus arctos*

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Counting animals is a common activity of wildlife managers but it is particularly difficult to count carnivores, because they tend to occur at low densities and often are elusive (Linnell et al. 1998). A few researchers have conducted complete censuses of brown bear (*Ursus arctos*) populations (e.g., Miller et al. 1997), whereas others focused on developing indices of abundance (Kendall et al. 1992, Clevenger and Purroy 1996). In recent years, DNA-based censuses of brown bear populations have been tested extensively (Bellemain et al. 2005, Mowat et al. 2005). Tellería (1986) suggested that population indices should concentrate on segments of populations that can be identified most reliably. For brown bears, females with cubs-of-the-year (hereafter, FWC) constitute the most easily identifiable population segment (Knight et al. 1995, Palomero et al. 1997). Females are accompanied by cubs for a long time, are more active during daylight hours (Knight et al. 1995), and have smaller home ranges (Blanchard and Knight 1991, Dahle and Swenson 2003a), and less home-range overlap compared with other age and sex classes (Mace and Waller 1997, Støen et al. 2005). In addition, litter sizes are limited (most often 1–3) and mothers, cubs, or both can have recognizable marks (Campo et al. 1984, Knight et al. 1995) that make them easier to identify than other individuals (Naves et al. 1999, Schwartz et al. 2003, Bellemain et al. 2007). Counts of FWC have been used to monitor brown bear populations and estimate the minimum number of adult females in relatively small populations in Europe (Campo et al. 1984, Palomero et al. 1997) and North America (Knight and Eberhardt 1984, 1985; Knight et al. 1995; Keating et al. 2002; Schwartz et al. 2002).

The utility of FWC counts is based on the assumption that trends in this important segment of the population are correlated with trends in the population (i.e., growth rate, λ) as a whole. This may be true only if the raw, and probably biased, counts of FWC are in some way corrected (Keating et al. 2002) and if demographic parameters (e.g., age distribution of the population, age of first reproduction, reproductive intervals) are reasonably stable during the period of interest (Eberhardt and Knight 1996, Boyce et al. 2001). Annual counts of FWC can be useful to monitor bear populations (Mattson 1997, Linnell et al. 1998, Wiegand et al. 1998) by providing information regarding minimum population size, population trends, and reproductive success (Knight and Eberhardt 1985, Harris 1986, Servheen 1989, Palomero et al. 1997). In addition, the technique is relatively inexpensive and unobtrusive. However, several problems have been reported, including differences in sighting capability, sampling effort, and reporting rate of sighted FWC (Boyce 1995, Mattson 1997, Solberg et al. 2006), so more studies are necessary to define the reliability of the method (Craighead et al. 1995).

Criteria used to discriminate among different FWC often are based on the spatial and temporal distance among sightings and family group descriptions (number of cubs, size, color, and markings; Knight et al. 1995, Bellemain et al. 2007). Distance criteria have been used in USA (Knight et al. 1995), Spain (Campo et al. 1984, Palomero et al. 1997), and Scandinavia (Zakrisson 2001, Kristoffersen 2002). Information gathered from radiotracking FWC can improve the criteria based on distances between sightings, adding objectivity when distinguishing among family groups (Zakrisson 2001, Kristoffersen 2002).

The objective of our study was to improve the criteria to differentiate unique FWC using the distance in space and time among sightings. Specifically, given the number of days between observations, we determined the likelihood of a FWC moving a given distance. The use of this approach reduces the probability of erroneously classifying a FWC seen multiple times as >1 FWC (i.e., making a type I error).

Methods

Radiotelemetry data

We gathered data on FWC from 9 study areas in Europe, collected between 1981 and 2003 (Table 1). During the period in which females and cubs are

Table 1. Mean number of locations per brown bear female with cubs-of-the-year (FWC), by period and country of origin in Europe, 1981–2003.

		Number of locations by period	
Group	FWC (*n*)	Early spring to 30 Jun mean (range)	Jul to denning mean (range)
Native bears			
Southern and central Europe[a]	6	27.5 (27–28)	70.4 (14–150)
Sweden[b]	15	42.5 (20–54)	58.8 (32–123)
Released bears			
Southern and central Europe[c]	5	54.8 (33–82)	60.4 (16–137)

[a] One FWC from Croatia (Huber and Roth 1993), 1 from Greece (Mertzanis et al. 2005), 2 from Slovenia (Kaczensky et al. 2003), 1 from Romania (Mertens and Promberger 2001), 1 from Spain (Naves et al. 2001).

[b] Fifteen FWC from Sweden (Scandinavian Brown Bear Research Project; Zedrosser et al. 2006).

[c] Two FWC from Austria (Rauer et al. 2003), 1 from Italy (Mustoni et al. 2003), and 2 FWC from Pyrenees (France–Spain; Quenette et al. 2001).

together and active (i.e., excluding the denning season), we selected 1 location/day for each FWC, because our aim was to analyze straight-line distances on a daily basis. When >1 locations were available for a day, we chose the location that would result in the elapsed time between successive locations being closest to 24 hours. For every day with available locations, we calculated Euclidean distances between locations for each FWC using intervals from 1 to 180 days, or the maximum interval allowed by available data. We developed the distance data set for each FWC by calculating the distances between all pairs of daily locations within the sample period (e.g., distances traveled between day 1 and 2, day 1 and 3, day 2 and 3, day 2 and 4). Thus, the data set for each FWC contained distances corresponding to elapsed times among observations.

Most FWC reduce their movements during the mating season, possibly to avoid sexually selected infanticide (Kristoffersen 2002, Dahle and Swenson 2003b), a major cause of cub mortality in spring (Swenson et al. 1997), and are spatially segregated from other bears after emerging from dens (Miller et al. 1997, Haroldson et al. 2002). Thus, we considered 2 periods of bear activity: (1) early spring to the end of June, and (2) July to denning. The first period was from the first observation of each FWC (Mar–May) to June 30, the end of the mating season in Europe (Dahle and Swenson 2003c, Solberg et al. 2006, Fernández-Gil et al. 2006). The second period was from the beginning of July to den entry, including the season of hyperphagia. In portions of southern Europe, some bears may not den during some winters (Huber and Roth 1997), including some FWC (Naves et al. 2001). In those instances, we also used winter locations up to February. In addition to biological reasons, we considered the 2 periods defined above because surveys may be carried out only during a specific period in some areas (Servheen 1994); therefore, we intended to provide a distance-based tool for each period.

Groups of FWC

Because the habitat of small populations of bears in southern and central Europe has some common features (e.g., fragmented forest cover, mostly deciduous forest, anthropogenic influence), we pooled data from the 9 populations. In several populations, female bears had been released during the 1990s to augment existing populations. The Scandinavian Brown Bear Project offered information from a boreal forest to contrast possible geographical differences among areas, thus we also included data from Sweden in our analyses (Table 1). Therefore, we divided the sample into 3 groups: native FWC ($n = 6$) in temperate forests of southern and central Europe, native FWC ($n = 15$) in boreal forests of Sweden, and released FWC ($n = 5$) in temperate forests of southern and central Europe.

Statistical analysis

After developing data sets of distances moved by FWC for each time lag, we calculated the 80, 90, and 95 percentiles of distances for each FWC and time lag. Any distance above these values was very unlikely to have been traveled by the same family group. Thus, it may constitute an objective criterion to differentiate FWC. To test whether the division of the data base according to periods, geographical origin, and released versus native status was statistically supported, we used generalized linear models (GLM, McCullagh and Nelder 1983, Crawley 1993) to examine the explanatory ability of period and the 3 groups of FWC (explanatory variables) on the 80, 90, and 95 percentiles of the maximum distance traveled by FWC (dependent variable). In GLMs, we used the Type I error of PROC GENMOD (SAS Institute, Inc. 2000), which does not use iterative checking of explanatory power of all variables included in the model, but includes them in the given order. This procedure is frequently used when correcting for some factors. Because distance traveled depends on elapsed time between observations, we first included the variable 'time', followed by 'period,' and 'FWC group'. We also tested whether these relationships differed among individual bears (i.e., included individual bear as a variable along with elapsed time, period, and group). Statistical analyses were performed with SAS (2000).

In addition, we used nonlinear regression with all FWC groups and the 2 periods to describe relationships between travel distance and time. We used a nonlinear approach, because distances traveled between 2 observations are expected to be larger when time lags are longer, but a threshold is also expected, because movements ultimately are constrained by the home range (Zakrisson 2001, Kristoffersen 2002).

Using the predictive equation from statistical models, we determined the likelihood that an observed FWC had moved a particular distance during a given time. We applied Table Curve (Systat Software, Inc. San José CA, USA) to fit predictive curves to 80, 90, and 95 percentiles of distance traveled as a function of time for every FWC group and period. Among the potential curves generated for each period and group, we selected the curve with the largest R^2. Depending on the length of each period and available data (there were some gaps in data sets), the fitted curves had different lengths. We extended curves to the point (i.e., time-lag) where the amount of data did not decrease compared to shorter time lags between observations (e.g., for the early spring–end of Jun period of around 90 days, we only extended curves for a maximum of 55 days because we still had 35 observations to calculate percentiles for this time lag).

Results

When accounting for elapsed time between observations (χ^2 = 37.1, $P < 0.001$), distance traveled by each FWC depended on period of the year (χ^2 = 196.9, $P < 0.001$) and FWC group (χ^2 = 398.0, $P < 0.001$). In addition, the variable individual FWC was also significant (χ^2 = 3,208.6, $P < 0.001$).

The nonlinear regression equations for a given FWC group and period provided a statistically-based (e.g., 80%, 90%, 95%) method of discriminating between 2 observations belonging to the same FWC and 2 observations belonging to distinct FWC (Table 2, Fig. 1, 2). In some instances, the 95 percentile was not obtainable because of small sample size. Figs. 1 and 2 show the 80 percentile regression equations fitted for every FWC group and period, as well as its upper 95 prediction interval. This is the most conservative approach to differentiate FWC, because most individual distances traveled by the females included in a given group and period are below that upper threshold. For example, 96.2% of the observations of native FWC in the boreal forest during the early spring–end of June occurred below the fitted curve, with individual FWC ranging from 80.4% (more mobile FWC) to 100% (less mobile FWC). Likewise for July–onset of denning, 97.5% of the observations were below the 95% prediction interval curve of the 80 percentile regression (individual range = 85.4–100%).

Based on the upper 95% prediction interval of the curve fitted to the 80% percentile in the early spring–June period (Fig. 1), 2 observations 30 days apart were unlikely to be of the same individual if >13 km apart for FWC in the boreal forest, >15 km (released FWC) and >7 km (native FWC) in southern and central Europe.

Discussion

The distance between sightings of a FWC can help determine whether these sightings were of the same FWC. We found that distance traveled by FWC, corrected for elapsed time between observations, differed between periods (early spring–end of Jun, Jul–denning) and among FWC groups (native FWC in boreal forest; released and native FWC in southern and central Europe). Distances larger than the thresholds established by our fitted curves (Fig. 1, 2) are unlikely to be from the same FWC. Without additional criteria, distances below those thresholds may be of the same FWC, but the method does not allow differentiation of FWC. Therefore, distance-based criteria provided here should be used with additional criteria when possible, such as family group size and other characters, and may be most

Table 2. Regression equations that describe distances moved by brown bear females with cubs (FWC) in Europe according to upper percentiles of distance traveled as a function of time, group of FWC, and period. y = distance traveled; x = number of days separating observations; a, b, and c are parameters from the models.

		Group of FWC[a]		
Period	**Percentile**	**1**	**2**	**3**
Early spring to the end of Jun	80	$y = a+bx^{c}$ $a = 1.1$ $b = 476.6$ $c = 0.6$ R^2: 50.6%	$y = a+b/x^{0.5}$ $a = 10359.7$ $b = -8433.3$ R^2: 26.5%	$y = a+bx^{c}$ $a = -2019.5$ $b = 4965.5$ $c = 0.2$ R^2: 15.9%
	90	$y = a+bx^{c}$ $a = -243.6$ $b = 1257.1$ $c = 0.5$ R^2: 69.5%	$y = a+bx^{c}$ $a = 11701.7$ $b = -7629.6$ $c = -0.6$ R^2: 20.7%	$y = a+bx^{c}$ $a = -876.4$ $b = 5423.2$ $c = 0.2$ R^2: 16.6%
	95	Insufficient data	$y = a+b/x^{(0.5)}$ $a = 13266.9$ $b = -8032.8$ R^2: 19.8%	Insufficient data
Jul to denning	80	$y = a+bx^{c}$ $a = -1040.9$ $b = 3903.4$ $c = 0.2$ R^2: 4.8%	$y = a+bx^{c}$. $a = -326.7$ $b = 8135.5$ $c = 0.2$ R^2: 32.7%	$y = a+bx^{(0.5)}$ $a = -520.8$ $b = 3598.9$ R^2: 21.1%
	90	$y = a+bx^{c}$ $a = 1039.2$ $b = 3867.5$ $c = 0.2$ R^2: 3.01%	$y = a+bx^{c}$ $a = 17706.4$ $b = -10235.1$ $c = -0.5$ R^2: 15.2%	$y = ax^{b}$ $a = 11835.4$ $b = 0.3$ R^2: 17%
	95	$y = ax^{b}$ $a = 6942.4$ $b = 0.1$ R^2: 3.3%	$y = a+b/x^{(0.5)}$ $a = 19452.2$ $b = -9928.4$ R^2: 13%	$y = a+b/x^{(0.5)}$ $a = 30340$ $b = -26469$ R^2: 12.1%

[a] Groups of FWC: 1 = native bears from southern and central Europe, 2 = native bears from the boreal forest of Sweden, 3 = released bears in southern and central Europe.

useful when trying to distinguish groups with the same number of animals (2 cubs is the most common litter size; Schwartz et al. 2003).

The variability in travel distances among groups and periods was large. It is important to note that our equations were fitted to the upper 80, 90, and 95 percentiles, which constitute the upper part of distance distribution. Thus, the curves do not represent the central tendency of the data. The inherent high variability of extreme values, and the individual variation within FWC groups, explains the generally low R^2 values of the non-linear regressions (Table 2, Fig. 1, 2). Fitting curves as we have done estimates the maximum distances that FWC within the 3 groups and 2 periods may move in a given time lag, in the presence of individual variation. In fact, most of the females moved less than our models predict; that is, our curves represent a highly conservative criterion that would avoid error type I to a large and quantifiable degree. However, in some groups females occasionally moved large distances. Most of these cases were related to human disturbances that moved the bears away from their normal areas of use (Naves et al. 2001, Mertzanis et al. 2005). The lowest R^2 was found for the native FWC group in southern and central Europe after July (Fig. 2), probably because we extended the period for FWC that did not den. The upper 95% prediction interval of the 80 percentile fitted curve included 100% of the distances traveled by 5 of the 6 females of this group and period and 95.6% of the distance values for the remaining FWC. That is why we also included the 95 percentile fitted curve for that group and period (Fig. 2c), which is very conservative and more accurately described the distance traveled by most of the FWC; 99.9% of the observations occurred below the 95 percentile fitted curve, although this value was 69.4% for the most mobile female (which was often disturbed by human activity; Mertzanis et

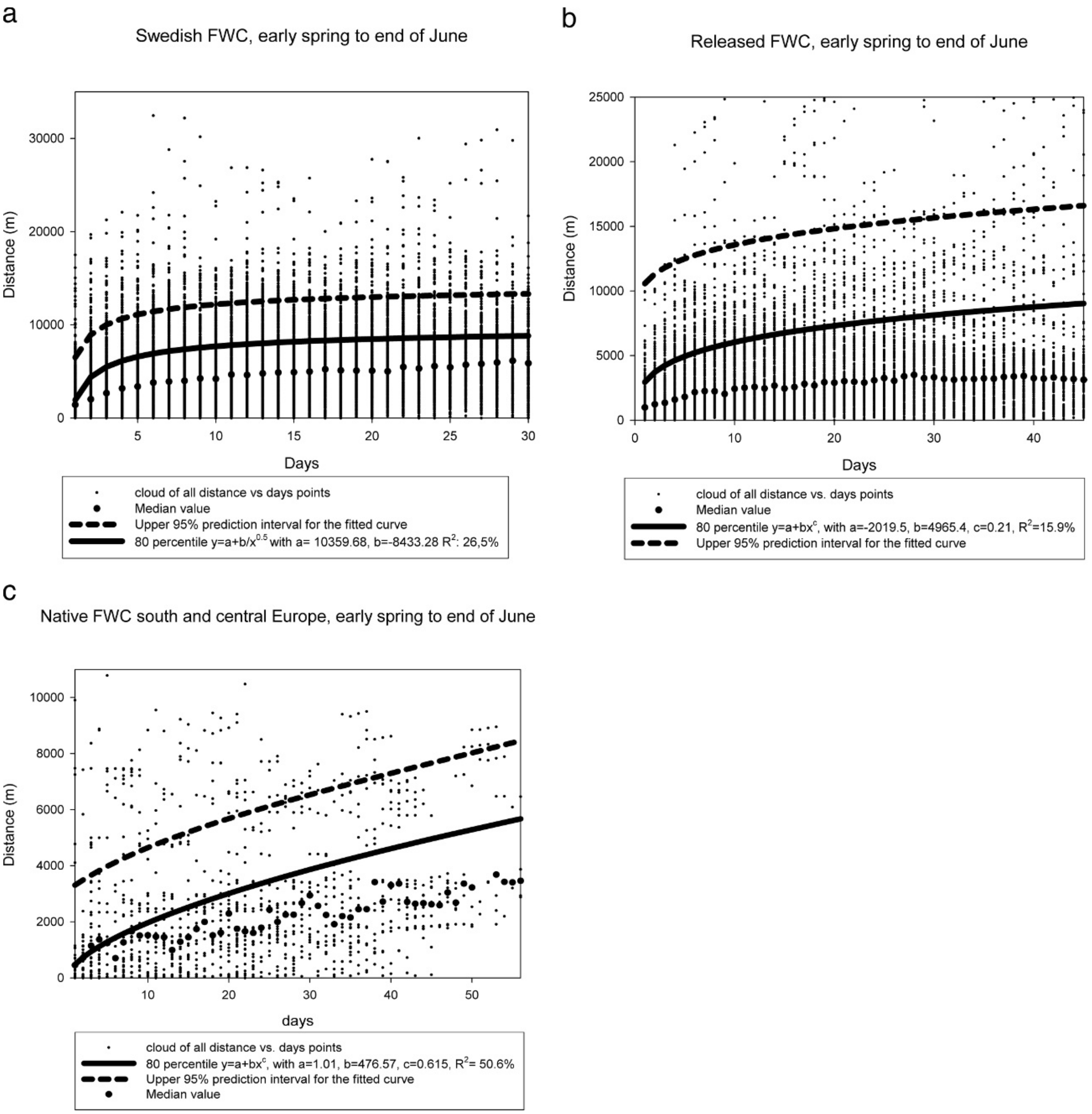

Fig. 1. 80 percentile fitted curve and its upper 95% prediction interval, based on nonlinear regression of travel distance versus elapsed time between locations for 3 groups of female brown bears with cubs (FWC) in Europe, early spring–30 Jun, 1981–2003. Small points are distance traveled versus time lags, larger points are median values of observations for all females in each group. 1a: Native FWC in the boreal forest of Sweden. 1b: Released FWC in southern and central Europe. 1c: Native FWC in southern and central Europe.

al. 2005), 100% for the 3 least mobile FWC, and >99% for the 2 remaining FWC.

For the purpose of estimating a minimum number of FWC, we suggest that the use of maximum distances is more reliable than the central tendency of the data. We have shown median distances traveled (Fig. 1, 2) to emphasize that the curves were fitted to maximum distances represented by an upper percentile and its upper 95% prediction interval as the most conservative option.

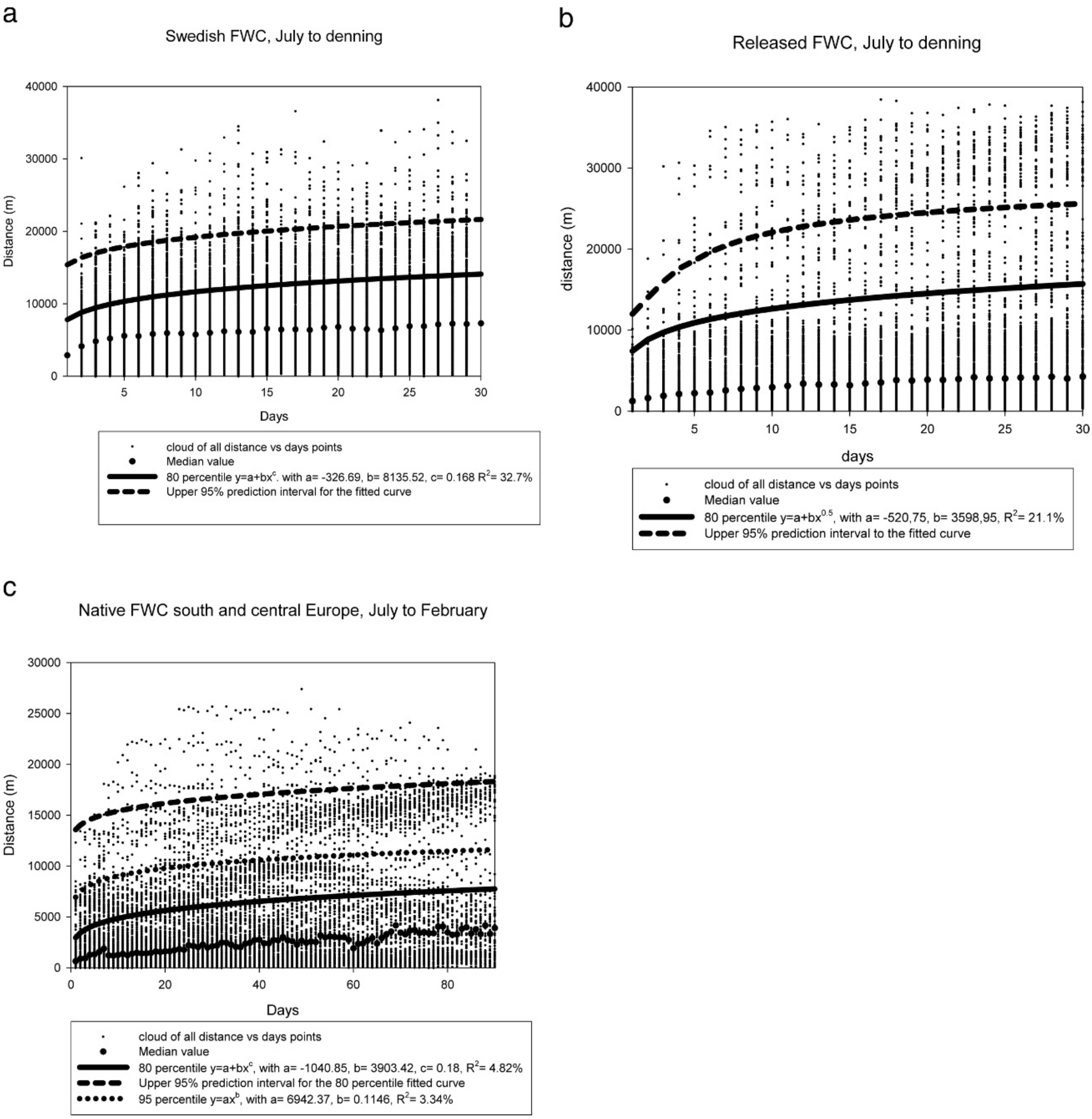

Fig. 2. 80 percentile fitted curve and its upper 95% prediction interval, based on nonlinear regression of travel distance versus elapsed time between locations for 3 groups of female brown bears with cubs (FWC) in Europe, 1 Jul–onset of denning, 1981–2003. Small points are distance traveled versus time lags, larger points are median values of observations for all females in each group. 2a: Native FWC in the boreal forest of Sweden. 2b: Released FWC in southern and central Europe. 2c: Native FWC in southern and central Europe; 95 percentile fitted curve is shown, and the period includes Feb because some FWC did not den.

Movement patterns differ among brown bear populations inhabiting different habitats in Europe (Dahle and Swenson 2003a). In general, released females in southern and central Europe and native FWC inhabiting boreal forests in Scandinavia moved farther than native FWC in southern and central Europe, regardless of the time of the year. Movement patterns of native bears were more consistent, whereas movements of some released females were highly variable, even when they have cubs-of-the-year, until they become acquainted with new areas. Actually, 87.7% of all distance values for these females were below the upper 95% prediction interval of the 80 percentile fitted curve, but for the most mobile female this percentage dropped to 50%. This variation among released bears requires further investigation and cautious application of this distance-based criterion, but this finding may have implications for reintroductions. Observations of native FWC in the boreal forest may be separated by distances close to the maximum even when separated by relatively short times (Fig. 1, 2). Distances traveled by native and released FWC in southern and central Europe did not reach an asymptote for either of the periods we examined. Therefore, the longer the time lags between observations, the greater the distances separating them.

We believe that our method to differentiate unique FWC improves former approaches by statistically relating the distance separating 2 observations of FWC to the lag between them. For example, in Yellowstone this lag was not accounted for by Blanchard and Knight (1991). They created a mobility index using standard diameters of annual home ranges of 31 FWC, using twice the mean value as a criterion to determine if FWC were the same, while also including other sources of information (Knight et al. 1995).

Management implications

The methodology we present provides additional, objective distance-based criteria to estimate the minimum number of FWC for brown bears in areas of Europe. Keating et al. (2002) suggested that the number of FWC should be at least as high as that estimated. Therefore, it is often advisable to use the most conservative predictive models to avoid assigning observations of the same FWC to different FWC. Both upper 95% prediction intervals, shown in all the curves, and 95% percentile fitted curves, shown for native FWC in southern and central Europe, are conservative approaches (Table 2).

Because our models are based on maximum distances traveled, FWC separated by short distances (those well below the fitted curves) are not clearly distinguishable, so our findings are probably more reliable in areas with low bear densities (Solberg et al. 2006). Thus, the application of our method will result in conservative estimates, because some observations of different FWC will be considered to be the same FWC. Although the percent of home-range overlap among FWC is the lowest compared to any other bear–bear overlap (Mace and Waller 1997), Støen et al. (2005) have reported high degrees of home-range overlap by related females. When the application of family group-based criteria is not definitive, distance-based procedures may be a useful, additional tool to differentiate and count minimum numbers of unique FWC.

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Paper II

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DISTANCE-DEPENDENT EFFECT OF THE NEAREST NEIGHBOR: SPATIOTEMPORAL PATTERNS IN BROWN BEAR REPRODUCTION

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Abstract. In mammals, reproductive synchrony and reproductive suppression usually are found in social, group-living species, which often display hierarchical relationships among related animals. Some individuals, particularly younger, philopatric females beyond the age of sexual maturity, may not raise offspring because they are suppressed by other individuals. Although brown bears (*Ursus arctos*) are a solitary species, the existence of socially induced delayed primiparity of philopatric females has been documented. Here we show further evidence for interactions of a population-regulatory nature that are typically associated with social species. We found that an adult female's probability of having cubs in a given year was influenced by whether or not her nearest neighboring adult female had cubs. At short distances ($\leq$10 km) between the home range centroids of neighboring females, females with cubs had a negative effect on their neighboring female's probability of having cubs of the year. At distances >10 km and $\leq$20 km, the effect reversed, and it disappeared beyond 20 km. We argue that reproductive suppression is probably caused by resource competition among females living close to each other. Previously, similar population regulation mechanisms have been found only in group-living mammals. Thus, social interactions and behavior in solitary carnivores may be more flexible than usually assumed.

Key words: brown bears; females; population regulation; reproductive competition; reproductive suppression; reproductive synchrony; Scandinavia; sexually selected infanticide; sociality; Ursus arctos.

Introduction

Reproductive synchrony refers to several females giving birth within a few days or weeks, i.e., parturition is temporally clustered (Ims 1990). In mammals, it has been usually described for social, group-living species, from rodents to ungulates and large carnivores (e.g., Rutberg 1984, Johannesen et al. 2000, Packer et al. 2001, Gilchrist 2006). Also, group-living and cooperatively breeding mammals often display hierarchical relationships among related animals, in some cases manifested by reproductive suppression (Creel and Macdonald 1995, Moelhman and Hofer 1997). This generally affects young, philopatric females through behavioral or physiological mechanisms (Wasser and Barash 1983, Brant et al. 1998, Hackländer et al. 2003).

There are several possible causes of spatiotemporal patterns in reproduction (Ims 1990). Environmental factors, like food availability, can play an important role in synchronizing reproduction (Hudson and Cattadori 1999), but also internal factors, like biological clocks and social signals exchanged among female individuals within a population, may synchronize reproduction in birds and mammals (Ims 1990). In addition, the existence of male-induced reproductive synchrony has been observed in lions (*Panthera leo*), with the turnover of males causing birth synchrony within the pride following infanticidal killing by males (Packer and Pusey 1983).

However, some factors facilitate reproductive asynchrony rather than synchrony. Competition for breeding among females can explain why older females suppress reproduction in younger ones to reduce competition for limited resources, which has been shown for different mammal groups, such as rodents (Eccard et al. 2002, Hodges et al. 2002, Wolff et al. 2002), carnivores (e.g., Moelhman and Hofer 1997), and primates (e.g., Digby 1995). Female reproductive suppression, likely instigated by adult females, was suggested to explain delayed primiparity in brown bears (Støen et al. 2006*b*), which could be in accordance with the reproductive-competition hypothesis (e.g., Wolff et al. 2001, 2002). Sexual selection also may favor reproductive asynchrony in species where paternal investment in young is unimportant (Ims 1990). Reproductive asynchrony can increase the opportunity for optimal male choice because each

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receptive female can attract more males when no other receptive females are present, and, if space and other resources are limiting, it can be advantageous for females with size-oscillating territories to reproduce out of synchrony with their neighboring territory holders (e.g., Ims 1990).

In this study we investigated whether there are spatiotemporal reproductive patterns in brown bears (*Ursus arctos*), i.e., if reproductive females living near each other influenced each other's reproduction. Brown bears exhibit two-, three-, and four-year reproductive cycles, but can give birth every year if the cubs of the year are lost. A number of different factors may favor either reproductive synchrony or asynchrony in Scandinavian brown bears. Environmental factors, such as between-year differences in food availability, could promote reproductive synchrony among neighboring females, i.e., most females giving birth in years with favorable food conditions. In some populations of North American black bears (*Ursus americanus*) reproduction is controlled mainly in a density-independent way by nutritional factors that fluctuate in abundance from year to year (Rogers 1976, 1987, Bunnell and Tait 1981, Beecham 1983, Eiler et al. 1989, Pelton 1989, McLaughlin et al. 1994). Sexually selected infanticide by males (Hrdy 1979), a major reason for bear cub mortality in parts of Scandinavia (Swenson et al. 1997, 2001), also could promote reproductive synchrony, because infanticide shortens the time to the mother's next estrus (Swenson et al. 1997, Bellemain et al. 2006*a*), and affects several females simultaneously within the home range of a perpetrating male.

Dominance behavior during the mating season, leading to female reproductive suppression, might cause reproductive asynchrony in brown bears. We have already found evidence for female–female competition and dominance behavior in Scandinavian brown bears, where related females are spatially structured into matrilineal assemblages (Støen et al. 2005): (1) natal dispersal is inversely density dependent (Støen et al. 2006*a*), (2) there is a delayed primiparity of philopatric females, probably driven by resource competition within female hierarchies that causes reproductive suppression in young females (Støen et al. 2006*b*), (3) competition among female siblings forces the smaller one to disperse (Zedrosser et al. 2007), (4) unrelated females are excluded from matrilineal assemblages (Støen et al. 2005), and (5) home range size of both adult and subadult females are inversely related to density (Dahle and Swenson 2003*c*, Dahle et al. 2006). Also, Beckmann and Berger (2003) found that black bears were distributed primarily in an ideal-despotic manner in their study sites. Moreover, the lack of paternal care in brown bears, and the females' oscillating home range during their multiyear reproductive cycle (Haroldson et al. 2002, Dahle and Swenson 2003*b*) may promote reproductive asynchrony rather than synchrony (Ims 1990). Brown bear females roam to mate and mate with several males (Dahle and Swenson 2003*b*, Bellemain et al. 2006*b*), so a lower number of females available to males in the breeding season, which would be facilitated by reproductive asynchrony, may increase mating possibilities for the females in estrus.

MATERIAL AND METHODS

Study species and study areas

The brown bear is a large carnivore with a promiscuous mating system (Pasitschniak-Arts 1993, Schwartz et al. 2003, Bellemain et al. 2006*b*). The mating season lasts from late May to early July (Dahle and Swenson 2003*b*). Implantation of the embryos is delayed (e.g., Spady et al. 2007), and female bears give birth to 1–4 offspring while hibernating in dens during winter (Pasitschniak-Arts 1993). Offspring separate from their mothers when they are 1.4–3.5 years old (McLellan 1994). In Sweden, females reproduce every two to three years (Dahle and Swenson 2003*d*). In south-central Sweden, 95% of the litters are weaned as yearlings (Dahle and Swenson 2003*a*), whereas only 53% of the litters are weaned as yearlings in northern Sweden (Dahle and Swenson 2003*d*). Females usually separate from their offspring during the mating season prior to mating (Dahle and Swenson 2003*b*; see Plate 1). In Scandinavia young females reach sexual maturity at the age of 3–5 years (Swenson et al. 1995), whereas they are usually older in North American populations (McLellan 1994, Hilderbrand et al. 1999).

Brown bears are solitary, but hierarchies develop, for instance, when they aggregate at food sources (Craighead et al. 1995, Gende and Quinn 2004). They are usually not considered to be territorial (Pasitschniak-Arts 1993, Schwartz et al. 2003), but natal dispersal and home-range size have been shown to be inversely density dependent, suggesting some form of territorial behavior in brown bears (Dahle and Swenson 2003*c*, Dahle et al. 2006, Støen et al. 2006*a*).

Our data came from two study areas. The southern study area is situated in Dalarna and Gävleborg counties, south-central Sweden, and Hedmark County, southeastern Norway (61° N, 18° E) and covers the southern part of the southernmost brown bear subpopulation in Scandinavia. Elevations range from $\sim$200 m in the southeast to about $\sim$1000 m in the west. Most of the area is below the timberline, which is at $\sim$750 m. Lakes and bogs are common, but most of the hilly landscape is covered with intensively managed coniferous forest, dominated by Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*). The northern study area is situated in Norrbotten County in Sweden (67° N, 18° E). The area is rolling, with elevations $<$300 m in the east, but is dominated by mountains that rise to $>$2000 m in the west. Northern boreal coniferous forest dominates, but there are extensive subalpine birch (*Betula pubescens*) forests. Detailed descriptions of the study areas can be found in Dahle and Swenson (2003*d*) and Zedrosser et al. (2006). For capture and marking procedures, see Arnemo et al. (2006) and Arnemo and Fahlman (2007).

We analyzed data from 76 radio-marked females $\geq$4 years old (20 from the north, 56 from the south) during the period 1987–2006. Most of the bears were captured in spring, after den emergence, when yearlings were with their known, previously radio-collared mother; and/or the mother was known through genetic analyses (Bellemain et al. 2006*b*). The bears were located weekly or biweekly during their active period using standard triangulation methods from the ground or the air (Dahle and Swenson 2003*a*). The females were systematically observed from helicopters in spring to determine whether they had cubs, that is, to know if they gave birth that year. If not accompanied by cubs, the females were captured in spring and examined for lactation to determine if they had suckled cubs. In addition, we visited dens in the southern study area to determine whether young had been present outside the den, which was based on tracks and markings from the young climbing in nearby trees. In the northern study area, virtually 100% of the adult bears were radio-marked. Up to 80% of the adult females and 50% of the adult males (Swenson et al. 2001, Solberg et al. 2006) were radio-marked and relatively evenly distributed in the southern study area, with some variation during the 20-year study period.

Home-range centroid estimation for the annual active season

We used females with at least six relocations (range, 6–23; median, 16) to calculate annual home-range centroids, which were needed to determine neighbors, distance between them, and density. The distance between a focal female and its nearest neighbor in a given year was calculated as the straight-line distance between their annual home-range centroids. In the southern area, the mean date of den emergence was 20 April and that of entry was 28 October for radio-marked females (Friebe et al. 2001), whereas it was 10 May and 9 October, respectively, in the northern area (Manchi and Swenson 2005). Thus, we used only locations from May to September. To minimize autocorrelation, centroids were estimated using only the first position in a week if several positions were available for the same week. Female dyads were excluded from the analysis when this distance exceeded 40 km, because, even if the proportion of adult marked bears was very high, we did not know every breeding age female in the population. Thus, the probability that we knew the true nearest female decreased with increasing distance, as there was more space for unmarked females.

Statistical analysis

In order to test if reproductive females living near each other influenced each other's reproduction, we used logistic regression to evaluate the effect of the following variables on the probability of an adult female having cubs of the year in a given year: (1) age category of the focal female (4–6, 7–12, >12 yr); (2) distance to the nearest known (radio-marked) neighboring adult female ($\leq$10 km between home-range centroids, >10 and $\leq$20 km, >20 km up to 40 km); (3) the nearest neighboring adult female having cubs of the year or not (yes, no); (4) the nearest neighboring adult female was the focal females' mother (yes, no); (5) study area (north, south); and (6) environmental condition index. The spring body mass of yearlings in each year and study area was used to construct an index of the general food condition of the study populations for the previous year, while they were cubs (see Zedrosser et al. 2006).

Focal females had reproduced at least once before or during the first year of inclusion in the analysis. Our most general model included all of the above variables and meaningful two-way interactions among them. Among the ecological determinants of reproductive success, intraspecific competition and density-dependent effects have received much attention (e.g., Koskela et al. 1999). We evaluated the possible influence of density on the outcome of the analysis by using a local density index calculated for each year and study area, based on radiolocations of all collared bears, and local density using location of individual bears identified from DNA in scats collected by hunters during an intensive census (see Zedrosser et al. 2006 for a detailed description). Density (log-transformed) was inversely related to distance to the nearest neighbor (F = 142.3, df = 1, 427, $P < 0.001$); thus, at a first stage we only included distance to the nearest neighbor in the model. To verify that possible effects of nearest neighbor distance were not solely an artifact of local density, we cut density into 20 narrow categories of equal size. For the first two distance categories ($\leq$10 km, and >10 km and $\leq$20 km), we selected all the observations that fell within a density category, selecting from the distance category that had the fewest observations. We then randomly drew a subsample ($N = 174$ observations), balanced in terms of local density, from observations in the two distance categories and refitted the logistic regression model to this sample. Second, we also ran a model with density, including an interaction density–distance, and a model replacing distance by density everywhere in the model, to determine whether both density and distance were similar measures in terms of their effect on the probability of a female having cubs in a given year.

Model selection was based on the Akaike Information Criterion (AIC; Akaike 1974) using stepwise removal of model terms until the model with the lowest AIC value was reached. To achieve greater parsimony, we further reduced the resulting model by removing terms with effects that had P values > 0.1. Preliminary analysis and diagnostics suggested a nonlinear relationship between the probability of a female having cubs and the distance to the nearest neighboring female. Hence, we first fitted distance to the nearest neighboring female using natural splines (piecewise cubic polynomials with smooth transitions) in a basic model with the predictors distance

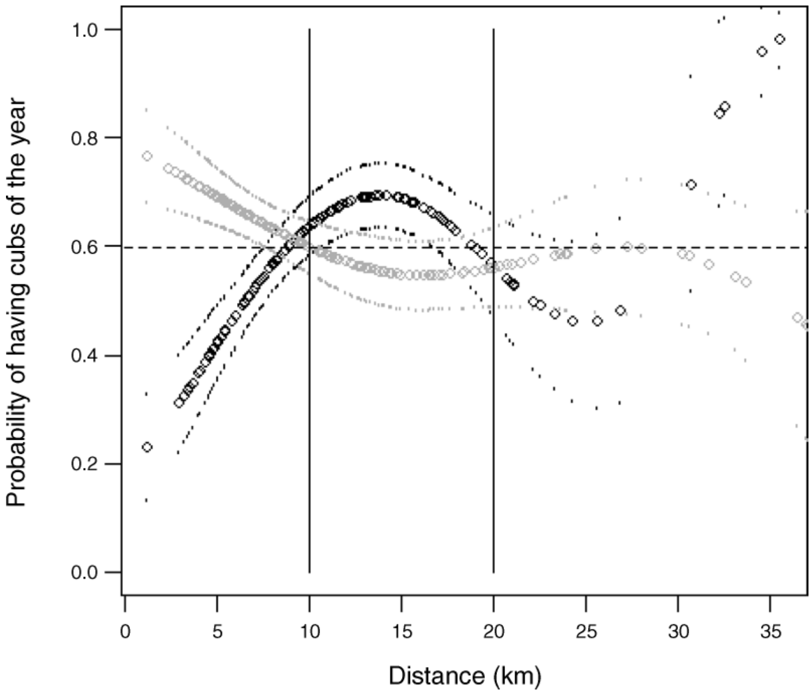

FIG. 1. Predicted probability of a female having cubs of the year and associated standard error boundaries from the logistic regression model with the effect of distance from the nearest neighboring adult female modeled as a natural spline (knots at 15 and 30 km). Predictions for females with nearest neighboring females that have cubs of the year are represented by large black circles, predictions for females with nearest neighboring females without cubs of the year are represented by large gray circles. Standard error limits are marked with small circles. The dashed line is a visual reference representing the mean annual probability of having cubs of the year (0.6) for our sample population.

to nearest neighboring female and the nearest neighboring female's reproductive status (having cubs of the year: yes or no), including the interaction between the terms. The best version of this model with splines based on AIC was one with knots at 15 and 30 km. After inspection of fitted values from this model, we selected cut points at 10 and 20 km for a categorical representation of distance.

We confirmed the goodness of fit of our logistic regression model with a binary response variable by using the Pearson residuals chi-square test (Hosmer et al. 1997, Crawley 2002).

We also checked for a potential lack of independence due to individual females that were used repeatedly in the model (as a result of testing over multiple years) by including bear identification as a random effect in a generalized linear mixed model version of our best model derived from model selection. We omitted the random effect from the final model because effect size estimates and their standard errors were nearly identical in the models with and without the random effect. We used the statistical package R 2.5 in all statistical analyses (*available online*).[7]

RESULTS

We obtained 335 pairings between female home-range centroids for the period 1987–2006 (dyads per female; mean = 4.4, SD = 3.9, range = 1–16). The basic model with distance as a smoothing spline (Fig. 1) and the equivalent model with distance as a categorical variable (Fig. 2) provided nearly identical results. Because the model with distance from the nearest neighbor as a categorical variable had a lower AIC (ΔAIC of the model with splines = 5), we utilized the categorical representation of distance in the final model.

This model indicated an effect of the reproductive status (having cubs of the year; yes or no) of the nearest neighboring adult female, modulated by the distance between that female and the focal female, on a focal female's probability to have cubs in a given year. At distances $\leq$10 km, a female's odds of having cubs were on average 65.9% lower in years when her nearest neighboring female had cubs (Figs. 1 and 2). The effect of the reproductive status of the nearest neighboring female reversed at distances $>$10 km and $\leq$20 km; females had 123.9% greater odds to have cubs when their nearest neighboring female also had cubs. The probability of having cubs for females whose centroids were separated from that of their nearest neighboring female by $>$20 km to 40 km did not seem to be affected by their neighbor's reproductive status (Table 1). The model further showed differences in the probability of having cubs depending on age (the effect sizes are shown in Table 1). The probability of a female having cubs in the southern study area was higher than in the north

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[7] ⟨http://www.R-project.org⟩

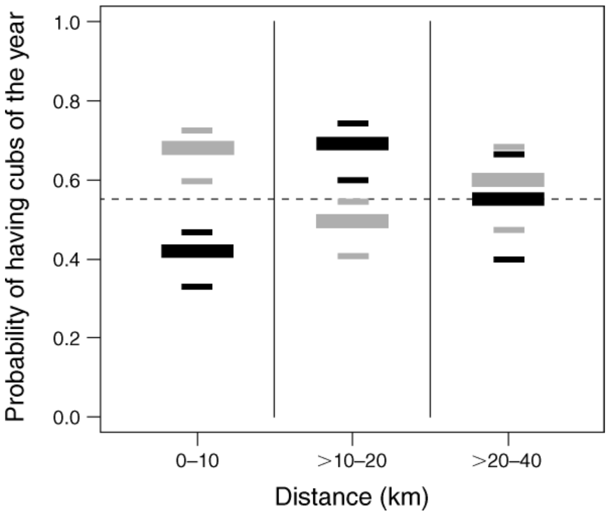

FIG. 2. Predicted probability of a female having cubs of the year (large horizontal bars) and associated standard error boundaries (small horizontal bars) from the logistic regression model with the effect of distance from the nearest neighboring adult female modeled as a categorical variable (cuts at 10 and 20 km). The figure shows the pattern for the most common age class in our study, 7–12-year-old females. Predictions for females with nearest neighboring females that have cubs of the year are represented by large black bars, predictions for females with neighbors without cubs of the year are represented by large gray bars. Standard error boundaries around the predicted probabilities are marked with small bars. The dashed line is a visual reference representing the mean annual probability of having cubs of the year (0.55) for 7–12-year-old females in our sample population.

(odds ratio = 1.62). Neither the nearest neighbor being the focal female's mother nor the yearling condition index remained as predictors in the final model.

Distance to the nearest neighbor might be understood as a manifestation of density effects. However, after balancing in terms of density and after its inclusion in the model, the effect that persisted qualitatively was the nearest neighbor's reproductive status (with or without cubs) and its distance to the focal female; and its magnitude for the first distance category (<10 km separating centroids) actually increased ($\beta = -1.65$ density controlled vs. $\beta = -1.08$ without control). This suggests that the effect of distance to the nearest neighbor (and its reproductive status) that we obtained originally was indeed the appropriate measure in this study.

DISCUSSION

The probability of an adult female brown bear having cubs in a given year was significantly affected by the distance to the nearest neighboring female and whether or not she had cubs, and this effect was not just an effect of local density. The effect of distance to the nearest neighbor on female reproductive success has been found before (Mappes et al. 1995), but to our knowledge this is the first such finding in a wild population of a large, nonsocial mammal. In addition, we found that the pattern changed spatially. At short distances, ≤ 10 km between home-range centroids, a female was less likely to have cubs when her nearest neighbor had cubs. Ten km approximates the radius of a median home range of lone females in Scandinavia (217 km^2 in the south, 280 km^2 in the north; Dahle and Swenson 2003*c*, Støen et al. 2006*a*). Thus, at short distances there would be an extensive home-range overlap among the females. We suggest that reproductive suppression of subordinate females by dominant females causes this spatiotemporal pattern. In Scandinavia we have previously documented several phenomena suggesting female–female competition (see *Introduction*). Our findings are also in accordance with female-induced reproductive suppres-

TABLE 1. Results of the final logistic regression model of the effect of whether the nearest neighboring female had cubs of the year on the probability of a Swedish brown bear female having cubs of the year in a given year, depending on the distance separating home-range centroids of both animals.

Explanatory variables	β	SE	*Z*	Lci†	Odds ratio	Uci†	Pr(>|*Z*|)
(Intercept)	1.27	0.42	3.01	1.55	3.54	8.07	0.003
NNC‡, no	0.00						
NNC, yes	−1.08	0.33	−3.24	0.18	0.34	0.65	0.001
Distance, 0–10§	0.00						
Distance, 10–20	−0.76	0.36	−2.12	0.23	0.47	0.94	0.034
Distance, 20–40	−0.34	0.49	−0.70	0.27	0.71	1.86	0.486
Study area, north	0.00						
Study area, south	0.48	0.30	1.61	0.90	1.62	2.91	0.107
Age, 4–6 years	0.00						
Age, 7–12 years	−0.97	0.31	−3.13	0.21	0.38	0.70	0.002
Age, >12 years	−1.21	0.35	−3.45	0.15	0.30	0.59	<0.001
NNC, yes; distance, 0–10	0.00						
NNC, yes; distance, 10–20	1.88	0.52	3.62	2.37	6.57	18.20	<0.001
NNC, yes; distance, 20–40	0.88	0.74	1.20	0.57	2.42	10.25	0.232

Notes: The neighboring effect persisted for all age categories, but annual breeding probabilities were different depending on age. Model selection was based on AIC. The first level of each categorical variable served as the contrast for the remaining levels of that variable.

† Lci and Uci indicate lower and upper 95% confidence limits around the odds ratios, respectively.

‡ NNC, nearest neighbor had cubs of the year.

§ Distance categories expressed in km.

PLATE 1. Female brown bear with a yearling cub. Photo credit: I. Kojola.

sion found in many mammal groups (e.g., Digby 1995, Moelhman and Hofer 1997, Wolff et al. 2002).

We propose that the mechanism involved for brown bears is a greater probability of encounter between two estrous females with overlapping home ranges, allowing one to dominate the other and suppress her estrus, rather than the probability of encounter between an estrous female and one with cubs. In our study areas, estrous females use large ranges in the mating season, suggesting that they roam to find mates, because these increased home ranges could not be explained by a seasonal change in food availability or by increased needs of estrous females to replenish body reserves after previous cub raising (Dahle and Swenson 2003*b*). The greater home-range sizes of estrous females would bring them into contact with more females, giving the opportunity for dominant females within hierarchies to suppress estrus in subdominant females (Støen et al. 2006*b*). The situation is quite different when female brown bears have cubs. They minimize their range size during the mating season, are spatially segregated from other bears after emerging from dens and, compared with estrous females during the mating season, females with cubs move shorter distances, are less active, and use different habitats (Dahle and Swenson 2003*b*, Swenson 2003, Ordiz et al. 2007). Thus, a dominant female with cubs would rarely meet a subdominant female during the mating season, greatly reducing the possibility for female-induced estrus suppression. Embryo loss and neonatal mortality do not appear to be common in brown bears (Mano and Tsubota 2002); thus, if they mate, they are expected to have cubs.

The pattern reversed at greater distances between neighboring females, home range centroids at 10–20 km, and the probability of a female having cubs was higher when its nearest neighbor had cubs. We suggest that the reproductive suppression of subordinate females declines with increasing distance between females' home-range centroids, which allows synchronizing effects to become evident. Variation in food availability is one factor that might be expected to have a synchronizing effect on reproduction in brown bears, but including the environmental condition index did not significantly increase the model's ability to explain whether or not a female had cubs in a given year. Sæther et al. (1998) also found little environmental variation in the population growth rate of Scandinavian brown bears, suggesting that variation in food is not a major factor for reproduction in this population. Another synchronizing factor could be sexually selected infanticide (SSI), which is a major cause of bear cub mortality in parts of Scandinavia (Swenson et al. 1997, 2001) and is not correlated with food shortage (Swenson et al. 2001). Infanticide usually involves the killing of cubs that the perpetrating male has not fathered and shortens the time to the mother's next estrus (Swenson et al. 1997, Bellemain et al. 2006*a*). Presumably, several females with cubs could be affected simultaneously within the home range of a perpetrating male, because males' home ranges are larger than those of females, and one male overlaps several females (Dahle and Swenson 2003*c*).

The lack of effect of a neighboring female having cubs beyond the distance of 20 km between females may be because that distance is too far for females to influence each other and infanticide by males to influence the reproduction of several females, if that was a synchronizing effect at intermediate distances (10–20 km between females). Male home range size is not large enough to influence several females >20 km apart, as the average radius of male home ranges in Scandinavia is ~16 km (Dahle and Swenson 2003*c*). Also, at distances >20 km apart we may have missed the true neighboring female more often.

The indication of reproductive suppression in brown bears suggests a mechanism for population regulation in the species. According to Wolff (1997), intrinsic population regulation can occur only in species in which females are territorial, offspring-rearing space is limited, and young females exhibit reproductive suppression. Wolff's model predicts that female territoriality, the threat of female infanticide, and the presence of male relatives in the natal home range are the proximate mechanisms for intrinsic population regulation in mammals. Agrell et al. (1998) summarized female mammals' counterstrategies to deter major losses in reproductive success provoked by infanticide. These strategies included aggression, female choice of dominant males, promiscuity to confuse paternity as defense against males, and territoriality, association with kin, and reproductive suppression as defense against females. Most of these strategies have been shown for Scandinavian bears, i.e., association with kin (Støen et al. 2005), female promiscuity, and choice of dominant males (Bellemain et al. 2006*a*, *b*), indications of territorial behavior (Dahle and Swenson 2003*c*, Støen et al. 2006*a*), and delayed primiparity possibly due to reproductive suppression (Støen et al. 2006*b*). Agrell et al. (1998) also included reproductive synchrony as a strategy to avoid loss of young caused by females. Although female-caused infanticide has been widely documented in mammals (e.g., Wolff 1993, Agrell et al. 1998), including brown bears (Hessing and Aumiller 1994, McLellan 1994), we consider it to be relatively uncommon in this species, because most of the known cases of infanticide were caused by males, and in our study areas, the three requirements of SSI were met (Bellemain et al. 2006*a*). Regardless, the threat of female-caused infanticide could delay reproduction by subdominant females until they could successfully rear offspring, as proposed for other species (Wasser and Barash 1983, Wolff 1997). However, female kin clustering and excluding nonkin, as observed in Scandinavian bears (Støen et al. 2005), also should reduce female infanticide by limiting interactions with unrelated females; each female in a kin cluster would maximize her inclusive fitness by not killing young related to her (Hodges et al. 2002). Based on experiments, Ylönen et al. (1990) suggested that mutual familiarity decreased antagonism toward the juveniles, with positive consequences for their survival. Thus, kinship or mutual familiarity between neighboring females might decrease the frequency of infanticide (Ylönen et al. 1997), in accordance with the kin selection theory (Hamilton 1963). In our study areas, the relationship between genetic relatedness and geographic distance between female dyads was strongest within a distance of 40 km and then rapidly disappeared; that distance probably reflected the geographic distribution of closely related females (Støen et al. 2005). The thresholds found in this study, i.e., 10 and 20 km, are well below 40 km and include many related females.

The interval between consecutive litters is an essential reproductive parameter determining brown bear population growth rates (Eberhardt et al. 1994), so reduced reproductive success of young females may influence population regulation. Taylor et al. (1987) emphasized that bear cub production and cub and yearling survival were the most likely parameters to be reduced by density effects. Also, delayed sexual maturity of juveniles recruited into the population is one of the characteristics of increasing and high population densities, which may result from resource limitation or intrinsic, often female-induced, social stress (see Wolff et al. 2002). Bear density was higher in the south (30 bears/1000 km^2) than in the north (11 bears/1000 km^2; Zedrosser et al. 2006), but we accounted for the possible effects of both population and density, and it did not alter the reproductive pattern that we found. In this sense, the lower odds of females having cubs in the north were likely reflective of the longer interval between consecutive litters in the north than the south.

Female reproductive success varies with social rank in many gregarious mammals, including primates, ungulates, and carnivores (Holekamp et al. 1996). Reproductive suppression can occur by endocrine means, with preovulatory stages usually affected, or by behavioral mechanisms, and both types of suppression can be related (e.g., Creel and Macdonald 1995). The social and physiological mechanisms mediating reproductive suppression might be viewed as reaction norms to the social environment, perhaps with sociality in solitary carnivores being more flexible than commonly observed (Dalerum et al. 2006). The results from this study on wild, free-ranging brown bears, a solitary species commonly considered to be nonterritorial, show that social interactions and behavior of large mammals without an obvious form of social organization may be more similar to social species than previously assumed.

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Paper III

Are Cantabrian Brown Bears Recovering?

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Communicating good news and partial success on wildlife conservation to the public is an important task, but suggesting that conservation goals are at hand with scarce or ambiguous evidence can be dangerous, promoting overconfidence and loss of a critical attitude. The critically endangered Cantabrian brown bear (*Ursus arctos*) population (NW Spain) has around a hundred bears in two subpopulations (Zedrosser et al. 2001), all together in barely 7,500 km^2 (Naves et al. 2003). Based on counts of unduplicated females with cubs, Palomero et al. (2007) concluded that the population was recovering. Palomero et al. (2007) estimated a 7.5% annual increase in the western population, and that this trend was a consequence of a reduction in mortality due to enhanced protection. Pérez et al. (2009) found some evidence of connection between both the western and eastern Cantabrian populations isolated for around 10 generations. However, it is unknown if this connection occurred previously but was undetected. These papers bring good news for one of the most endangered brown bear populations in the world (Servheen et al. 1999, Zedrosser et al. 2001), and the last stronghold for the western European lineage, the most ancient one of the Eurasian brown bears (Taberlet and Boubet 1994).

Nevertheless, if a trend estimate of an endangered population is wrong, negative consequences may arise. A type I error could lead to conservation prioritization and action responding to short-term noise rather than a longer term signal, with concomitant waste of scarce resources. However, a type II error can have adverse consequences on the success of conservation efforts because knowledge of the direction and magnitude of trends often determines the immediacy and scope of management action (see Maxwell and Jennings 2005). The paper by Palomero et al. (2007), concluding that the brown bears in the Cantabrian Mountains are recovering, is based on the females with cubs-of-the-year (hereafter F_{CUB}) index for 1989-2004. We argue that both the data set and the analyses used in that paper do not permit those conclusions. We discuss three major factors limiting the interpretation of an increasing trend based on the available F_{CUB} data and extrapolations at the population level: sampling effort during the study period, non-rigorous sampling procedures, and failure to consider alternative biological explanations for observed increases.

Sampling effort increased during the study period

The number of dedicated and qualified bear observers (*sensu* Palomero et al. 2006 and 2007) increased continuously between 1989 and 2004. Using data from Palomero et al. 2006:24 (Fig. 1.3, i.e., the same data analyzed by Palomero et al. 2007), we found a significant exponential increase in the number of observers in both Cantabrian populations. We performed a generalized linear model (GLM) fit with the annual number of observers as the response variable, with Poisson error distribution and a natural log link function. For the western population, the exponential rate of increase of observers was 0.112 (SE = 0.03; $p < 0.001$) during 1994-2004, whereas the bear population increase detected by Palomero et al. (2007) for the same period was 0.072 (SE = 0.036; $P < 0.05$). For the eastern population, the exponential rate of increase of observers was 0.118 (SE = 0.025; $p < 0.001$) during 1989-2004, whereas the population trend of F_{CUB} was not significant (0.0301; SE = 0.046; $P > 0.05$). We argue that, in addition to personnel from non-governmental organizations, an increase in the number of publically employed wildlife rangers among these bear observers also should be considered, as they were responsible of up to 28 % of the F_{CUB} data (Palomero et al 2007: 148). Further evidence of increasing effort is provided by the trend in number of F_{CUB} with > 4 observations/yr in the western population (GLM with Poisson error distribution and natural log link function: $\beta = 0.077$; SE = 0.030; $p < 0.01$; Palomero et al. 2007:149, Table 2). Existence of temporal trends in variance may reflect a trend, an increase in this case, in the accuracy of F_{CUB} annual counting.

Differences in F_{CUB} searching effort (in this case an increase in effort) can have very important consequences. Palomero et al. (2007) justified the exclusion of 1989-93 data from the western population because search effort was considered lower than in later periods. We argue that the detected trends in searching effort should have been specifically and carefully accounted for when estimating the trend of F_{CUB} within the period 1994-2004.

Data collection was not systematic and data sets did not meet probabilistic analytical requirements

Data collection on F_{CUB} in the Cantabrian Mountains was collected in an opportunistic way that was likely to yield repeated observations of some bears. Palomero et al. (2007) "obtained information from hunters and others within the areas occupied by the bear populations" and further "members of the team prospected areas where females with cubs or their sign had been observed". This procedure yields a very special data frequency distribution, very different from distribution frequencies of systematic field surveys (compare Table 2 in Palomero et al. 2007 with Table 4 in Keating et al. 2002; 80% of Yellowstone F_{CUB} were observed $\leq$5 times/ year, whereas in the Cantabrian Mountains 82% of F_{CUB} were observed > 5 times/ year). However, Palomero et al. (2007) used the Chao estimator as a "complementary effort to evaluate if the minimum number of F_{CUB} observed was far from the theoretical value", even recognizing that their data "did not strictly fit the requirements of its application …and the possible bias of the estimator". Given the virtually identical value of the Chao-corrected estimate and the observed one and the low numbers of annually observed F_{CUB}, it would be virtually impossible for them to be significantly different. Nevertheless, Palomero et al. (2007: 146) assumed that F_{CUB} present each year is estimated as the number of such animals actually observed, and used F_{CUB} observed to estimate population trend. They validated F_{CUB} observed with a probabilistic analysis, despite the fact that the distribution of the data was not appropriate for the approach they used. Other researchers also have considered the use of Chao2 estimator to be inadequate for their data sets of F_{CUB} in small populations (Brodie and Gibeau 2007).

Moreover, uncertainty should be addressed in the statistical analysis. The application of count protocols by different teams in the Cantabrian Mountains yielded substantially different results in the number of unduplicated F_{CUB}, which is surprising given the low numbers considered. For instance, the estimation of annual F_{CUB} for 1989-1995 by Wiegand et al. (1998; considering their upper range, see Table 5, p. 549) and by Palomero et al. (2007), i.e. the period in which both studies overlapped, yielded different number of estimated F_{CUB} in five of seven years. The estimation by Wiegand et al. (1998) was 1-2 F_{CUB} higher than that of Palomero et al. (2007) in four years (1989, 1991, 1992 and 1993;

that means a difference of 15%-33% for those years), whereas the estimation by Palomero et al (2007) was 1 F_{CUB} higher in one year (1994; which means a difference of 50% for that year). We feel that these issues should have been specifically and carefully accounted for when estimating F_{CUB} trend.

F_{CUB} trend may not reflect population trend

Biological factors other than population increase can complicate the interpretation of F_{CUB} trend. We think there are no available data to properly assess if F_{CUB} trends reflected true population trends in the Cantabrian Mountains. Although more detailed rule sets improve the criteria to count and distinguish F_{CUB} generally and in the Cantabrian Mountains specifically (Naves et al. 1999, Ordiz et al. 2007, Palomero et al. 2007), important data on reproduction parameters and age and sex structure are lacking. Palomero et al. (2007) suggested that the population trend was a consequence of a reduction in mortality due to enhanced protection. That is only one of several factors that could explain the detected F_{CUB} trend. Since 1996, 4 confirmed and 5 suspected cases of infanticide have been reported, with at least 2 of the affected females having cubs of the year in the following spring (AFG, JN, AO unpublished data). Thus, these females would be included in the F_{CUB} counts in 2 successive years. If the rate of infanticide would had been increasing (there were no observed events prior to 1996), the mean litter interval would decrease, resulting in increasing observations of F_{CUB} even in a stable population. Moreover, the very recent implementation of techniques like digital photography through spotting scopes in the Cantabrian Mountains increases the certainty of F_{CUB} identification, implying a higher probability of distinguishing observations of different F_{CUB} that might have earlier been assigned to the same F_{CUB}. This probably led to a decrease in Type II errors (sightings of different F_{CUB} groups mistakenly classified as the same).

The possible influence of environmental factors should be considered as well. Wiegand et al. (1998) suggested that favorable climatic conditions in the early 1990s might be partially responsible for the slightly positive trend of the Cantabrian population during that period. This has been addressed as a key factor influencing population dynamics in other areas (see Schwartz et al. 2006).

Some of the analyses by Palomero et al. (2007) do not support a conclusion that the population was recovering during 1989-2004. The geographic expansion of the F_{CUB} distribution was weak. The fact that within the considered period (1994-2004) no other temporal window (1995-2004; 1996-2004; 1997-2004…2002-2004) showed significant positive trend, call for a cautious interpretation of the results. We also point out that other analyses have shown a low availability of suitable habitat for the population (Naves et al 2003), which in the long term may be the greatest constraint for the viability of this population.

We recognize the usefulness of the F_{CUB} index, currently the only population index with a long data set to monitor the Cantabrian bear populations. However, one must carefully consider the limitations during data analysis and interpretation, because the trend of the population size does not necessarily follow the trend of the F_{CUB} index (Eberhardt and Knight 1996). We believe that further research is required to determine the trend of the brown bear population in the Cantabrian Mountains and the causes of the observed trend of the F_{CUB} index. We suggest that current population status and analysis of trend could be evaluated by a population viability analysis, but accounting for essential factors such as sampling effort. Thus, the principle of caution should prevail, especially in a critically endangered population, which is the current status of the brown bears in the Cantabrian Mountains.

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Paper IV

Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears

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Abstract Prey usually adjust anti-predator behavior to subtle variations in perceived risk. However, it is not clear whether adult large carnivores that are virtually free of natural predation adjust their behavior to subtle variations in human-derived risk, even when living in human-dominated landscapes. As a model, we studied resting-site selection of a large carnivore, the brown bear (*Ursus arctos*), under different spatial and temporal levels of human activity. We quantified horizontal and canopy cover at 440 bear beds and 439 random sites at different distances from human settlements, seasons and times of the day. Although human densities in Scandinavia are the lowest within bear ranges in Western Europe, we found an effect of human activity; bears chose beds with significantly higher horizontal and canopy cover during the day (07:00-19:00) than at night (22:00-06:00). In the berry season, with more intensive and dispersed human activity, including hunting, bears rested further from human settlements during the day than in the pre-berry season. Additionally, daybeds in the berry season were the most concealed. Large carnivores avoid humans at a landscape scale, but total avoidance in human-dominated areas is not possible. Apparently, bears have behavioral mechanisms to avoid human encounters that resemble those of prey avoiding their predators. Bears responded to fine-scale variations in human-derived risk, both on a seasonal and a daily basis. Also, bears occasionally kill people. Hence, people should avoid areas with dense vegetation to minimize potential interactions with bears, as a safety factor for both species.

Key-words Concealment behavior · Disturbance · Predator avoidance · Predator-prey relationships · *Ursus arctos*

Introduction

In order to maximize their fitness, prey modify their habitat use and movement patterns in response to predators, as they must balance risks (mainly predation) and potential benefits (e.g. foraging; Lima and Dill 1990; Kotler et al. 1991). In a humanized biosphere (e.g. Vitousek et al. 1986), man has become a universal predator. Human activity and developments induce mortality, and human recreation disturbs the dynamics or the eco-ethological characteristics of populations of many animal taxa (Trombulak and Frissell 2000; Blanc et al. 2006). Evolutionary adaptive behaviors have likely arisen after a long coexistence between predators and prey, and it has been argued that disturbance stimuli could even be analogous to predation risk from an evolutionary perspective (Frid and Dill 2002).

Species with large spatial requirements, such as large carnivores, use multiple-use landscapes at a large scale (Noss et al. 1996), and in human-dominated environments a very high proportion of adult mortality in large carnivores is human-induced (Woodroffe and Ginsberg 1998). Thus, large carnivores may alter their behavior to reduce encounters with humans, e.g. by becoming more nocturnal, avoiding areas with high human activity or hiding in dense vegetation (Boydston et al. 2003). It is well documented that prey can reduce their perceived risk and fear via behavioral, morphological or experiential modifications to the same degree that predator behavior can increase the perception of risk in prey (see Stankovich and Blumstein 2005), and prey are able to adjust their anti-predator behavior to fine-degree variations in the perceived risk (e.g. Martín and López 2004). However, it is not clear whether adult large carnivores that are virtually free of natural predation, which may have induced a loss of anti-predator behavior, and only recently (in evolutionary perspective) must cope with humans, are able to flexibly adjust their behavior to subtle variations in human-derived risk.

To address this issue, we used the brown bear (*Ursus arctos*) as a model species. It is the largest carnivore in Europe and North America and is threatened by human-caused mortality, habitat fragmentation and habitat loss (e.g. Servheen et al. 1999). Brown bears need large areas of habitat with sufficient availability of food and cover to satisfy their life-time requirements (e.g. Swenson et al. 2000). The persistence of brown bear populations depends on habitat quality, human density, and human behavior (e.g. Mattson et al. 1996). Indeed, brown bears tend to avoid human activity throughout their range (Mace et al. 1996; Kobler and Adamič, 2000). In a large area that included our study site, Nellemann et al. (2007) found that, for comparable habitat and terrain types, bear density increased substantially with increasing distance to towns and resorts. Bears also avoid humans by altering their temporal use of areas with high recreational activities (Naves et al. 2001; Rode et al. 2006a).

Cover is a key habitat factor that may lower the risk of mortality by reducing the chance of detection and hindering attacks (Mysterud and Østbye 1999), and it is important for many animal groups, including carnivores. For instance, black bears (*Ursus americanus*) select for a mosaic of habitat types that provide cover near food resources (Lyons et al. 2003); badgers (*Meles meles*) need cover for the selection of diurnal resting dens, even in a highly protected national park where disturbance by people is expected to be low (Revilla et al. 2001); hyenas (*Crocuta crocuta*) are able to persist in areas with increasing livestock pressure by relying on dense cover (Boydston et al. 2003); and the availability of cover for resting during daytime is probably the limiting habitat requirement for European lynx (*Lynx lynx*) in human-dominated areas (Sunde et al. 1998). Also, the availability of cover is important in determining how human activities influence brown bear habitat use (e.g. Suring et al. 2006). Bears may adjust to living in human-dominated landscapes by choosing denser habitat when closer to people. Brown bears in the Italian Alps tend to avoid areas of major human activity, and forage most intensively in areas with a high degree of cover (Preatoni et al. 2005).

Prey sensitivity to the risk of predation while resting is shown by the different strategies frequently used, e.g. hiding cryptically in the safest possible areas, orienting the detection senses toward the most likely direction of approach by a predator or forming groups (see Semeniuk and Dill 2005). However, behavioral avoidance of humans by large carnivores is difficult to study, because carnivores occur at low densities and are elusive. Improving our knowledge on animals' adaptive behaviors such as foraging, patch use, and habitat selection can be useful for conservation (Morris et al. 2009). For large carnivores, activities such as feeding (e.g. diet analyses) or movement (e.g. home-range estimations) are better documented than resting site selection, although animals devote much time to resting. For instance, Scandinavian brown bears rest ~12 h a day, with a short (~3 h) resting period in the night and the longest (~9 h) in the day (Moe et al. 2007). Legal hunting is the single most important cause of mortality for brown bears in Sweden and nonhuman-caused mortality accounted only for 13.5% of confirmed deaths of marked animals between 1984 and 2006 (Bischof et al. 2009). Thus, it can be expected that bears are very selective when choosing their daily resting sites, which makes the study of this selection very interesting.

We analyzed the concealment, i.e. horizontal and canopy cover, at resting sites (i.e. beds) of GPS-collared bears at different distances from human settlements, different times of the day, and in relation to seasonal shifts in human activities throughout the non-denning season. We aimed to understand the behavior and requirements of a large carnivore when choosing resting sites at a very fine scale and in relation to human-derived risk. If fine-scale adjustment occurs between bed selection and human-derived risk, we would expect to find that beds were a) more concealed during the day, when humans are more active, than during the night, b) more concealed than random sites, c) more concealed close to human settlements than further away, and d) more concealed in late summer-early fall (when human activity outdoors is most common and includes hunting) than in spring.

Material and methods

Study species and study area

Brown bears are large, omnivorous and shy, and usually use shelter when resting (e.g. Servheen et al. 1999). Here we refer to resting as a daily process, in opposition to denning, which refers to winter hibernation. Although brown bears are primarily diurnal throughout their range in North America (Munro et al. 2006), bears are often nocturnal where human activity is high, both in North America (e.g. Gibeau et al. 2002) and in Europe, where the highest activity levels occur during the crepuscular-nocturnal hours (Kaczensky et al. 2006; Moe et al. 2007). In Scandinavia, the brown bear has been hunted for a long time, trying to eliminate the species for hundreds of years. Bears were protected from hunting on state land in Sweden in 1913, but hunting became legal again in 1943 and has been managed by quotas since 1981 (Swenson et al. 1995).

The study was carried out in 2007 in Orsa Finnmark (Dalarna and Gävleborg counties, central Sweden) near the southernmost distribution of the Scandinavian brown bear population (61ºN, 15ºE). The 2100 km^2 study area is covered with managed productive forest (80%), mainly composed of Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch *Betula* spp. Heather, grasses and berry-producing shrubs dominate the understory vegetation (see Elfström et al. 2008, for further details) and bogs and lakes occupy the remaining area. The human settlements consist of a few scattered small villages (n = 24) and few seasonally used single houses. In 2007, human density in the municipalities ranged from 4.1 to 7.1 habitants.km^{-2} (Statistics Sweden 2008); our study area is located at the lowest density range, with 2 to 150 habitants per settlement. Bear density is about 30 bears.1000 km^{-2} (Bellemain et al. 2005).

Identification of resting sites to be visited in the field

Twenty-two bears were equipped with GPS-GSM collars (Vectronic Aerospace GmBh, Berlin, Germany). For details on capturing and marking see Arnemo et al. (2006) and Arnemo and Fahlman (2007). The collars were programmed to obtain a location every half hour, giving a maximum of 48 locations per 24 h. The coordinates and time were obtained by the NAVSTAR global positioning system (Rodgers et al. 1996). The locations were sent via SMS and downloaded to a 1:50 000 map in the ArcGIS (Geographic Information System) 9.0 software (Environmental Systems Research Institute, Redlands, California, Inc. 2004). We defined a cluster as a minimum of three consecutive locations within a circle of 30 m radius, where the bear spent $\geq$ 1.5 hours. We visited 518 clusters and recorded all bear sign within a 30 m radius set around the most central bear location of those composing the cluster. Most of the clusters (85%) contained at least one bed where the bear had been resting. To avoid doubts, a bed was defined as a resting site (hereafter, bed) only if it contained bear hairs. From late April to October (non-denning season; Friebe et al. 2001), we visited clusters corresponding to nocturnal and diurnal resting periods, $\geq$ 48 hours after the bear used the area, and after we confirmed that no marked bear was there, to avoid disturbance.

Measurement of horizontal and canopy cover

We measured the concealment of the bed closest to the centre of the cluster. A cloth cylinder (60 cm high, 30 cm wide; Ordiz et al. 2009) was placed in the bed and we walked in the four cardinal directions, and in one random direction, to measure the sighting distances (D), i.e. the minimum distance required for the device to be completely hidden (Mysterud and Østbye 1999). Thus, the shorter the D, the more horizontal cover the bed had. The average D value at beds was similar ($t = -0.36$, $n = 440$, $p = 0.72$) when obtained from the random (21.4 $\pm$ 13.8 m; mean $\pm$ SD) and the four cardinal directions (21.2 $\pm$ 10.8 m).

To compare bed site concealment with the surrounding habitat, we also measured D from a random direction at a randomly selected point 50 m from every bed. Canopy openness (CO) was measured above both the beds and the randomly selected point with a densiometer (Lemmon 1956) held on top of the cylinder. The lower the CO, the more canopy cover the bed had.

Temperature might influence the selection of bed sites. We installed a temperature logger (Easy Log OM-EL-USB1, Omega Engineering Inc., Manchester, England) at each of 6 permanent sites to record the temperature every 30 min during the field season. The loggers were placed in the main habitat types present in the study area, i.e. mature forest, intermediate-age forest, young forest, swamp forest, tree-rich bog, and clear cut (from Karlsson and Westman 1991). Finally, at each cluster we measured the distance from the selected bed to the edge of the closest different main habitat type.

Statistical analyses

We used generalized linear regression models to evaluate the effect of the following variables on D and on CO:

1. Day/Night: the core resting periods previously defined for this bear population were 00:00-03:30 and 09:00-18:00 (Moe et al. 2007). For this study, we adjusted them to outdoor human-activity periods, thus considering beds from 07:00 to 19:00 as daybeds; and from 22:00 to 06:00 as night beds. All times refer to GMT + 2 h.

2. Straight-line distance to the closest human settlement permanently inhabited.

3. Daylight length: minutes of daylight for every day within the study period (data from Astronomical Applications Dept, U.S. Naval Observatory Washington, DC 20392-5420).

4. Sex: male (n = 5) or female (n = 17; only 2 females had cubs during the whole season).

5. Age: adult (n = 18 bears $\geq$ 4 years old) or subadult (n = 4 bears < 4 years old).

6. Temperature: we used an average daily value of the 6 temperature loggers, based on values recorded between 01:00-02:00 for night beds; and between 13:00-14:00 for daybeds, as predictor values to be compared with the concealment of every bed.

7. Season: pre-berry (26 April-15 July) and berry season (16 July- 11 Oct). Brown bear behavior, habitat use and movement patterns change seasonally during the non-denning period (e.g. Mueller et al. 2004; Moe et al. 2007). Pre-berry includes the bear mating season (Dahle and Swenson 2003), and the berry season is the period of hyperphagia, when bears eat copiously to gain fat reserves for winter denning (e.g. Farley and Robbins 1995). Also, there is higher human activity in the entire area during the berry season (e.g. berry picking and hunting, including small game, moose *Alces alces* and bear hunting) than in the pre-

berry season. The boundary between seasons was set on 15 July, when berries began to be a main, consistent component in the scats of the bears, based on visual inspection in the field.

The most general models included all of the above variables and meaningful two-way interactions among them. Each model was run separately for D and CO. Because temperature and daylight length were highly correlated (r = 0.87), only daylight length was included in the final selection process, because it was a more explanatory variable in the analyses. Model selection was based on the Akaike Information Criterion (AIC; Akaike 1974) using step-wise removal of model terms until the model with the lowest AIC value was reached. Initially, generalized linear mixed models were used, with individual bear identification as a random effect. However, the random effect was omitted from the final models, because effect size estimates and their standard errors were nearly identical in the models with and without the random effect. We used the non-parametric Mann-Whitney test (*U*) to compare distances between beds and settlements during day and night and between seasons. *P* values lower than 0.05 were considered statistically significant. We used the statistical package R 2.7.0 (R Development Core Team, http://www.R-project.org) in all statistical analyses.

Results

We analyzed the concealment around 440 beds (220 daybeds and 220 night beds), and 439 random sites. Beds corresponded to 22 different bears; 20 ± 13.6 (mean ± SD) beds per individual. The mean distance from a bed to the closest different main habitat type was short, 10.7 ± 7.0 m.

According to our predictions, both horizontal and vertical cover were significantly larger (lower D and lower CO, respectively) at beds than at random sites, at day beds than at night beds, and at beds in the berry season than at beds in the pre-berry season (Table 1). Both horizontal and vertical cover increased closer to human settlements, and with increasing daylight length. Daybeds were the most concealed, especially for horizontal cover during the berry season (Fig. 1), and the odds for D declined 31.7% from night to day.

In the pre-berry season, the distance from bear beds to human settlements was similar for daybeds (1976 ± 1756 m) and night beds (1798 ± 1875 m; *U* = 3958, *P* = 0.28), whereas in the berry season the distance to human settlements was larger for daybeds (2681 ± 2275 m) than for night beds (1944 ± 1762 m; *U* = 11139.5, *P* = 0.002). During the day the bears rested further away from human settlements in the berry than in the pre-berry season

(*U* = 4579, *P* = 0.009), whereas at night the difference between seasons was not significant (*U* = 5174.5, *P* = 0.22).

Discussion

To avoid encounters, detection and capture, prey have developed behavioral defenses against predators. As a metric of wariness, much attention has been paid to the distance at which an individual approached by a predator initiates flight (e.g. Blumstein 2006a). Other surrogates of perceived risk include the amount of activity in the presence vs. absence of predators (Stoks et al. 2003), shifts in habitat choice (Kotler et al. 1991), frequency of vigilance or use of alarm signals (Blumstein 2007) and group size (Heard 1992). Most of these approaches are not strictly applicable for large carnivores (LC), which usually are scarce, solitary, elusive and nocturnal. However, radio-tracking techniques can allow the identification of responses of LC to human pressure, because LC usually avoid humans at a large scale. For example, the location of breeding and rendezvous sites of wolves (*Canis lupus*) depends more on the distribution of villages and roads than on habitat types (Theuerkauf et al. 2003), and Scandinavian bears try to avoid large human settlements and resorts (Nellemann et al. 2007) and select winter dens where human disturbance could be minimized (Elfström et al. 2008). However, total avoidance of people in human-dominated landscapes is not possible. We have used radio-tracking combined with fieldwork to estimate the "fear" (i.e. the perceived risk, sensu Stankovich and Blumstein 2005) of bears towards humans at a finer scale, by measuring the amount of concealment around their temporal resting sites (beds).

Most theoretical approaches assume the risk of predation to be negligible inside refuges, but bears do not use permanent refuges except for winter denning, and even dens are not completely safe. In our area, > 67% of abandoned winter dens had evidence of human activity within 100 m (Swenson et al. 1997). Bear beds are one-use resting sites chosen for rest during some hours, either at night or during the day (see above). For prey species, predation risk varies in space and time, which may be the reason why refuges, such as dense vegetation, are used in a flexible way, depending on the presence/absence of predators (e.g. Sih 1992). Escape theory suggests that prey monitor approaching predators to assess predation risk and will escape only when the risk reaches some level in relation to the cost of escaping (Cooper 2008). If cover is far away, so that the chances of escaping are reduced, an animal may flee sooner than if cover is at hand (Ydenberg and Dill 1986), and escaping implies the loss of benefit that could be obtained by not fleeing, plus costs of emerging, e.g. energetic expenditure or risk of injury (Cooper and Frederick 2007). Thus, presumably bears select beds in a way that avoids detection and the consequential need of fleeing and associated costs. As the human predator is visually oriented, we would expect beds to be as concealed as possible, as with ungulates selecting dense vegetation with limited visibility to conceal their fawns (Bongi et al. 2008). Indeed, we found more dense cover at beds than at random sites and at daybeds than at night beds, which would help bears avoid detection and the costs and risks of fleeing. The use of protective cover is commonly associated with high predation risk; hiding under vegetation may be especially adaptive during the day, because of predation by visually oriented hunters, and it is common that prey species use more open areas during the night than during the day, when they are exposed to visually-oriented predators (e.g. birds of prey; Moreno et al. 1996). Hunted brown bears appeared to show the same behavior.

In the berry season, when the human activity was more common, more scattered and more dangerous (hunting), bears seemed to avoid encounters with people by increasing the distance of their beds to human settlements, by having larger horizontal and canopy cover at daybeds than in the pre-berry season, and by being more active at night (Moe et al. 2007). Bears used denser vegetation for both horizontal and canopy cover at daybeds near human settlements. Interestingly, day/night did not mean light/dark at our boreal latitude (> 9 hours of daylight change in the study period), but rather reflected outdoor human activity (day) vs. human resting periods (night). Mueller et al. (2004) also found that bears in Alberta, Canada, moved away from human development in periods of high human activity (07:00–18:00) and were closer when human activity diminished (18:00–07:00). In our case, daylight length, which was a surrogate of temperature, and the human-associated variables (distance to human settlements and day/night) most influenced bear selection of cover in beds.

Both horizontal and canopy cover were greater at beds than at random sites (only 50 m away from the beds), which suggests a very fine-scale bear habitat selection. In our area, a median habitat patch size of 22500 m^2 suggests an average maximum exit distance of 85 m (Moe et al. 2007). Thus, a median habitat patch size usually would include the random sites 50 m from the beds, unless the beds were near the edges of habitat patches, as actually occurred (10.7 ± 7.0 m to the next habitat type). Indeed, bears use forest edges more than other large carnivores in Scandinavia (May et al. 2008), and Moe et al. (2007) found bear beds in dense habitats with more open surroundings. Likewise, Lyons et al. (2003) often located black bears near edges of closed canopy classes in North America. This could be due to the denser protective cover at edges than in mature stands, which may protect the animals from olfactory predators (e.g. bear hunting dogs) because turbulence and updrafts occur along edges and it has been reported that dogs have difficulty following scent when they cross from one habitat type to another (Conover 2007 and references therein). The use of edges also emphasizes the need for field work to study fine-scale habitat related behaviors. Also, GPS collars recording bear positions every 30 min provided highly detailed information on a 24 h basis, avoiding bias that habitat studies can incorporate if most locations are obtained at certain times of the day (Palomares and Delibes 1992).

A finer approach shows that bears are able to discriminate among different perceived risks. The presence of hunters (annually ~700 big-game hunters plus small-game hunters within the 2100 km^2 study area) and berry pickers likely explained the bears' choice of greater concealment during the day and the larger distances to human settlements in the berry season. The fact that cover at random sites associated with night beds did not differ between pre-berry and berry seasons, but random sites associated with day beds were more concealed in the berry season (Fig. 1), emphasized bear selection of denser habitats, not just denser bed sites, when human activity was more intense and dispersed. However, more openness at night might facilitate monitoring of a potential predator to determine its position and behavior to assess risk (Cooper 2008).

We have shown that the brown bear, like any prey, is able to discriminate among subtle differences of potential risk from the universal human predator. Brown bears have coexisted with *Homo* spp. for at least one million years in Eurasia (e.g. Stiner 1999), but scarcely 10-20 thousand years in North America. Thus, one would expect a greater anti-predator ("antihuman") behavior to have evolved in the Old World than in the New one. For instance, European brown bears show high activity levels during the crepuscular-nocturnal hours, in contrast to some North American populations (see Methods). Nocturnal habits help bears avoid people and likely have allowed them to survive in areas with relatively high human densities, a pattern also observed when comparing Eurasian and North American wolves (Woodroffe 2000). Also, the careful avoidance of people by Scandinavian bears, both on a daily and seasonal basis, depending on perceived risk, could be a result of the long-term human persecution that almost eradicated the species in Scandinavia around 1935 (Swenson et al. 1995) in addition to an effect of the current hunting regime.

The distribution of bears in relation to disturbance has been reported to vary with sex, age and social organization; bears closer to large settlements and resorts (<10 km away) were on average 27–51% younger than in areas beyond (Nellemann et al. 2007). Sexual dimorphism and differing reproductive strategies also led to sexual segregation in habitat use by bears in relation to human disturbance (Rode et al. 2006b). Female ungulates select habitats with more horizontal cover than males (Mysterud and Østbye 1999). We did not find differences in cover related to the age and sex of the bears, but our sample was biased towards adult bears (81%), and mainly females (77%). Intra-specific killing of bears, mostly affecting cubs, has been documented. In Scandinavia, 86% of known cases occurred during the pre-berry, mating season (Swenson et al. 2001), a pattern also observed in North America (Mattson et al. 1992). Thus, our results suggest that all bears prioritized human avoidance over bear avoidance, because the random effect (individual bear identification) did not modify the results, suggesting a general bear behavior to hide further away from human settlements during the day. Also, selected cover was denser in the berry season, whereas intra-specific predation mostly occurs in the pre-berry season.

Therefore, despite the low human density in our area, humans had a clear effect on brown bear selection of cover at resting sites. Bears realized shifts in human activities within very short temporal frames, and responded to the increasing danger posed by humans both on a seasonal and a daily basis, hiding further away and in denser cover when the chance to meet humans was greater, i.e. bears were able to finely adjust their selection to the perceived human-derived risk, suggesting the evolution of fine scale anti-predator behavior in this LC. Given the importance of storing fat during hyperphagia, the essential foraging season for successful bear hibernation and cub production (Farley and Robbins 1995), a large investment in security may also imply foraging costs for the animals (Brown and Kotler 2004).

Understanding the effects of human disturbance on wildlife is critical for its conservation (Kerley et al. 2002). The results of our study, carried out at the lowest human density within the distribution of bears in Western Europe, reinforce the importance of cover for LC and to reduce conflicts with people. Although most encounters between bears and humans result in the bear leaving without incident, several deaths have occurred recently in Scandinavia and elsewhere (e.g. Herrero 2002). Thus, people should be made aware to avoid areas with dense vegetation or rugged terrain, i.e., areas with low accessibility for humans, which appear indispensable for the occurrence and survival of LC (e.g. Naves et al. 2003; Fernández et al. 2006), to minimize potential interactions, as a safety measure for both LC and humans. Behavior can reveal vital information on the status of individuals, populations, habitats, etc., which can be most useful in conservation and management (Kotler et al. 2007). The involvement of managers in the process is essential, so that improved knowledge of behavioral responses can influence conservation (Caro 2007; McCleery et al. 2007).

Our results may be relevant in understanding the pattern of the extinction of mammals and birds after the arrival of humans to America, New Zealand or Madagascar. It has been traditionally assumed that the extinctions occurred in a size-dependent way; large species become extinct but small ones did not, because of the greater profitability obtained from large animals. However, small animals probably possessed adaptive anti-predator defenses to protect them against human predation, sensu the multi-predator hypothesis of Blumstein (2006b). Big animals would have been more naïve because they evolved with fewer predators. Thus, big animals may have been exterminated selectively because they were profitable and naïve. Bears in Scandinavia, and some other European areas, may have survived in some areas because some lived in remote areas far from people, and because some had learned to avoid people both spatially and temporally, as we documented here.

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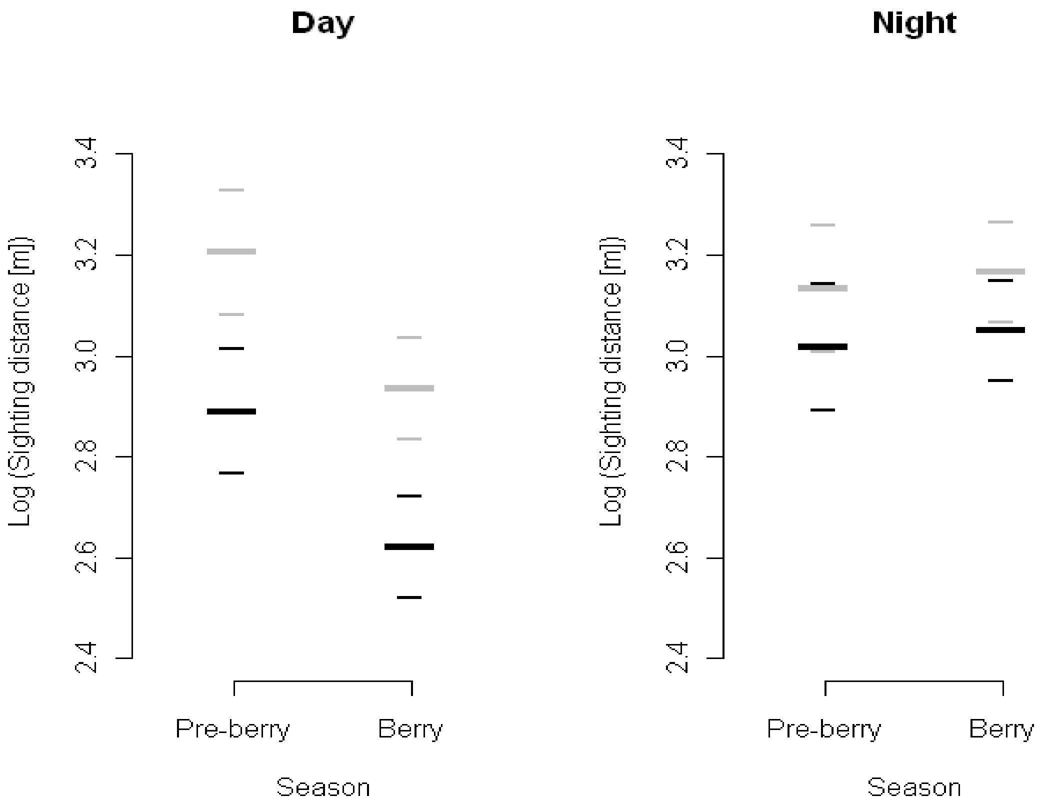
Tables

Table 1. Generalized linear models with the variables affecting horizontal and vertical cover at the resting beds of brown bears in Sweden. The variables, i.e. sighting distance and canopy openness, were log transformed to improve model performance.

Model	β	SE	t statistic	p value
Horizontal cover (log sighting distance)				
(Intercept)	2.936	0.252	11.64	<0.001
Day/Night	0.127	0.078	1.621	0.105
Bed/Random	0.315	0.058	5.417	<0.001
$\log_e$ (Distances to human settlement)	0.057	0.018	3.129	0.002
Daylight length	-0.001	0.000	-2.388	0.017
Season	-0.270	0.075	-3.588	<0.001
Day/Night:Season	0.302	0.085	3.563	<0.001
Day/Night:Bed/Random	-0.199	0.082	-2.416	0.016
Vertical cover (log canopy openness)				
(Intercept)	0.375	0.246	1.525	0.128
Day/Night	0.808	0.072	11.197	<0.001
Bed/Random	0.780	0.073	10.736	<0.001
Season	-0.145	0.062	-2.323	0.020
$\log_e$ (Distances to human settlement)	0.125	0.018	6.788	<0.001
Daylight length	-0.001	0.000	-5.691	<0.001
Day/Night: Bed/Random	-0.603	0.090	-6.725	<0.001

Figures

Fig 1 The horizontal cover measured as sighting distance in meters (mean ± SD) at brown bear resting beds (n= 440; black) and random sites (n= 439; gray), at day and at night, during the pre-berry and the berry seasons in Sweden.



Paper V

A practical method for measuring horizontal cover

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Abstract: We propose a new cover cylinder as a useful tool for a single observer to measure horizontal cover in the field. We compared it with 4 other methods for measuring horizontal cover at brown bear (*Ursus arctos*) beds, with all measurements taken 10 m from beds in the 4 cardinal directions. We also compared cylinder cover values from a fixed distance with an index of cover, namely a sighting distance, *D*, the minimum distance at which the cylinder could no longer be seen; we also compared measurements from a random direction and from the 4 cardinal directions. The cylinder provided measurements comparable to other devices, including a cardboard profile of a bedded bear, and was the most practical to use in the field. Measuring *D* was scarcely more time consuming than measuring cover from the fixed 10-m distance, and *D* is better for statistical analysis. We recommend the cylinder, and using the index of cover, *D*, taken from the 4 cardinal directions, when assessing horizontal cover for bears or other medium and large terrestrial vertebrates.

Key words: bears, cover cylinder, horizontal cover, sighting distance, Sweden, *Ursus arctos*

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Cover, a habitat element that conceals, shelters, or protects, is important for animals; it can protect against weather and lower the risk of predation (Mysterud and Østbye 1999, Ratikainen et al. 2007). Horizontal cover (hereafter, cover) may be an important factor affecting habitat choice, so proper measures of cover in the field are relevant to understanding habitat selection. However, methods to measure cover tend to be inefficient or subject to considerable bias (Collins and Becker 2001). We compared the efficacy of 5 devices used by 1 person to measure cover in the field. Three of these devices were described previously: the table board (Nudds 1977), cover pole (Robel et al. 1970, Griffith and Youtie 1988, Toledo et al. 2008), and cover board (Mysterud 1996). We also tested a cardboard profile of a bedded bear and a new, light, self-supporting, collapsible, easily carried cover cylinder that we designed (Fig. 1). We compared (a) the practicality of these 5 devices for measuring cover at brown bear (*Ursus arctos*) resting sites, (b) cover measurements obtained from the cylinder when standing 10 m from the resting site, versus an index of cover (the sighting distance *D*), the minimum distance at which the cylinder was completely blocked from view, which provides a continuous variable for statistical analysis (Mysterud and Østbye 1999), and (c) results from the cylinder when taking measurements from the 4 cardinal directions versus from 1 random direction. We sought the most effective device and method to quantify horizontal cover that could be applied by a single observer in the field.

Methods

Study area

The study took place in 2007 in Sweden, near the southernmost distribution of the Scandinavian brown bear population (61°N, 15°E). The area was 80% covered with highly managed forest, mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birch (*Betula* spp.). The understory vegetation was dominated by heathers (*Calluna vulgaris*), grasses, and berries (*Vaccinium*

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Fig. 1. The 700-g, collapsible cover cylinder developed to measure horizontal cover in the field measures 60 cm high x 30 cm diameter. The 30-cm upper section is red and the lower section is white (left photograph).

myrtillus, *V. vitis-idaea* and *Empetrum hermaphroditum*). For further details on the study area, see Elfström et al. (2008).

Comparison of methods

We compared techniques to assess cover in an ongoing study on the effect of human disturbance on brown bear resting site selection. To find resting sites, we used data from 22 bears equipped with global positioning system (GPS)-global system for mobile communication (GSM) collars (Vectronic Aerospace GmBh, Berlin, Germany). For details on bear capturing and marking see Arnemo et al. (2006) and Arnemo and Fahlman (2007). We defined a bed as a resting site (hereafter, bed) only if it contained bear hairs.

We used the following devices to measure the cover of beds:

1. Table board (Nudds 1977): originally 1.5 m high, 30 cm wide, divided into 3 50-cm sections. To compare it with other devices, we only used the lower 2 sections (upper red, lower white; hence, it was only 1.0 m high for this study).
2. Cover pole (Griffith and Youtie 1988): 1 m high, 2.5 cm wide; 10 alternating black and white 10-cm bands.
3. Cover board (Mysterud 1996): 30 cm high, 40 cm wide; 40 black and white grid cells, 6 x 5 cm each.
4. Cardboard profile of a bedded bear (modified from a bear profile published by the Swedish Association for Hunters and Wildlife Management): 40 cm high, 120 cm long.
5. Cover cylinder (designed by us): 60 cm high, 30 cm in diameter, with 2 30-cm sections, upper red and lower white, collapsible and made of steel spring wire and light cloth (Fig. 1).

We placed all devices consecutively inside the bed and estimated how much of each device was visible. The same observer took all the measurements at each bed to avoid individual bias and to standardize the same height from which all the measurements were taken. For the table board, the cover pole, and the cover cylinder, we obtained separate values for upper and lower sections. We divided the cover pole into an upper and lower section with 5 bands each. We gave a score to all the devices and sections, except the cover board, according to the percentage that was visible: 1 if <25%; 2 if 26–50%; 3 if 51–75%; and 4 if >75% visible. For the cover board, we counted the number of squares totally visible (Mysterud 1996). To compare devices, we took all measurements at 10 m from 43 bear beds, from the 4 cardinal directions (Nudds 1977, Griffith and Youtie 1988). Secondly, using the cover cylinder we measured *D*, the minimum distance at which the device could no longer be seen, at 439 beds from 1 random and the 4 cardinal directions. That is, *D*

Table 1. Linear regression with the cardboard bear, i.e. the device that most accurately represented the shape of a resting bear, as response variable, and the alternate methods as predictors (cover board, cover cylinder, cover pole, and table board).

Model	β	SE	*t*	*P*
Cover board ($R^2 = 0.77$)				
Intercept	0.336	0.031	10.805	<0.001
Cover board	0.906	0.092	9.845	<0.001
Cover cylinder ($R^2 = 0.74$)				
Intercept	0.044	0.062	0.71	0.484
Cover cylinder	0.794	0.087	9.094	<0.001
Cover pole ($R^2 = 0.53$)				
Intercept	0.148	0.08	1.835	0.077
Cover pole	0.660	0.116	5.701	<0.001
Table board ($R^2 = 0.49$)				
Intercept	0.106	0.094	1.124	0.27
Table board	0.671	0.127	5.271	<0.001

readings reflected the distance at which the cylinder was completely covered.

To obtain a cover value for each device and bed, we added the values from the 4 cardinal directions and calculated the observed percent of the maximum possible value (i.e., the value that would be obtainable without any cover). To compare the measurements obtained with different devices, we used linear regression models with the cardboard bear as the response variable, given that this was the most accurate representation of the shape of a resting bear, and the alternate methods as the predictor variable. To compare the 10-m fixed distance vs. *D*, we correlated the average value obtained from the 4 cardinal directions at 10 m and *D*. Finally, we compared (paired *t*-test) *D* from a random direction and from the average value of the 4 cardinal directions. We used the statistical package R 2.8.1 (R Development Core Team 2008) in all statistical analyses

Results

The upper sections of the table board, the cover pole, and the cover cylinder were on average 19% more visible at the 10-m distance than their respective lower sections (16% for the table board, 20% for the pole and the cylinder). From the results of a linear regression analysis, the visibility of the cover board and the cover cylinder showed the highest correlation ($R^2 = 0.77$ and $R^2 = 0.74$ respectively) with the cardboard bear (Table 1; Fig. 2).

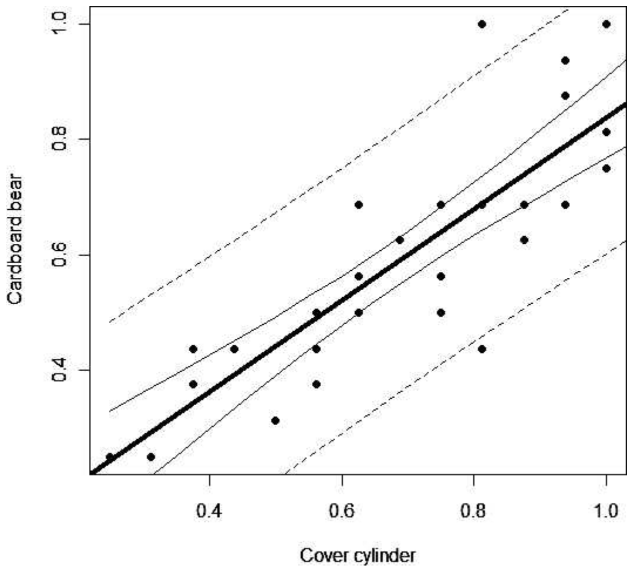

Fig. 2. The linear relationship (thick line) between the measurements of cover obtained with the cover cylinder and the cardboard bear ($R^2 = 0.74$). Dashed lines represent the 95% prediction intervals and solid lines the 95% confidence intervals.

Because of the ease of use of the cover cylinder (see Discussion), we used it for further comparisons in 439 beds. The measurements ranged from 0% (the devices fully covered by vegetation) to 100% (the devices fully visible). The lower section was fully covered more often than the upper section (7.7% versus 2.5%); thus, for comparative purposes we only show results from the upper sections. The correlation coefficient between cover values at 10 m and *D* was 0.75 when using the average *D* of the 4 cardinal directions, and 0.48 when using *D* from a random direction. The average *D* was similar (paired *t*-test: $t = -0.36$, $n = 439$, $P = 0.72$) from a random direction (21.4 m, SD = 13.8 m) and from the 4 cardinal directions (21.2 m, SD = 10.8 m), and the correlation coefficient between them was 0.51.

Discussion

A single observer had problems using 3 of the 5 devices. The table board was heavy (5 kg), and had to be held in the vertical position. The cover pole was lighter (1 kg) and easier to carry, but did not stand by itself on hard substrates and often required help from a second person. The cardboard bear was impractical to put up, required a second person to hold it, and frequently did not fit well inside the beds. In addition, it broke quickly with daily use under outdoor conditions. The cover board required time to count the squares and a second person to hold it. The cylinder and the cover pole were circular, allowing observation from different directions without turning the device, which was necessary for the other devices. The cover pole may require interchangeable spikes to stand by itself on different substrates (Toledo et al. 2008), a disadvantage compared with the light (700 g), self-supporting cylinder, which was the easiest to transport and use. The high and similar relationship between the cover board or the cylinder and the cardboard bear (Table 1) suggested that device selection was more constrained by practical reasons than by measuring accuracy. Given the cylinder's practicality, we consider the cylinder as the best option to measure horizontal cover.

The average *D* was 21.2 m (SD = 10.8 m), which was only twice the 10-m fixed distance. In practice, measuring *D* was not much more time consuming and provides a continuous variable for more rigorous statistical analysis (Mysterud and Østbye 1999). This also avoided the use of more subjective categorical values that must be given to the observed portion of the device from a fixed distance. In addition, the fixed distance should be changed depending on the study area or vegetation types (Nudds 1977, Collins and Becker 2001), which causes difficulties in comparing results from different study areas or vegetation types. Averaging 4 directions gave a better concealment description than using only 1 direction, maybe because beds were often close to a tree or large rocks. This is probably reflected by the higher correlation between measures at 10 m and average *D* of 4 directions ($r = 0.75$) than 10 m versus a random *D* ($r = 0.48$). Although the average *D* value was similar from a random direction (21.4 m, SD = 13.8 m) and from the 4 cardinal directions (21.2 m, SD = 10.8 m), the relatively low correlation coefficient ($r = 0.51$) may indicate that 4 readings provided more accurate information than only 1. Readings from 4 cardinal directions are frequently used (Griffith and Youtie 1988), but using only 1 random direction is also advised (Mysterud 1996, Mysterud and Østbye 1999). Directional values are useful when describing specific characteristics of cover, such as testing whether the animal had more cover in the direction of prevailing winds or better vision in open habitats (Mysterud and Østbye 1999). Depending on study areas characteristics, measuring *D* from 4 cardinal directions or from a random direction is a trade-off among accuracy, effort, and objectives.

Management implications

Measuring cover quickly and reliably in the field is important, because projects normally have cost and time constraints. We recommend the cover cylinder as a practical device that is useful for a single observer. Other methods, including the improved design of the cover pole described by Toledo et al. (2008), are not self-supporting on bedrock or other impenetrable surfaces, thus requiring 2 people to take measurements. Device size depends on species and study area (Nudds 1977, Toledo et al. 2008), but the proposed 60 cm high x 30 cm in diameter cylinder may be practical for studies of many medium to large terrestrial vertebrates, including all bear species. Also, the cylinder is very quick to use, because it opens and folds quickly due to its steel spring wire structure.

Interpretation and comparison of data collected can be confounded by inconsistent design and measurement criteria. It is advisable to ensure taking measurements from the same height if several observers participate, or if comparisons are to be made among studies carried out by different researchers (e.g. Toledo et al. 2008).

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Paper VI

Behavioural effects of hunting in a large carnivore

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Abstract Non-lethal, behavioural effects of predation may be more influential on the dynamics of prey species than direct demographic, lethal effects. Human recreation, especially hunting, can also force prey to increase vigilance and can influence distribution and habitat use even more than predation by natural predators. Demographic consequences of hunting are well documented for large carnivores (LC), but behavioural effects of hunting on LC dynamics remain unexplored. Whereas prey species evolved anti-predator adaptations under natural predation in multi-predator systems, LC have had less time at evolutionary scale to adapt to a specific predator, modern humans, who caused LC extinctions and population reductions in wide areas of their former distribution. This is of special interest, given the potential apex role of LC in the ecosystems they inhabit.

We studied the movement patterns of brown bears (*Ursus arctos*) in Scandinavia as a model species, before and after the start of the annual bear hunting season. Bears increased movements in 9 of the 48 daily half-hour periods after hunting started. The largest effect was in the morning (06:00-09:00), when hunting effort was highest; 51% of 104 bears were shot during that period in 1998-2008. Bears modified their movement pattern in a critical time of the year, during hyperphagia, when they must store fat reserves before hibernation. Non-lethal effects of hunting should be a relevant issue for the conservation and management of LC, most especially when hunting occurs in highly sensitive periods of the year. This concern applies to many species under hunting pressure.

Key words: behaviour, conservation, disturbance, hunting, large carnivores, mortality, movement

Predation causes mortality, but also predation risk potentially affect population dynamics indirectly by forcing animals to invest in anti-predator behavior and thus discard more profitable activities (e.g. Lima 1998; Frid & Dill 2002). Animals may perceive human recreation, especially hunting, as a predation risk that forces them to increase vigilance (Jayakody et al. 2008) and may influence their habitat use and distribution even more than predation by natural predators (Theuerkauf & Rouys, 2008). In addition to direct demographic consequences, risks caused by hunting can induce non-lethal effects on the behavior of animals (e.g. Valeix et al. 2009). Non-lethal effects of predation risk, also referred to as indirect, trait-mediated or non-consumptive effects, are now recognized as common and large for many taxa (e.g. Preisser & Bolnick 2008), and include temporal and spatial changes in activity patterns, increased vigilance, and reduced foraging time (Fenn & Macdonald 1995; Abramsky et al. 2002; Brown & Kotler 2004). Indeed, non-lethal effects can even drive trophic cascades (e.g. Schmitz et al. 2004) and can be even more important for population dynamics of prey than direct demographic, lethal effects; however, they are rarely considered in conservation or wildlife management (Creel & Christianson 2008).

Recognition of the importance of the non-lethal effects of natural and human predation applies to a large variety of prey populations (e.g. Madsen 1998; Preisser et al. 2007; Stankowich 2008). However, predator-prey and predator-avoidance theory may also provide insight into the effects of human activity on wildlife (Frid & Dill 2002). Such an approach may be useful to study the effects of human hunting on large carnivores (hereafter, LC). Compared with the evolutionary arms race between prey and their predator species (Vermeij 1987), there has been less time for co-evolution between LC and modern humans, e.g. ~40 000 years in Europe and ~15 000 in America (Olson 2003). Thus, whereas prey species evolved anti-predator adaptations under natural predation and in multi-predator systems (Sih et al. 1998), LC have had less time to adapt to a specific predator, modern humans. A very high proportion of adult mortality in the LC guild is human-induced, i.e. hunting has direct and large demographic effects on LC (e.g. Woodroffe & Ginsberg 1998) and has caused population reductions and extinctions of LC worldwide. Where predation exerts a strong influence on prey demography, individuals often alter their daily behavior (e.g. Berger 1999 and references therein). Thus, it can be expected that hunting induces non-lethal effects on LC, as has been shown in other mammals (e.g. Pauli & Buskirk 2007). Assessing the nature of the large and increasing alterations that humans cause to trophic interactions requires an understanding of how demography and behavior are altered (Searle et al. 2008). Thus, studying the effect of hunting on LC behavior and, indirectly, on LC population dynamics is of special interest given the regulatory role that many LC play in the ecosystems they inhabit (e.g. Ale & Whelan 2008).

We explored non-lethal, behavioural effects of hunting on brown bears in Scandinavia as a model species. Legal hunting is the single-most important cause of mortality for brown bears in Sweden and natural mortality (i.e. nonhuman-caused mortality) accounted only for 13.5% of confirmed deaths of marked animals between 1984 and 2006 (Bischof et al. 2009). Brown bears in Sweden are exposed to annual hunting seasons in a critical period of the year, the hyperphagia period. Brown and black bears (*U. americanus)* eat copiously in summer and autumn to achieve fat reserves for hibernation and reproduction (e.g. Welch et al. 1997). In that period, most bear populations rely on soft and hard mast, e.g. berries and acorns, both in North America and Europe (e.g. Rode & Robbins 2000; Naves et al. 2006). In central Scandinavia, 92% of the scats analyzed in the autumn contained berries, which represented ~81% of the annual digestible energy (Dahle et al. 1998). However, bears consuming berries are constrained by fluctuations in berry availability and physiological factors (e.g. Welch et al. 1997).

In North America, bears are primarily diurnal (e.g. Munro et al. 2006), and are active for up to 17–18 hours/day during hyperphagia, feeding ~80% of the time (Welch et al. 1997).

In Europe, bears are active only ~12 hours/day during hyperphagia, with a marked resting period at mid-day and the highest activity levels occur during crepuscular and nocturnal hours (e.g. Moe et al. 2007). The reasons for these differences may be related to the more intensive and long-term persecution of LC in Europe, where human populations are denser and have been present much longer (Woodroffe 2000). Therefore, bears in Europe may be more constrained in the time they can spend feeding daily. Additional limitations posed by outdoor human activities, including hunting, which usually are most intense during summer and autumn, may affect bear behavior in a highly critical period by reducing the time bears allocate to feeding or resting in order to increase vigilance or fleeing. This may leave the animals unable to utilize a spatial or temporal resource to its full potential, as has been documented in a variety of animals (see Kitchen et al. 2000).

Annual brown bear hunting seasons start on 21 August in Sweden and bears are hunted until quotas are filled after a period of ~2 months. The mean date of den entry for female bears in our study area is 28 October (Friebe et al. 2001). This means that hunting encompasses ~65% of the hyperphagia season (which starts in mid July, see Methods) for females, and even more for males, which enter dens later. Even if bear hunting is stopped due to filled quotas, bears still encounter moose (*Alces alces*) hunters. The moose hunting season lasts until bears have denned, and even longer, and the hunters have traditionally used the same dogs and hunting techniques for moose as for bears. Behavioural responses to humans may be energetically expensive and disruptive to bears (McLellan & Shackleton 1989). This is especially important in northern ecosystems, where bears hibernate 5-7 months per year (e.g. 100% of 603 radio-collared bears monitored in Scandinavia during1984-2008 hibernated), and require a large storage of fat. The body mass of Scandinavian bears increases dramatically from spring to autumn, before hibernation starts; ~65% increase for adult females, ~35% increase for adult males (Swenson et al. 2007).

We compared the diurnal movement patterns of bears in the week prior to hunting with those during the first week of hunting, and examined relationships between changes in movement patterns and hunting-related mortality of bears. An eventual alteration of bear movement patterns after hunting started would increase the constraints posed to bears by a berry-based diet. Also, to conserve exploited species is important to understand their behavioural responses to hunting and to incorporate such knowledge into models to predict their future vulnerability (Croes et al. 2007). Our study may help reveal the existence of behavioural effects of hunting on LC, which should be taken into account for their conservation and hunting management.

METHODS

Study species and study area

The brown bear is one of the few large-bodied monogastric animals that obtains most of its energetic requirements from plants, which forces bears to spend a high proportion of their daily activity on feeding (Naves et al. 2006). There are two main periods of brown bear activity and one of inactivity within the year (e.g. Ordiz et al. 2007). The first active period, after leaving the den in early spring, includes the mating season, which in Europe lasts until early July (Dahle & Swenson 2003). Bears may gain little or even loose body mass during this period (Swenson et al. 2007). Afterwards, from mid-July to den entry in October, is the season of hyperphagia (e.g. Nielsen et al. 2004; Moe et al. 2007), when bears accumulate fat. From late October to early spring the bears hibernate and live from the fat reserves.

The study area was situated in Dalarna and Gävleborg counties, south-central Sweden (61º N, 18º E) and covers the southern part of the southernmost brown bear subpopulation in Scandinavia. Elevations range from ~ 200 m in the southeast to ~ 1000 m in the west. Most of the area is below the timberline, which is at ~ 750 m. Lakes and bogs are common, but most of the hilly landscape is covered with intensively managed coniferous forest, dominated by Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*). Heather, grasses and berry-producing shrubs dominate the understory vegetation (see Elfstrom et al. 2008 for further details). In 2007, human density in those counties ranged from 4.1 to 7.1 habitants/km^2 (Statistics Sweden 2008); our study area is located at the lower density range, with 2 to 150 habitants per settlement, the lowest human density within brown bear ranges in Western Europe.

Capture, handling and radiotelemetry

All brown bears in this study (30 females, 5 of which had dependent young in certain years within the study period, and 12 males) were captured as a part of a long-term project on brown bear ecology in Scandinavia (e.g. Swenson et al. 1997). Radio-marked brown bears were darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark). For ethical reasons we did not capture females with cubs-of-the year. In the case of females with yearling offspring, the standard capture procedure was first to immobilize the yearling and then the mother. We used helicopters because it is the only method that allows continual recapture of individuals (Zedrosser et al. 2007). All captures were carried out in mid-April in the southern study area, shortly after the bears emerged from their winter dens, to avoid the danger of drowning in open water and high ambient temperatures. To avoid stress and physiological side-effects (hyperthermia) during immobilization, we kept intensive chasing very short; the average time from the initial sighting of an individual from the helicopter until it was fully immobilized was 8.4 min (Zedrosser et al. 2007). We used 2.5 mg of tiletamine, 2.5 mg of zolazepam and 0.02 mg of medetomidine per kg body mass to immobilize the bears (Arnemo et al. 2006). Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg of medetomidine; Kreeger and Arnemo 2007). A family group was always processed at the same location at the same time, and recovery from anaesthesia was timed so all individuals recovered at approximately the same time. Bears were equipped with GPS-GSM collars (Vectronic Aerospace GmBh, Berlin, Germany), programmed to obtain a location every half hour, yielding a maximum of 48 locations per 24 h. The coordinates and time were obtained by the NAVSTAR global positioning system (Rodgers et al. 1996). The weight of the collar varied from 520 to 1570 gr. depending on the weight of the bear, and represented from 0.8 to 2% of the weight of the bear. There is no evidence of adverse effects of the collars on the bears. Within the long-term research project on brown bears in Scandinavia the capture-related mortality rate is 0.9% (N=1079), the lowest among Scandinavian large carnivores, and none of 10 deaths was related to the collar (Arnemo et al. 2006). The project uses an experienced professional capture team (including veterinary surgeons) and a specific capture protocol (Arnemo and Fahlman 2008). All capture and handling were approved by the appropriate Swedish ethical committee (Uppsala Djurförsöksetiska Nämd). For further details on bear capturing and marking, see Arnemo et al. (2006) and Arnemo & Fahlman (2008).

Study period

We compared the movement pattern of the bears during the week prior to hunting and the first week of hunting, from 2003 to 2008. The moose hunting season starts in September, thus bear hunters were the only large-game hunters present in the field during our study periods. Summing all bears and days, the 42 bears were followed a total of 940 days; 475 in the week prior to hunting and 465 in the first week of hunting. Each day was divided into 48 periods of 30 min. Distances were calculated as the straight-line distance between subsequent GPS-locations at 30-min intervals for individual bears. Lacking GPS locations due to low GPS coverage (see Moe et al. 2007) resulted in lacking distance calculations for two periods, both before and after the lacking GPS location. This reduced the number of distance calculations from a potent of 45 120 to the 25 395 that we used in the study.

Statistical analysis

We chose a Bayesian approach to analyze the data, in order to deal with the relatively large amount of missing data, the repeated measurements of individual bears with dependence between measurements, and because the measurements within 24 hours were likely to be time-correlated. We used a linear model, where the response variable (square root of distance) was assumed to be a function of a random bear effect (42 levels), and the following fixed effects: time interval (48 levels), hunting period (before and after start of hunting), age effect and day length (both continuous variables), and family structure (3 levels). Since males do not have dependent young and most females were without dependent young, the two variables holding information on gender and whether the bear had dependent young or not, were partly confounded. We therefore combined these two variables into a new "family structure" variable (0= male, 1= female without dependent young and 2 = female with dependent young). The time correlation was included in the model by assuming that the time effect of a given time interval depended on the previous time interval using an autoregressive (AR1) structure on the time effects. The random noise term of the model was assumed to be normally distributed with zero expectation and a variance depending on the time of the day and hunting. Finally, the random bear effects were assumed to be normally distributed.

The unknown model parameters were estimated by Bayesian posterior means using Markov Chain Monte Carlo (MCMC) methods, implemented in the software WinBUGS (Lunn et al. 2000). The estimated posterior distributions for the model parameters provided point estimates (mean) and uncertainty intervals (as lower 2.5% and upper 97.5% percentiles of the estimated distribution). We considered effects to be statistically significant if the uncertainty intervals of the corresponding parameters did not contain the zero value.

The MCMC approach for parameter estimation is an iterative process allowing the missing values to be predicted by the given model and the current estimates of the unknown model parameters (data augmentation). By the MCMC estimation method it is also straight forward to obtain posterior mean estimates and uncertainty intervals for any combination of the main model parameters. We used this possibility to study derived parameters, including the time-dependent differences in the effect of hunting period and the time-dependent ratios of variance coefficients. The variance coefficients can provide information on whether the bears showed more variable behavior after hunting started. In order to evaluate model fit, we used the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002), as well as the significance considerations of the individual parameters. The DIC is a MCMC counterpart to the more familiar AIC and BIC criteria and a smaller value indicates better model fit.

RESULTS

Initial analyses were conducted to determine whether the error terms could be assumed to have common time-dependent variance before and after hunting started. The reduced model had a DIC of 170 489, whereas the full model had a DIC of 170 476, indicating that the variation in travelled distances was different before and after hunting, at least for some time periods of the day. Furthermore, the full model fit indicated that age and day length were non-significant (the zero value was well inside the 95% uncertainty intervals). DIC for the reduced model without age and day length effect was 170 473, indicating that these two variables could be removed from the model. The model used in the final analyses, therefore, was reduced to only include random individual bear effects, time-dependent hunting effects, and family structure effects.

During the week prior to hunting, bears showed the highest movement levels during crepuscular and nocturnal hours, with marked resting periods at mid-day and during the darkest part of the night (Fig. 1a). During the first week of hunting, bears moved significantly more in the morning, in 6 of 7 half-hour periods from 06:00 to 9:30, and in the evening, in 3 of 7 half-hour periods from 16:00 to 19:30 (Fig. 1b). This change in behavior corresponded in time with the hours in which most bears were killed in the first week of bear hunting during 1998-2008 (n= 104 killed bears) in Dalarna and Gävleborg counties (Fig. 1c). The periods with significantly larger movements after hunting started comprised 19% of the day and 51% of the bears where shot then, especially in the morning (48 % of shot bears) between 06:00 and 09:00 (12.5 % of the day). Overall, females with dependent young (n= 5) moved on average 3.17 m more per 30 minutes than males (95% CI=0.72, 7.24) and 2.99 m more per 30 minutes than lone females (95% CI=1.49, 5.02).

The variance of the noise term was different after hunting compared to before, at least for some hours of the day. However, these differences may be due to a general increased level of distance travelled by the bears after hunting started (heterocedastic noise depending on the expectation level). The ratio of the time-dependent variance coefficients (after/before hunting) was not significantly different for 47 of 48 time points. Hence, it did not appear that the initiation of hunting increased the variation in how the individual bears moved in 30-minute intervals, but it seems that there was a general increase in movement rates associated with the increased disturbance in the forest.

DISCUSSION

The beginning of the hunting season had a clear influence on the daily movement patterns of brown bears. During summer, before bear hunting started, bears in our study area showed a marked daily resting period between 09:00 and 18:00, with foraging periods before and after, and a ~3 h resting period after midnight (Moe et al. 2007), i.e. the pattern that we found for the week before hunting (Fig. 1a). This pattern changed after hunting started, because bears increased their movements both in the morning (from 06:00 to 09:30, time allocated for foraging before hunting started) and in the evening (from 16:00 to 17:30, time allocated for resting before hunting started).

Bears consuming berries are highly constrained by fluctuations in berry availability and factors such as intake rate, physiological capacity of digestion, and metabolic efficiency of gain in body mass (Welch et al. 1997). Indeed, bears may have difficulty meeting their energy requirements on diets of vegetation, because of the combination of their large absolute energy requirements, limited foraging time, relatively small bite size, and the low protein content of fruit, which increases energy metabolism (Rode & Robbins 2000; Rode et al. 2001). Bears feeding only on fruits during hyperphagia have higher maintenance cost and lower efficiency of growth compared to bears feeding on mixed diets of protein (e.g. salmon) and fruits. In fact, bears that fatten on fruits without access to salmon are 50% smaller than salmon-feeding bears, which ingest >7 times more digestible energy per hour than fruit-feeding bears (Robbins et al. 2007). Berry-based diets are the most common for brown bear populations inhabiting boreal latitudes, both in North America and Eurasia (e.g. Dahle et al. 1998; Nielsen et al. 2004; Mineev 2007). Basically these are the brown bear populations managed under hunting-regimes. Given the absolute importance of storing fat during hyperphagia, which is essential for successful hibernation and cub production (Farley & Robbins 1995), increasing movement patterns after hunting starts constitutes a non-lethal effect of hunting that adds to the limitations of a berry-based diet. There was no compensation in the time that bears could allocate for foraging, i.e., the bears did not increase their movement during night (00:00 - 03:00), maybe because they need light to feed on berries.

Ruminants can reduce the costs of vigilance by chewing food during vigilance bouts, which is possible when food is concentrated in space and unconcealed (Benhaiem et al. 2008). However, bears feeding on berries move constantly, presumably at an optimum rate for many hours a day, to feed only at sites with the highest berry densities, cropping the most visible berry clusters, to maintain high intake rates (Welch et al. 1997). This requires full attention to locate and pick berries in the foliage and would reduce bears vigilance while feeding. At viewing sites in Alaska, bears that were not displaced by tourists devoted more time to vigilance and reduced time for foraging (Rode et al. 2006).

Animals may modulate the risk of predation through behavioural means, such as apprehension, i.e. directing attention towards ascertaining the types and whereabouts of predators, time allocation, and vigilance, which implies costs for other essential behaviours, e.g. foraging and resting (e.g. Brown & Kotler 2004). For instance, prairie dogs *(Cynomis ludovicianus)* subjected to hunting increased alertness eightfold and decreased foraging and resting sharply after shooting started, with dramatic consequences at population-level processes (Pauli & Buskirk 2007). The levels of anti-predation behavior in response to a given level of predation risk can change instantaneously (Ydenberg & Dill 1986), and over evolutionary time (Cresswell 2008). Nocturnal activity patterns of European LC (e.g. brown bears and wolves, *Canis lupus*), compared to their North American counterparts (Woodroffe 2000), could be interpreted as a relatively recent, but adaptive behavior to avoid visually-oriented hunters. This may explain the marked daily resting period of bears in Europe (e.g. Kaczensky et al. 2006). After hunting started, the collared bears increased the daily feeding-movement rate that they had before hunting, in the periods (19% of the day) when 51% of the killed bears were shot in the area in 1998-2008. This likely show that bears were most disturbed when the hunting effort was highest. Hunters often use dogs to track and locate the bears or shoot bears while waiting at posts (Bischof et al. 2008), thus bears may have been forced to move more after hunting started to avoid both dogs and hunters. None of the collared bears we followed were killed during the first week of hunting, but, in addition to the physiological expenses generated by the increased movement, threats may increase metabolic rates (Abrahams & Dill 1989). Prairie dogs, as bears, also survive the winter on somatic stores, and even during and after shooting the juveniles tended to remain above ground, probably because they needed to increase body mass to survive the winter (Pauli & Buskirk 2007). We did not find any effect of age or daylight length in the comparison of movement patterns, but females with young (n=5) generally moved more than lone females or males. Although the sample size of females with young was low, this might be because they segregate spatially and temporally from other bears, sometimes occupying areas less secure (e.g. closer to people; Mueller et al. 2004) or less rich in food, which may have induced larger movements.

Hunting is often considered a necessary part of wildlife management and conservation, e.g. providing justification for protection of wildlife habitats and maintaining populations at desired levels. However, hunting may have negative demographic effects beyond the killing of individuals (e.g. Swenson et al. 1997; Packer et al. 2009). To conserve exploited species, it is important to understand their behavioural responses to hunting and to incorporate such knowledge into models to predict their future vulnerability. Targeted animals may adjust their daily activity patterns to prevent encounters with humans. This may affect the distribution, dispersal patterns, and social organization of hunted species (e.g. Croes et al. 2007). Non-lethal effects can result in a lack of a linear relationship between mortality and harvest rate or between responses of prey with predator numbers. This can have important consequences for understanding population dynamics and management; i.e., the effects of predation, including hunting, can only be determined by considering both non-lethal and lethal effects (Cresswell 2008). According to the results of our study, these concerns may well apply to the hunting of LC. Also, non-lethal effects may be particularly strong in large-bodied and long-lived species (Heithaus et al. 2008), which LC, especially brown bears, are.

Hunting seasons often overlap with important phenological periods of the year, such as ungulate hunting during rutting seasons or bird hunting along migratory routes, which can reduce the rate of fattening and forthcoming reproduction (Fox & Madsen 1997; Bechet et al. 2004). It has also been shown that driving hunts for ungulates in the autumn disturb bears, and thereby induce nutritional stress in an essential foraging season (e.g. Mertzanis et al. 2005). In southern Europe, Naves et al. (2006) recommended that oak (*Quercus* spp.) forests and berry fields should receive high conservation priorities as critical bear foraging habitats, and hunting pressure for wild boar should be reduced there to decrease disturbance of bears. In North America, Rode et al. (2001) suggested that issues such as competition with domestic livestock or security (e.g. opportunity to feed throughout the 24-h day) must be addressed to provide essential foraging opportunities for bears. In addition, bear-human interactions might be curtailed by recognizing important foraging sites and reducing human activities in those areas. Legal hunting is the single most important cause of bear mortality in Sweden, especially since 1998, when harvest quotas increased (Bischof et al. 2009). Hunters aim to kill bears before the quota is filled, which generates a large hunting effort in the first week of hunting, a phenomenon also reported elsewhere (e.g. Ruth et al. 2003). In Scandinavia, bears gain more body mass before hibernation and lose more during hibernation than southern European bears, probably because hibernation is twice as long in Scandinavia (Swenson et al. 2007). Given the effect we found of hunting on bear behavior, the importance of hyperphagia for bears, and the large overlap of hunting and the hyperphagia season, hunting managers should consider reducing disturbance as much as possible, either by reconsidering hunting methods or hunting periods. This can also apply for other species and areas under hunting regimes that result in a sudden increase of mortality and disturbance at the beginning of hunting seasons, either for singular or multiple species. Hunting can probably create a general disturbance that differs from other human activities, because it takes place over large and more inaccessible areas, where the presence of people is not otherwise common.

The impact of intimidation on prey demographics has been shown to be at least as strong as lethal effects for a variety of animals (Preisser et al. 2005). Our study provides evidence of behavioural effects of hunting on the circadian movement pattern of a LC in a critical foraging period, and further research is needed to show their costs. Changes in movement patterns could be used as early indicators of the extent and severity of human disturbance on carnivores, which may have other unforeseen consequences (Kolowski et al. 2007). For instance, there is a strong correlation between female bears' condition in the autumn and subsequent reproductive success (see Welch et al. 1997); bears give birth in the dens, and mothers must obtain large reserves of energy to sustain the cubs. Further research should aim to document whether the potential consequences of hunting disturbance in the autumn affects fitness, e.g. female bears´ condition and forthcoming reproductive success.

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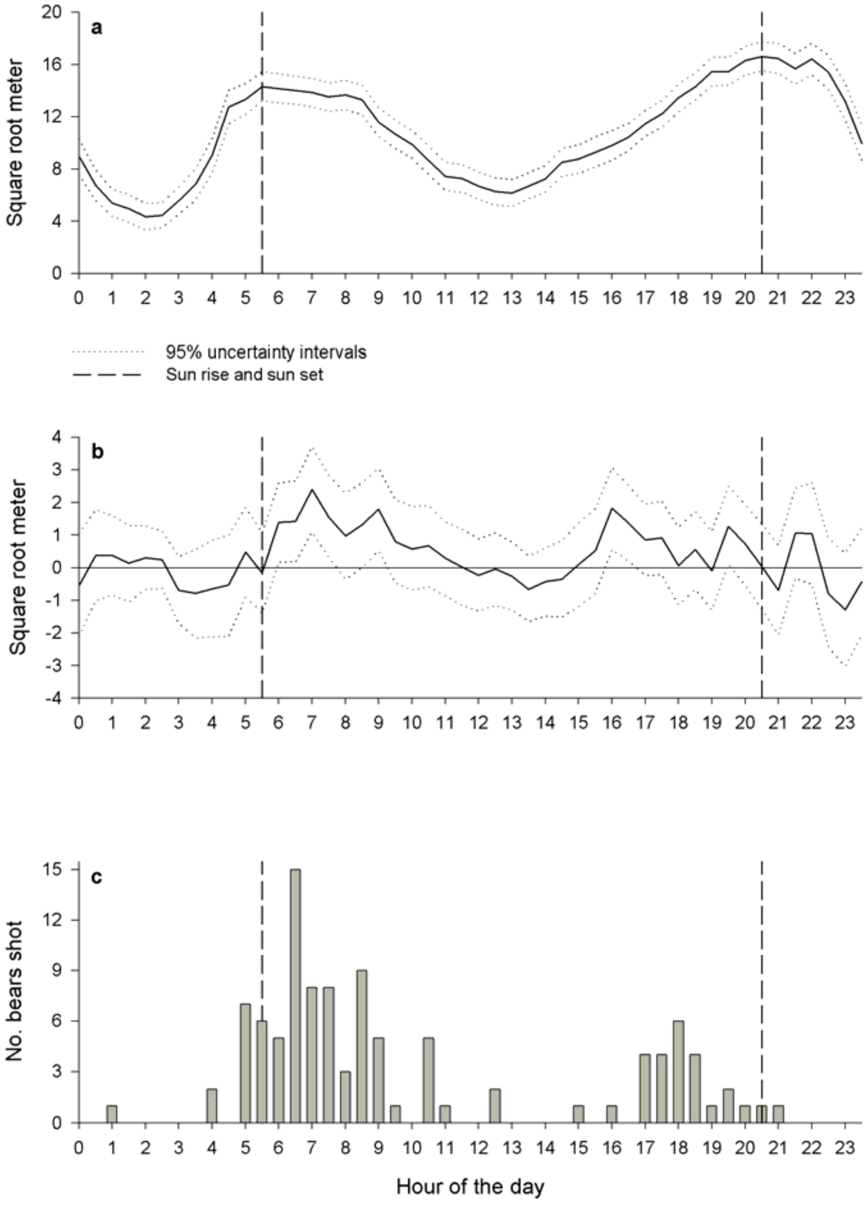
Figures

Figure 1. Distance (√m) between consecutive GPS locations at 30-min intervals during the week prior to hunting (a), the expected difference (see text) in these distances (√m) between the week prior to hunting and the first week of hunting (b) for 42 brown bears in Dalarna and Gävleborg, Sweden, 2003-2008; and the number of brown bears shot during the first week of hunting in these counties 1999-2008 (c).



Paper VII

Saving large carnivores but losing the apex predator

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Running head: *Losing apex predators*

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Large carnivores (LC) often play a key ecological role, because of their position at the apex of trophic systems. Changes to their populations reverberate through ecological communities, consequently their widespread decline in numbers and shrinking distribution due to human persecution has brought about a loss and re-configuration of biological diversity in many systems, marine and terrestrial alike (Ray et al. 2005). Although many LC populations are now under conservation-minded management, political and economic constraints make compromises necessary. A common compromise is to permit a limited harvest, with the premise of sustainability and the objective to increase tolerance and funding for LC recovery and conservation. Here we question whether a LC that has to look over its shoulder for human hunters can still perform its ecological role at the apex of a trophic system. We use knowledge about carnivore ecology, trophic interactions, and the effects of human harvest to argue that exploitation of large carnivores, even if sustainable numerically, undermines the popular rationale for large carnivore conservation, namely the restoration and preservation of ecosystem functionality (Sergio et al. 2008). Our argument centers around (i) the necessity of behavioral adjustments in LC to anthropomorphic risk, which may limit the contribution of contemporary LC to the "landscape of fear" (Ripple & Beschta 2004) and (ii) the observation that many of the same features that put LC at the apex of trophic systems also make them vulnerable to human exploitation and persecution, with implicit consequences for their ecological functionality and evolution.

The effects of LC on their communities, which often stand in stark contrast to their relatively low abundance, include the facilitation of resources and predator-prey interactions (Sergio et al. 2008). LC can greatly impact their prey, as exemplified by the high mortality rates that terrestrial predators can induce among large herbivores (Prins & Iason 1989) or the impressive consumption rates attributed to large marine predators (Steneck & Sala 2005). LC also have non-lethal effects on prey ecology. Predation risk affects prey population dynamics and habitat utilization indirectly by forcing individuals to invest in anti-predator behavior, and thus trade off reproduction or foraging efficiency (Lima 1998), a phenomenon appropriately captured by the term "ecology of fear" (Brown et al. 1999). Although non-lethal effects are rarely considered in conservation or wildlife management, they are powerful enough to drive trophic cascades (Schmitz et al. 2004).

What are the features that define the typical LC? Clearly, one of them is physical size, but also low densities and the propensity for large home ranges and long movements (Ray et al. 2005). There are additional, somewhat anthropomorphically tainted, attributes of LC, such as fierceness, fearlessness, and intelligence or cunning. Ironically, it is precisely those combined features that typify placement of LC at the apex of trophic systems that also guarantee their persecution by humans; low abundance appeals to our desire for the rare and elusive, fierceness and intelligence challenge sportsmen, and high predation rates make them loathed competitors for game and depredators of livestock. Perhaps the greatest and oldest reason behind their persecution is that LC instill fear in us, much like they do in their prey species.

Whereas LC are reviled and feared by some, they are revered by others and are frequently used as flagship species for conservation efforts. This focus on single species is often justified ecologically, as its benefits can extend beyond the target species to entire communities (Sergio et al. 2008), which even has prompted some to suggest the re-establishment of Pleistocene communities of LC and other large mammals in North America (Donlan 2005). Even when recovery proposals are less ambitious, conservation efforts for LC remain highly controversial, and managers are forced to make compromises. One of these is the willingness to allow sustainable harvest, whether it is with the intent to generate additional political and financial support from sportsmen (Lindsey et al. 2007) or to respond to calls to reduce the real or perceived threat to humans (Packer et al. 2005), livestock and game animals (Basille et al. 2009).

We question whether a LC that has to look over its shoulder due to human harvest, even if it is numerically sustainable, can perform its ecological role to its full potential. First, we suspect that trading off avoidance of humans with foraging activities will reduce the efficiency with which managed populations of LC numerically control prey populations. Second, anthropomorphically induced alterations of movement patterns and the use of space and time (Boydston et al. 2003) likely impact and possibly diminish their contribution to shaping the landscape of fear. For example, hunted Eurasian lynx (*Lynx lynx*) trade off prey abundance with avoidance of humans during habitat selection (Basille et al. 2009), arguably impacting their ability to numerically and behaviorally affect their main prey, roe deer (*Capreolus capreolus*).

LC are targeted because they frighten, compete with and challenge humans. Individuals in which the features of a high-quality apex predator are especially pronounced are likely also the most vulnerable to human-caused mortality. Individuals with the greatest movements and largest home ranges are most likely to encounter hunters, fishermen or capture devices, such as traps and nets. Large individuals are more easily detected (Fenberg & Roy 2008) and are also specifically sought after by trophy hunters (Birkeland & Dayton 2005). Aggressive individuals and those with the greatest predation rates are liable to be more noticeable and hence draw the attention of damage control efforts (Inskip & Zimmermann 2009) and sport hunters (Lindsey et al. 2007). Hunting and fishing bias towards exceptional individuals in terms of ecological performance may reduce the ecological impact of LC populations in the short term and in the long run may reduce the quality of traits that define apex predators. The removal of exceptional individuals may be particularly detrimental for LC, due to their low population sizes and consequently greater contribution of such individuals to population dynamics and ecological impact. Hunting by humans may have already shaped the LC of today in terms of life history and behavior. In brown bears (*Ursus arctos*) for example, there is evidence of reduced aggression towards people (Swenson 1999), a shift towards more nocturnal behavior (Kaczensky et al. 2006), and greater and earlier reproductive investment (Zedrosser 2006) in populations in Europe compared with North America, where bears have a much shorter history of human persecution. The evidence keeps accumulating for morphological, behavioral and life-history changes in wild populations due to hunting and fishing (Allendorf & Hard 2009) and, as a recent review of 40 human-exploited systems suggests, humans are substantially more prolific in causing trait changes than other agents of selection (Darimont et al. 2009). Ultimately, we have to accept that harvesting wildlife, even if it is sustainable, changes populations. More specifically, we have been urged to assume that exploitation results in genetic changes in wild populations (Allendorf et al. 2008) and are warned about the consequences of ignoring the potential for evolutionary effects (Stenseth & Dunlop 2009).

We have dethroned top carnivores in most ecosystems, which leads to the obvious question of whether humans have successfully assumed the role of top predator in terms of ecosystem functionality. The overall impression is that current human hunting is not functionally redundant to predation by wild apex carnivores (Berger 2005). Glaring examples are the persistent problems associated with high ungulate populations following predator eradication or “management” in Europe and North America (Allombert et al. 2005), both cultures with strong ungulate-oriented hunting traditions. Furthermore, even in cases where hunters prompt numerical responses in prey, functional responses may be lacking (McShea 2005). In marine ecosystems, the top-down control exerted by human predators is substantially different from that of natural predators, increasing the likelihood of fluctuations in species abundance (Sala & Sugihara 2005).

In part due to conservation efforts, the future of some LC populations looks less dismal today than just a few decades earlier (Basille et al. 2009, Enserink & Vogel 2006). However, in the case of apex predators, it is not simply the species we are protecting, but its ecological role. Systematic harvest even though allowable from the perspective of species conservation, may impede ecosystem functionality. In recent years, the population increase of wolves and brown bears in the Greater Yellowstone Ecosystem, due to successful conservation measures, has been used as an argument for their delisting from the US Endangered Species Act, without considering whether these LC had recovered sufficiently to play a normative ecological role (Pyare & Berger 2003). Similarly, Heithaus et al. suggested that predators in marine environments should be managed for the maintenance of both density- and risk-driven ecological processes, and not for demographic persistence alone, given the importance of non-lethal effects of large predators (Heithaus et al. 2008).

What we know about LC ecology and the nature of human exploitation of wildlife casts strong doubts upon whether a LC subjected to exploitation and pre-emptive control can effectively fulfill its ecological role as “king of the beasts”. As soon as adult individuals of an apex carnivore are routinely preyed upon, it, by definition, ceases to be an apex carnivore and its role may be diminished to that of yet another competing predator in the ecosystem. We concede that conservation and wildlife management operate under biological, financial and political constraints. All of these require compromises, and the choice is often made for us when we have to pick between allowing sustainable harvest of LC or face stronger, perhaps prohibitive, opposition to recovery and preservation efforts. Nonetheless, we urge wildlife managers, before eagerly accepting demographically sustainable exploitation, to evaluate whether the ecological justification for LC conservation is still addressed or whether it is only the target species and an image of wildness that is preserved.

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