ENCOUNTERS BETWEEN BROWN BEARS AND HUMANS IN SCANDINAVIA – CONTRIBUTING FACTORS, BEAR BEHAVIOR AND MANAGEMENT PERSPECTIVES

Møter mellom bjørn og mennesker i Skandinavia – medvirkende faktorer, bjørnens atferd og forvaltningsperspektiver

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# Encounters between brown bears and humans in Scandinavia – contributing factors, bear behavior and management perspectives

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# Contents

Summary i
Sammendragiii
Sammanfattningv
List of papers
Introduction 1
Objectives of the thesis and their rationale
What factors are involved when humans are injured or killed by bears in Scandinavia? (Paper I) 3
How do bears normally behave in encounters with humans? (Papers II, III, IV)
Bear behavior and increased risk of aggressive responses in encounters with humans (Papers III, V)
How do encounters with humans affect bears? (Papers IV, VI)
Materials and Methods
Study area7
The bears – population, capture and handling7
Bear movement and activity
Fieldwork
Human injuries following a bear attack
Summary of results
Factors involved when people are injured by bears (Paper I)11
Single bears avoid confrontations with humans (Paper II)12
Are females with cubs more aggressive than single bears? (Paper III)
The effects of disturbance go beyond the initial reaction (Paper IV)
Does behavior near den entry explain higher risks of human injury at that time? (Paper V)
The consequences of being disturbed in the den (Paper VI)
Discussion
How dangerous are Scandinavian brown bears to humans?
Who is the prey in the human-bear relationship?
Management perspectives
Future research perspectives 32
Acknowledgements 41
Compilation of papers

### Summary

Conflicts between large carnivores and humans can negatively affect attitudes and increase fear among the public. Because encounters between brown bears and humans are becoming more common in Scandinavia, the aim of this thesis was to evaluate bear-human encounters to determine risk factors for humans and how bear-human encounters affect bears.

Our results show that the Scandinavian brown bear poses a very low risk to humans, even though incidents do occur (31 persons injured and 2 killed during 1977-2012; all men). Both single bears and females with cubs respond to approaching humans by leaving and the majority of encounters go unnoticed by humans. However, females with cubs use more open habitat than singles, which may expose them to encounters with recreational forest users. This could explain why presence of cubs is the primary factor involved when unarmed people are injured. The bears' responses to approaching humans indicate that bears perceive humans as a serious threat, as they respond to meetings with humans by becoming more nocturnal for several days, which could have fitness consequences.

Incidents resulting in injuries have increased with the number of bears shot and the bear population size. However, this relationship was only significant for armed men. Most of the injured armed men were hunting when injuries occurred, and the presence of dogs and dens were the most common aggravating factors, often coinciding with the bear den entry period. The risk of injury thus appears to be primarily linked with which type of activity people are engaging in, especially hunting with dogs.

Bears significantly reduced activity prior to den entry whether or not they had arrived at their dens, which could affect fight-or-flight responses in encounters with hunters and hunting dogs. We documented high den abandonments during October/November, five times higher than during winter, possibly attributable to hunter activity at this time. The lower

i

abandonment rate during winter is probably due to increased costs of leaving the den, which can be considerable.

We conclude that Scandinavian brown bears avoid confrontations with humans and are generally not aggressive. Our results can be used by managers to help prevent injuries by developing recommendations for recreational users and hunters on how to best avoid risky situations, and evaluate potential impacts of human activity on the bear population. It can also be used in information campaigns to address public fear and lack of acceptance of the brown bear.

### Sammendrag

Konflikter mellom store rovdyr og mennesker kan føre til negative holdninger til rovdyr og øke frykten for rovdyr blant folk. Møter mellom brunbjørn og mennesker har blitt vanligere i Skandinavia, og formålet med denne oppgaven var derfor å identifisere risikofaktorer for mennesker og hvordan disse møtene påvirker bjørner.

Våre resultat viser at Skandinaviske brunbjørner utgjør en svært lav risiko for mennesker, selv om skadetilfeller forekommer (31 personer skadet og 2 personer drept i perioden 1977-2012; alle menn). Både enslige bjørner og binner med unger forlater stedet når mennesker nærmer seg, slik at de fleste av disse møtene skjer uten at menneskene oppdager det. Binner med unger oppholder seg derimot i et mer åpent terreng enn enslige bjørner, og dette kan innebære at bærplukkere, turgåere og andre som oftest bruker slikt terreng har større sannsynlighet for å møte binner med unger enn enslige bjørner. Dette kan forklare hvorfor det ofte er binner med unger som er innblandet når ubevæpnede personer blir skadet av bjørn. Bjørnene reagerer på slike møter med mennesker med å bli mer nattaktive i flere døgn etter møtet, noe som tyder på at bjørner oppfatter mennesker som en alvorlig trussel. Dette kan også medføre negative konsekvenser for bjørnens fitness.

Antallet tilfeller der mennesker er blitt skadet av bjørn økte med antall skutte bjørner og en økt bjørnebestand, men denne sammenhengen var bare signifikant for bevæpnede personer. De fleste bevæpnede personene ble skadet i forbindelse med jakt, og de vanligste forklaringsfaktorene var tilstedeværelsen av hund og forekomst av hi. Tidspunkt for skadetilfellene sammenfalt med perioden for når bjørnen går i hi. Risikoen for skade ser derfor i hovedsak ut til å avhenge av hvilken aktivitet personen bedrev når den ble skadet, der den vanligste aktiviteten var jakt med hund.

Bjørner reduserte sin aktivitet betydelig i perioden før higang, uavhengig av om de befant seg nær hiet eller ikke. Dette kan påvirke "flykt-eller-kjemp"-reaksjoner hos bjørnen i møter

iii

med jegere og jakthunder. Vi dokumenterte et høyt antall bjørner som forlot hiene i perioden oktober til november, fem ganger høyere enn gjennom resten av vinteren, noe som kan skyldes økt jaktaktivitet senhøstes. Årsaken til at færre bjørner velger å forlate hiet utover vinteren, kan være den økte energikostnaden dette medfører som kan være betydelig.

Vi konkluderer med at Skandinaviske brunbjørner unngår konfrontasjoner med mennesker og at de generelt ikke er aggressive. Våre resultat kan benyttes av forvaltningen for å forhindre at skadesituasjoner oppstår gjennom å utarbeide anbefalinger for hvordan mennesker som oppholder seg i skogen i forbindelse med rekreasjon eller jakt best kan unngå risikofylte bjørnemøter, samt for å vurdere potensielle effekter av menneskelig aktivitet på bjørnebestanden. Resultatene kan også benyttes i informasjonsvirksomhet som omhandler folks frykt og manglende aksept for bjørn.

### Sammanfattning

Konflikter mellan stora rovdjur och människor kan ha en negativ effekt på attityder och öka rädslan hos allmänheten. Möten mellan brunbjörn och människa blir allt vanligare i Skandinavien, och syftet med denna avhandling var därför att utvärdera sådana möten för att identifiera riskfaktorer för människor och hur dessa möten påverkar björnar.

Våra resultat visar att skandinaviska brunbjörnar utgör en väldigt låg skaderisk för människor, även om olyckstillfällen sker (31 skadade och 2 dödade personer mellan 1977 – 2012; alla män). När människor närmade sig björnar gick både ensamma björnar och honor med ungar undan, vilket innebär att majoriteten av dessa möten inträffade utan människans vetskap. Honor med ungar vistas däremot i öppnare habitat än ensamma björnar, vilket kan innebära att bärplockare, skogsvandrare m.fl. som oftast rör sig i sådan terräng har större sannolikhet att möta denna kategori av björn än ensamma björnar. Detta kan förklara varför det oftast var honor med ungar som var inblandade när obeväpnade människor skadades av björnar. Björnar reagerade på möten med människor genom att bli mer nattaktiva under flera dygn efter mötet, vilket tyder på att björnar uppfattar människor som ett allvarligt hot. Detta kan också medföra negativa fitnesskonsekvenser för björnen.

Incidenter där människor skadades av björn ökade med antalet skjutna björnar och ökande björnpopulationsstorlek, men detta samband var däremot endast signifikant för beväpnade män. De flesta av de beväpnade personer som skadades var ute på jakt vid skadetillfället, och de vanligaste förklarande faktorerna var närvaro av hundar och förekomst av iden. Tidpunkten för incidenterna sammanföll med björnens idesgångsperiod. Risken för skada verkar därför i huvudsak bero på vilken typ av aktivitet som personen ägnade sig åt där jakt med hund var den mest vanligt förekommande aktiviteten när människor skadades av björn.

Björnar minskade sin aktivitet signifikant innan idesgången vare sig de befann sig vid idet eller ej, vilket skulle kunna påverka "fly-eller-fäkta" reaktioner vid möten med jägare och

v

jakthundar. Vi dokumenterade ett högt antal björnar som övergav sina iden under oktober/novemer - fem gånger högre än under vinterårstiden - vilket kan bero på ökad jaktaktivitet under senhösten. Att färre björnar överger idet under vinterperioden beror troligtvis på den ökade energiåtgången som följer med att överge idet, vilken kan vara omfattande.

Vi drar slutsatsen att skandinaviska brunbjörnar undviker konfrontationer med människor och att de generellt inte är aggressiva. Våra resultat kan tillämpas inom förvaltningen för att minska risken att skadesituationer uppstår genom att utforma rekommendationer för hur människor som vistas i skogen för rekreation eller jakt bäst undviker riskfyllda björnmöten, samt för att utvärdera potentiella effekter av mänsklig aktivitet på björnpopulationen. Resultaten kan även användas i informationsinsatser för att minska rädsla och förbättra allmänhetens acceptans för björn.

## List of papers

# Paper I

Sahlén, V., Støen, O.G., Ordiz, A., Arnemo, J.M., Brunberg, S., Kristoffersson, M., Kindberg, J., Swenson, J.E. Human injuries and fatalities caused by brown bears in Scandinavia 1977-2012. Manuscript

# Paper II

Moen G.K., Støen, O.G., Sahlén, V., Swenson, J.E. 2012. Behaviour of solitary adult Scandinavian Brown Bears (*Ursus arctos*) when approached by humans on foot. PLoS ONE 7(2):e31699

# Paper III

Sahlén, V., Støen, O.G., Ordiz, A., Swenson, J.E. Behavioral differences between females with dependent young and single Scandinavian brown bears when experimentally approached by humans. Manuscript

## Paper IV

Ordiz, A., Støen, O.G., Sæbø, S., Sahlén, V., Pedersen, B.E., Kindberg, J., Swenson, J.E. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. Journal of Applied Ecology 50(2):306-314

## Paper V

Sahlén, V., Friebe, A., Sæbø, S., Swenson, J.E., Støen, O.G. Den entry behavior in Scandinavian brown bears *Ursus arctos*; implications for preventing human injuries. Submitted manuscript

## Paper VI

Evans, A.L., Sahlén, V., Støen, O.G., Fahlman, Å., Brunberg, S., Madslien, K., Fröbert, O., Swenson, J.E., Arnemo, J.M. 2012. Capture, anesthesia, and disturbance of free-ranging brown bears (*Ursus arctos*) during hibernation. PLoS ONE 7(7): e40520

**Synopsis** 

"Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less"

Marie Curie

### Introduction

Few animals generate such controversy and spark as intense debates as large carnivores, nor is it surprising that they do. The mutual history, and present day concerns, of carnivores and humans involve competition for resources (wild game) (Boertje et al. 1988, Swenson et al. 2007), conflicts over damages to livestock and property (Mishra 1997, Patterson et al. 2004), and human safety concerns (Packer et al. 2005, Conover 2008, Gurung et al. 2008, Packer et al. 2011). As a result, large carnivores have been persecuted by humans to the point of near extinction on a global scale (Gittleman et al. 2001), but shifting attitudes and changes in management goals have paved the way for recovery (Kellert et al. 1996), and large carnivore populations are now increasing in many areas (Enserink and Vogel 2006, Packer et al. 2009, Wydeven et al. 2009). The Scandinavian brown bear Ursus arctos has increased from a few hundred individuals in the mid-1900s to over 3000 individuals at present (Swenson et al. 1995, Kindberg et al. 2011). However, as the population has grown in size and expanded its range into areas that have been uninhabited by bears for almost a century, new research and management challenges have arisen (Swenson et al. 1998). Encounters between bears and humans have become more common and often create headlines in the printed media, which can affect people's perception of carnivores and associated risk (Hart et al. 2011). People in Norway expressed greater fear of bears than lynx Lynx lynx or wolverine Gulo gulo (Røskaft et al. 2003) and a Swedish survey documented an increase in fear of and decreasing tolerance for the brown bear among the public (Sandström and Ericsson 2009).

Knowledge of a species is often linked to a person's attitude toward that species (Lescureux et al. 2011, Glikman et al. 2012). There is thus a prevailing view among ecologists and managers that better understanding of a species can change people's attitudes toward the species and management of that species, although this may or may not be true (Blekesaune and Rønningen 2010). However, a better understanding of a species' behavior

and responses to humans is necessary to ensure the best management practices for that species. The large brown bear population in Scandinavia and its continued expansion demands a thorough understanding of bear-human encounters, both to address concerns regarding human safety, but also to understand what challenges the expanding brown bear population will present as the overlap between areas inhabited by both bears and human continues to grow.

The aim of this thesis is therefore to describe behavioral reactions of brown bears when encountering humans, both in terms of how it affects human safety, but also the effect such encounters have on bears.

### Objectives of the thesis and their rationale

# What factors are involved when humans are injured or killed by bears in Scandinavia? (Paper I)

Human injuries and deaths following animal attacks occur around the globe involving a variety of carnivore species, e.g. cougars *Felis concolor* (Beier 1991), sloth bears *Melursus ursinus* (Bargali et al. 2005), polar bears *U. maritimus* (Herrero and Fleck 1990), and black *U. americanus* and brown bears in North America (Herrero 2002) and Europe (Swenson et al. 1999b, De Giorgio et al. 2007). These attacks can be predatory in nature, i.e. the attacking animal acts as a predator and the human is essentially treated as prey (Beier 1991, Treves and Naughton-Treves 1999, Herrero et al. 2011). In the case of bears, most attacks are defensive/retaliatory, i.e. the attack response has been triggered by a provocation by the human, intentionally or not (Quigley and Herrero 2005). Understanding what factors are involved when bears, or any species, attack people is an important step to successfully minimize or prevent such incidents from occurring and provides important information on the potentially best practice, i.e. how people should behave if they happen to find themselves in such a situation.

Swenson et al. (1999b) reviewed the factors involved when humans were injured by bears in Scandinavia, which were, in order of decreasing significance; wounded bear, presence of cubs, presence of a carcass, vicinity of a den, and presence of a dog. However, between 1976 – 1995 only 7 incidents had occurred where a person had been injured by a bear (Swenson et al. 1999b), and from 1995 until present there appeared to have been an increase in the injury rates. The first objective of the thesis was therefore to investigate if the increasing number of injuries was related to the increasing and expanding bear population, and what factors were involved when people were injured or killed by bears in Scandinavia.

### How do bears normally behave in encounters with humans? (Papers II, III, IV)

An inherent problem of studying the behavior of elusive animals, such as the brown bear, when they encounter humans, is that one is often limited to describing the behavior of the animals that have been observed directly (McLellan and Shackleton 1989, Swenson et al. 1999b). Although the information garnered from such studies is very valuable, most encounters between man and animal may go unnoticed by humans. However, the development and increasing quality and accuracy of GPS-technology enables researchers to answer questions about animals' behavior, even when the animal cannot be observed (Cagnacci et al. 2010, Tomkiewicz et al. 2010).

The second objective of the thesis was therefore to document the normal behavior of brown bears during encounters with humans, using GPS technology to document both bear and observer movements. We designed experimental approaches in a way that the bears would be aware that humans were approaching, for two reasons: 1) we wanted to document the effect of encounters with humans and not the effect of general disturbance, and 2) we wanted to eliminate the potential effect of the bear being surprised. In addition, one complaint often raised by people is that the fear of encountering a bear inhibits them from engaging in outdoor activities, such as berry or mushroom picking, which is very popular in Scandinavia (Blekesaune and Rønningen 2010). Observers therefore simulated recreational forest users, talked in normal tone of voice to each other, and approaches were standardized in relation to relative wind direction.

# Bear behavior and increased risk of aggressive responses in encounters with humans (Papers III, V)

In a review of human injuries caused by bears in Scandinavia, Swenson et al. (1999b) showed that the most important variable was a wounded bear and most of the people were

involved in a hunting activity at the time the injury occurred, thus risk of injury was highest in the fall. The second most important factor was encountering a female with cubs. Our third objective was to investigate the bears' behavior in regard to these two factors, in order to better understand why these situations would be related to a higher risk of human injury. In the case of the timing of injury, we focused in particular on the movement around the den, as the presence of a den was an important factor associated with injuries later in fall (Paper I). A secondary objective was thus to identify potential predictors of the timing of den entry. The ability to predict the den entry period could be useful for bear managers as they, for example, could impose hunting restrictions during the most sensitive den entry period to minimize the risk of injury to humans and the risk of disturbance to the bears. In the case of females with cubs, our objective was to compare the reactions of females with cubs to those of single bears to approaching humans. We wanted to identify any potential differences and assess whether females accompanied by cubs were more aggressive than single bears.

### How do encounters with humans affect bears? (Papers IV, VI)

The fourth objective of the thesis was to evaluate how human disturbance affects bears. Many wildlife species avoid human activity and infrastructure, e.g. reindeer *Rangifer tarandus* (Vistnes and Nellemann 2008), wolverine (May et al. 2006), and grizzly bears *U. arctos* (Gibeau et al. 2002), either by avoidance or by reduced population densities (Benítez-López et al. 2010). The Scandinavian brown bear is no exception (Nellemann et al. 2007), but social organization factors affect the pattern of avoidance (Elfström and Swenson 2009, Elfström et al. 2013, Steyaert et al. 2013). This avoidance occurs even at smaller scales and in response to periodically increasing human activity (Ordiz et al. 2011, Ordiz et al. 2012), much in the same way prey species are affected by the presence of predators (Laundré et al. 2001, Berger 2007). We therefore wanted to evaluate if there were any long-lasting effects on bear behavior resulting from human encounters.

In 2009, the SBBRP began collaboration with cardiologists from Örebro University Hospital, which involved capturing bears in their winter dens for comparative physiological studies. This provided us with a rare opportunity to document bear responses to, albeit a very intense, human disturbance occurring while the bear was in the den. We knew from previous studies that most documented den abandonments occur because of human disturbance, and that this can incur considerable costs, especially to pregnant females (Swenson et al. 1997). Such abandonments are often discovered after the bear has left the original den location, with little information about the new den or the movements before arriving at the new den. Therefore, we documented movement patterns following den abandonments to better understand how disturbance resulting in den abandonments affect bears.

### **Materials and Methods**

### Study area

The study area was located in south-central Sweden (61°N, 15°E), in Dalarna and Gävleborg counties. It lies within the northern boreal forest zone and is dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. The landscape is hilly with elevations ranging from ~200 to ~1000 m above sea level (Dahle and Swenson 2003). Forestry production characterizes the landscape, with young forests, clearcuts (Swenson et al. 1999a), and an extensive road system consisting of gravel and paved public roads of varying sizes and quality ((Nellemann et al. 2007), Paper V). The human population density in the area is 4-7 inhabitants/km<sup>2</sup>, and there are a few villages and single cabins, primarily seasonally inhabited (Paper V). The area is popular for outdoor activities, such as berry and mushroom picking, hiking, fishing, and hunting.

### The bears – population, capture and handling

The bear population in the study area is part of the southernmost core reproductive area for Scandinavian brown bears, and the density is about 30 individuals per 1000 km<sup>2</sup> (Bellemain et al. 2005, Solberg et al. 2006). Hunting of brown bears is permitted in Sweden and quotas are set at the county level by the County Administration Boards. The hunting season spans from 21 August until 15 October, unless quotas are filled earlier. The dense bear population in the area makes it attractive to bear hunters, and landowners (who hold hunting rights) welcome a large number of guest hunters. Quotas are typically filled within the first two weeks of the hunting season. Moose hunting, which is the predominant hunting activity, is permitted in some parts of the area from the first Monday in September until the end of September. There is a two-week break for the moose rut, after which hunting is permitted in the entire area until the end of February.

The Scandinavian Brown Bear Research Project (SBBRP) has studied bears in the area since 1985, primarily by capturing already marked females and their offspring, but also by capturing and marking new bears (all age classes). Most bears are captured and handled during spring, after they have left their dens, and early during the breeding season. Capture and handling procedures are described in Arnemo et al. (2011), and capturing was approved by the Swedish Environmental Protection Agency (permit Dnr 412-7327-09 Nv) and Uppsala's Ethical Committee on Animal Experiments (Djuretiska nämnden i Uppsala), approval number C47/9.

### Bear movement and activity

The bears were equipped with GPS collars, mainly GPS Plus-3 or GPS Pro-4 collars), which are fitted with dual-axes motion sensors (activity sensors), VHF transmitters, and a GSM modem (VECTRONIC Aerospace GmbH, Berlin, Germany), as well as VHF transmitter implants (400L or 700L, Telonics). GPS location data are transmitted via the GSM network to a base station from which they can be downloaded remotely. Activity data (and any missing GPS locations) can be physically downloaded from the collars once they have been retrieved. Collars can be programmed remotely using text messages via the GSM network, and we used different location fix intervals depending on the requirements of the study; 1-min (Papers II, III, IV), 10-min (Paper VI), and 30-min (Papers IV, V, VI) intervals. Movement was investigated using ArcGIS 9.x and 10 (ESRI) and the statistical programming language R (R Core Development Team, 2011). Activity was recorded by measuring acceleration, generating data points on a 5-min interval, and was used to determine movement at, near, and between dens, and activity levels at den locations (Papers V, VI).

### Fieldwork

We carried out experimental approaches in July – October to document the behavior of single bears and females with cubs when approached by humans on foot, both in terms of immediate reactions and after the approach (Papers II – IV). We located the bears using VHF triangulation and last known GPS locations sent to the observers' cell phones via SMS. Observer movements were recorded using handheld GPS units programmed to fix positions every 10 m. The experimental approaches were standardized with regards to relative wind direction and observer passing distance. After the approach, we visited the locations where the bears had been at the time of the approach (initial sites) and, in the cases where the bears relocated to a new stable site, also the new locations (second sites). At the sites, we recorded environmental variables that could influence the bears' responses to the approaching observers, primarily habitat type and horizontal vegetation cover (Papers II – IV). Horizontal vegetation cover was estimated by measuring the sighting distance at the location (Papers II – IV). We also visited den locations determined from the GPS and activity data to verify the presence of dens and document den types (Papers V, VI).

#### Human injuries following a bear attack

The factors involved when people have been injured by brown bears was investigated by collating information from scientific articles, books, media (newspapers and electronic articles), police reports, and other official records, following incidents where a person had been attacked and injured (required medical treatment) or killed by a bear from 1977-2012 (Paper I). We defined incidents as each case where a bear had injured or killed one or more people, and used the term casualties for each person injured or killed. Thus, one incident could involve one or more casualties. All incidents where people had been injured were then

followed up by interviewing the person injured by phone or in person, to confirm and supplement our information.

### **Summary of results**

### Factors involved when people are injured by bears (Paper I)

We obtained annual estimates of the Swedish bear population based on estimates from literature for the years where this was available. For the years without literature estimates, we calculated growth curves based on standard exponential growth curves, using estimates available in the literature for the closest years before and after. We tested the effect of estimated population size and number of bears shot on the number of incidents, as well as on armed and unarmed people separately.

Between 1977 and 2012, the number of incidents resulting in human injury or death following bear attacks increased and was positively related to the bear population size and number of bears shot during hunting, both of which increased during the period. However, this was only true for armed people; the same pattern was not documented for unarmed people. In total, there were 32 incidents in Scandinavia where bears injured 31 and killed 2 people, excluding 2 capture-related incidents where 3 researchers were injured. All injured or killed people were males aged 12-75 years, and the majority was involved in some form of hunting activity. Most incidents occurred during fall, coinciding with the mose hunting season and the period in which bears enter their dens. The majority (69%) of incidents occurred in October, September and November, and the presence of a den was a factor in 41% of all incidents (Fig. 1).

Most armed men were involved in a hunting activity when the incident occurred, and in 18 of 24 incidents the injured person shot at the bear before being injured. In Scandinavia, bears and moose are often hunted using trained hunting dogs, where the dogs are released to search for the prey in question. When they locate their prey, they bark to keep it at bay, allowing the hunter to sneak up to the site and shoot the prey. The presence of a dog was a factor in 21 of the incidents involving armed people and dogs had chased and barked at the bear in the 19

incidents for which we had information on the dogs' behavior. For unarmed people, the presence of cubs was the most common factor involved when incidents occurred. Bear attacks in Scandinavia appear to be defensive rather than predatory in nature.



**Fig. 1** Number of people injured or killed by brown bears by month in Scandinavia, 1977-2012

In summary, the presence of dogs has become a more important factor in recent years, incidences of injury increased among armed but not unarmed people, and most injuries occurred during the fall hunting season. We therefore concluded that the increasing injury rates are not directly related to the bear population increase, but rather reflected an increasing interaction between hunters and bears, as indicated by the increasing number of bears shot. The general risk of being injured or killed by bears does not appear to have increased for people living in areas with bears, but is linked to the type of outdoor activity people are involved in.

### Single bears avoid confrontations with humans (Paper II)

We conducted 169 approaches on 30 bears (21 females, 9 males) during June until October 2006-2009. We passed the bears at  $54 \pm 61$  m (mean  $\pm$  SD), but were only able to

detect the bears (seen or heard) in 15% of the approaches. None of the bears behaved aggressively toward the observers and all bears walked or ran away after the initial observation.

We analyzed the responses of bears using generalized linear mixed models and linear mixed models, with an AIC-based backward elimination, selecting the final models based on the lowest AIC values. Bears left their initial site in 80% of all approaches and younger bears left more often than older bears, possibly indicating differences in experience, although this difference decreased later in the season. The bears' flight initiation distance (FID), i.e. the distance from the observer that the bear reacted by leaving, was longer when the bears were active than when passive, when there was less horizontal vegetation cover (sighting distance was longer) at the initial site, and for younger bears than older. Bears that left after they had been approached moved on average  $1173 \pm 1094$  m and settled into their second sites, which were densely vegetated. The second sites of active bears had more cover than the initial sites, whereas the initial sites and second sites of passive bears did not differ in sighting distance. We suggest that this was due to passive bears already having selected a protected resting site.

We conclude that the probability of encountering a bear is low, partly because they choose resting habitats that are typically too dense for hiking, but also because our results suggest that bears avoid confrontations with humans. Our results also suggested that even when encounters do occur, bears are normally not aggressive toward humans.

### Are females with cubs more aggressive than single bears? (Paper III)

We conducted 42 approaches on females with cubs (19 on females with cubs of the year, 23 on females with yearlings) in 2008-2011. Because of the high risk of displacement following disturbance (Paper II), all approaches were carried out after the main breeding season had ended (i.e. July – October), to minimize the risk of infanticide. We compared the responses of the females with cubs with the responses of 23 female and 8 male single bears during 108 approaches (76 on females and 32 on males) in the same time of year in 2006-2009. We used generalized linear mixed models, model dredging and a combination of AIC model and variable weights to assess the bears' responses.

We passed the bears' initial sites at  $50.6 \pm 53.7$  m. We saw or heard females with cubs in 26% of the approaches and single bears in 14% of the approaches, indicating a trend for FC to be more easily detected than single bears. As in Paper II, the majority of bears left as a result of being approached (95% of FC, and 88% of single bears), but here the decision to leave was primarily influenced by the proximity of the observers and the density of the vegetation at the IS. Contrary to our prediction, FID was not longer for FC than single bears, which may be because climbing up a tree may be a more effective alternative defensive response for the youngest bears than fleeing. We could not detect any effect of sighting distance on FID, which primarily was dependent on the bears activity at the time (active bears had longer FID than passive), and a weaker effect of age (younger bears left earlier than older). The weak effect of age documented for this dataset is consistent with finding that the effect of age decreased with season that we documented in Paper II.

Active bears responded to the approach by moving longer distances than passive bears, and FC, particularly active FCOY, moved farther than single bears, indicating a stronger immediate reaction to the disturbance than other categories of bears (Fig. 2).



**Fig. 2** Mean distance moved (m) after disturbance for active (A) and passive (P) Scandinavian brown bears in relation to family status (Fam Stat) with the categories: females with yearlings (FY), females with cubs of the year (FCOY) and single bears (S).

All bears tended to move longer distances after disturbance when there was more vegetative cover at the initial site, indicating that the bears may have had less ability to assess the oncoming threat, and therefore reacted more strongly. Females with cubs and singles differed in the density of vegetative cover at initial and second sites, which was true irrespective of habitat type (Fig. 3), and both active and passive females with cubs chose denser habitats for their SS following disturbance, which differed from single bears (this paper, Paper II).



Fig. 3 Average sighting distance in initial sites (IS) and second sites (SS) for approached Scandinavian brown bear females with cubs (FC) and single bears (S) in different habitat types (see Table 1 for habitat type definitions), in order of habitat type (e.g. G-FC =mid-aged forest, females with cubs). Longer sighting distance indicates less horizontal vegetation cover (i.e. more open habitat). The error bars show the standard error of the mean.

None of the bears, whether female with cubs or single, displayed any aggression toward the observers and females with cubs showed the same patterns as single bears in terms of staying or leaving and FID, and moved greater distances than single bears following disturbance. We therefore concluded that females with cubs are not more aggressive than single bears, and suggest that the pattern we documented in Paper I for the risk of injury to unarmed people, may be because females with cubs choose more open habitat, as this makes them the more likely category of bear that recreational forest users would encounter.

### The effects of disturbance go beyond the initial reaction (Paper IV)

We used data from 293 experimental approaches to evaluate whether there were longlasting effects of disturbance beyond the immediate reactions we documented in Papers II and III. We analyzed the movement data with a Bayesian model formulation that used Markov chain Monte Carlo (MCMC) methods for estimation. A baseline of movement was determined using GPS movement data from 6 days prior to the approaches. Disturbance effects were assessed against a baseline linear model, where significant positive differences indicated more movement, and significant negative differences indicated less movement (than the baseline). We corrected for daylight hours to remove any effects of shortening days during fall.

In the week before the approach, bears showed a bimodal movement pattern, with two active peaks and two resting periods, with the activity peaks occurring mainly during crepuscular and some nocturnal hours (Fig. 4a). At the time of the approach, there was an increase in distance travelled, followed by a reduction in movement (Fig. 4b), which reflected the pattern observed here and in Papers II and III, where bears left their initial site and relocated to a second site.



**Fig. 4a**) Estimated time effect (every 30 min during the 24 h day) on daily activity pattern of brown bears in south-central Sweden during the week before the experimental approach. The figure shows the main resting period during midday and the second around midnight.



**Fig. 4b**) Estimated time effect on daily activity pattern of bears on the day of the approach, showing the initial escape after the disturbance event, followed by a reduction in movement. Vertical lines show the range of time when most approaches were conducted (start at  $11:26 \pm 59$  min, end at  $12:41 \pm 68$  min). The curves represent the mean of the distance travelled and the 95% credible intervals.

In comparison with the week prior to the approach, bears exhibited significant increases in movement during nocturnal hours, and significant decreases in movement during daytime in the days following the approach (Fig. 5). This pattern persisted even when controlling for daylight hours, seasonal movement increases, and effects of the individual. As in Paper III, the movement patterns of the bears were more altered (i.e. the disturbance effect was greater), when the vegetative cover at the initial site was denser, but here (Paper IV) we also documented an increased disturbance effect when observer-bear distances were shorter.



**Fig. 5** Estimated differences in distance travelled by brown bears in south-central Sweden, every 30 minutes during the 24 h day, comparing the post-disturbance movement pattern of the bears, after they were experimentally approached, with the pre-disturbance movement pattern of the previous week. Two continuous vertical lines show the range of time when most approaches were conducted. The average percentage of bears' movement variation at night (+) and daytime (-) after the approaches is indicated for all significant time periods with duration  $\geq$  1h 30 min. Differences at 30-min intervals were considered significant when the mean and the 95% credible intervals were all above or below zero.

By decreasing movement during daytime and switching to more nocturnal activity, bears may forgo foraging efficiency for safety, which can have consequences for weight gain and fat storage before the hibernation period. We conclude that research on the effects of human activity on large carnivores should also account for nonlethal effects that may lead to ecological and evolutionary consequences. The results from this paper, Paper II, and Paper III show that bears generally seek refuge in densely vegetated areas, and forestry and bear management should consider securing such potential refuges and emphasize that managers should issue recommendations to outdoor recreationists to avoid densely vegetated areas; something that should benefit bears and people alike.

### Does behavior near den entry explain higher risks of human injury at that time? (Paper V)

We analyzed activity data using statistical process control (SPC) to define when bears had significantly reduced their activity (predenning activity levels (PDA)) prior to hibernation, and compared this to GPS movement data. We used activity data with established threshold values to define when bears reached hibernation activity levels (HA). This information was used in conjunction with GPS data to document bear movement around the den prior to hibernation, including the number of visits from 1 August until arrival at the den site, as well as the rate of den abandonment. We used generalized linear mixed models to assess which demographic and human infrastructure variables affected timing of arrival at the den site (within a 50 m buffer zone of the den), time spent in the den area (<150 m from the den), and den abandonment, assessing the importance of the variables using model and variable AIC weights.

Bears began PDA either before (PDAB, 58%) or after (PDAA, 42%) arriving at the den area. Bears beginning PDA before arriving in the den area averaged  $2164 \pm 1690$  m and  $1.8 \pm 1.8$  days from arriving in their den area. There was no difference between PDAB and PDAA bears in when they reached HA, or how long they spent in their den area prior to HA once they arrived there, but PDAB bears reached HA levels significantly faster than PDAA bears, i.e. less time between the onset of PDA and the onset of HA. Females were more likely to be PDAB bears than males. PDA activity levels did not appear to be dependent on having located a den site, which suggests physiological rather than behavioral triggers for reductions in activity.

On average, bears arrived at their den sites on 24 October  $\pm$  11.4 days, but timing of arrival ranged from 6 October until 1 December. Timing varied between years, and depended on the reproductive category of the bear (females with cubs of the year, females with yearlings, single female, pregnant female or male). We found some influence of distance to
minor gravel roads, small permanent settlements, and hunting cabins/smaller summer dwellings on the timing of den entry, which may reflect social organization factors on the den selection of males and females, and younger and older bears. Younger bears tended to arrive at their den sites later than older bears. Bears spent  $4.6 \pm 3.8$  days in the den area before reaching HA, and the time spent in the area was mainly related to the bear's age. Younger bears spent longer time in the den area before HA, and as younger bears typically have less well established home ranges, this suggests that time spent may be dependent on a bear's experience and potentially familiarity with the area.

We documented high den abandonment rates (22%), but den abandonments were more common early in the den entry period (primarily before mid-December), which coincides with the moose-hunting season. Males were more likely to abandon their dens than females, and bears that had visited their den area before arriving at the den site were less likely to abandon their den. Most of the previously documented den abandonments have coincided with human disturbance, thus it is likely that the intensive moose-hunting activity, including the use of free-running dogs, affect the bears during this time. Bears that are familiar with their den areas may be aware of most regularly occurring disturbances, and may therefore either be aware of or select against them, thus reducing the risk of abandonment. The reduced human activity during midwinter and the potentially higher costs of den abandonment at that time of the year (Paper VI) are the most likely explanations for the lower abandonment rates documented after 15 December.

We concluded that denning arrival occurred over such a long time period that enforcing any hunting restrictions to minimize the risk of injury to hunters would be impractical for managers, fiercely unpopular among hunters, and could interfere with moose management objectives. Our results further suggested that any increased risk of bears exhibiting aggressive defensive responses near dens (Paper I) may have less to do with the presence of the den and

more to do with physiological changes associated with PDA; for example reductions in body temperature that may inhibit muscle functions necessary for effective flight behavior. We encourage further studies on the link between physiological changes, movement, and behavior.

#### The consequences of being disturbed in the den (Paper VI)

As a follow-up of potential health and behavioral effects of being captured in the den, we conducted an observational study of subadult bears' movements following den capture, using a combination of activity and movement data. Prior to the capture, all bears were in anthill (n = 6), soil (n = 4), rock (n = 2), or uprooted tree (n = 1) dens. After capture and handling, the bears were placed back into their original dens. The bears abandoned their dens on 12 of 13 occasions after remaining in the den  $3.2 \pm 3.6$  days after the capture. In 7 of 13 events, bears utilized intermediate resting sites ( $1.8 \pm 0.5$  sites) before arriving at their new permanent dens after  $12.4 \pm 7.0$  days. Intermediate sites were either beds or nest dens, and the new permanent dens were primarily beds or nest dens (n = 5) or rock dens (n = 4); the remaining were either uprooted tree (n = 1), anthill (n = 1), or soil (n = 1) dens.

Bears that abandon their dens during midwinter are likely to have a difficult time locating a new suitable den due to the snow cover. The new permanent dens in this study were of poor quality, with little bed material and poor insulation. This is likely to confer additional costs in terms of increased heat loss, which could add considerable strain to an already energetically costly period. We were unable to compare weight gains with bears not captured in the den, due to a lack of comparable data, but all bears survived and had gained weight until summer (one was however killed at the end of June due to interspecific predation).

We conclude that bears that abandon their dens suffer increased costs in terms of energy, but that they appear to be able to cope successfully with such costs. However, we advise against capturing older females that could potentially be pregnant while in the den, as den abandonment among pregnant females increases the risk of litter loss (Swenson et al. 1999).

#### Discussion

#### How dangerous are Scandinavian brown bears to humans?

In relation to other causes of death, animal-related or otherwise, the risk of being injured or killed by a large carnivore is very small (Conover et al. 1995, Linnell et al. 2002). In spite of this, many people living in areas populated by large carnivores experience fear to an extent that it keeps them from engaging in outdoor activities that are often deeply rooted in tradition, thus experiencing loss in perceived quality of life (Blekesaune and Rønningen 2010). There are relatively few recorded incidents of human injury or death caused by large carnivores in Scandinavia; in fact, in our review of human injuries caused by bears we verified only 33 casualties in 32 incidents in 1977-2012, which equates to slightly less than 1 incident per year (Paper I). This is quite a low number, especially when viewed in the light of a bear population that exceeds 3000 individuals, with considerable overlap between bear range and areas of human activity (forestry, hunting, other recreation, and settlements).

During our experimental approaches, when bears were aware of the approaching human, the vast majority left their location, before or after we passed them (Papers II – IV). We passed the bears at close distances, but were only able to detect them 15% of the time (Paper II), although we tended to detect females with cubs more often than single bears (Paper III). Importantly, we did not experience any threatening or aggressive behaviors directed at us as observers. This reaffirmed our view that the majority of human encounters with bears go unnoticed by humans, and that bears avoid confrontations with humans. This also explains the relatively low incidences of injury we documented (Paper I).

However, incidents do occur, with injuries ranging from minor to severe, including death (Paper I). The bear attacks resulting in injury in Scandinavia do not appear to be predatory in nature, which is similar to what has been documented in North America (Quigley and Herrero 2005), although a large number of black bear attacks with fatal outcomes were

classified as predatory (Herrero et al. 2011). The majority of incidents occurred during daytime hours, whereas predatory attacks tend to occur during nocturnal hours (Packer et al. 2011), and only two attacks resulted in fatalities.

None of the injuries were caused by food-conditioned bears; although, the bear involved in the most recent fatality was shot by managers at a slaughter remain site containing illegal material (dumping of domestic animal species is forbidden) near the site where the incident occurred (Kristoffersson, pers. comm.). Food-conditioned or habituated bears is a common factor in incidents between bears and people in North America, particularly in national parks (Herrero 1976, Herrero et al. 2005); a difference which most likely relates to differences in waste disposal and waste management. Instead, the factors most commonly involved in encounters resulting in human casualties in Scandinavia involved armed men engaged in hunting activities during fall, often including the presence of dogs and dens (Paper I). Indeed, the higher incidence of injuries was only significantly related to bear population increase for armed people, suggesting that the increasing injury rates has more to do with hunting activity and the increasing number of bears shot during the hunting season than an increase in general risk to people that live, work or enjoy outdoor activities within the bear range.

Bear hunting has become increasingly popular and as harvest quotas have increased, so have the number of hunters pursuing bears. As the quotas are set at county level, there is almost a "scramble" effect, with the most intense hunting effort during the first two weeks (end of August/first week of September). Despite this, few incidents involving hunters occur during this time; rather most incidents occurred from September onwards. The increasing risk of injury also coincides with the den entry period, and presence of a den is an important factor associated with injuries during October and November. We documented significant changes in bear activity that began even before they had arrived at their dens for half of the bears (Paper V). Activity decreased gradually during the fall period, and is likely connected

to physiological changes, such as decreases in body temperature, that could affect the efficacy of flight as a defensive response. The increase in injury risk may therefore be due to an interaction between hunting activity and aspects of brown bear behavior in the period leading up to den entry. The use of dogs as a hunting method may exacerbate this, especially in the presence of a den as a dog can be a tenacious pursuer, which further affects the bears' ability to successfully escape.

The most important factor associated with injuries of unarmed people was encounters with females with cubs. The assumption has been that bear females exhibit increased parental aggression associated with defense of offspring, which has been documented in a variety of taxa (Maestripieri 1992, Hubbard and Nielsen 2009). This was not supported by our experimental approaches, as females with cubs exhibited similar reactions as single bears; in fact, there was a tendency for them to leave more often and at similar distances to single bears (Paper III). However, females with cubs used more open habitat than single bears, possibly due to social organization factors, such as avoiding dangerous conspecifics (Steyaert et al. 2013), or to seek better foraging opportunities for herself and her cubs. Their use of more open habitat therefore makes them the category of bear most likely encountered by people, as the day habitat of single bears is generally too dense for hiking or berry picking (Paper II).

The Scandinavian brown bear is considered to be less aggressive than its American counterpart (Swenson et al. 1996), which has been suggested to be related to the severe bottleneck and continuous hunting pressure the population has experienced (Swenson et al. 1995, Swenson 1999). Herrero (1972) also related differences in aggression levels between black and grizzly bears to differences in habitat. Black bears, which primarily occur in forest habitats, have the option of seeking refuge as a form of defense, whereas grizzly bears, primarily occurring in open tundra habitat, have to rely on other defensive action. Both

removal of bold individuals and availability of alternative defensive responses may have contributed to the lower aggression levels exhibited by Scandinavian brown bears, and one should therefore consider such effects before extrapolating our results to other, unstudied, bear populations.

We conclude that the brown bear in Scandinavia is not aggressive, but that it can respond aggressively in threatening situations, particularly when wounded. Hunting situations combine the elements of surprise and threat, which could be why these are particularly associated with risk. There has been a trend of reduction of human injuries since 2008, which may be attributable to a combination of accumulating experience of bears among hunters, and an intensification of an information campaign by the SBBRP and the Swedish Association for Hunting and Wildlife Management (SAHWM) (Paper I). However, many hunters fire shots at the charging bear in order to stop the attack, which often only results in a wounded bear that can continue its attack. A study from North America suggests that use of weapons does not deter, nor alter, the outcome of attacks (Smith et al. 2012), and as attacks in Scandinavia appear defensive in nature, we suggest that authorities should advise against the use of weapons as a method of defense against a charging bear. There is a possibility of exacerbating the situation by wounding the bear, thus increasing the severity of the attack and injuries, although this was not the case in the study from North America.

#### Who is the prey in the human-bear relationship?

We documented dramatic responses by brown bears to our experimental approaches, in both immediate reactions and longer lasting effects (Paper IV). Bears responded to our disturbance by leaving in most instances (Papers II – IV), and generally relocated to a new site with denser horizontal vegetation cover. Bears appear to select daybeds with respect to human activity (Ordiz et al. 2011), and the choice of denser habitat therefore suggests that

bears seek a refuge where they can hide from people. The habitat selection of brown bears, on landscape and smaller scales, is affected by human infrastructure and activity, which is reflected in for example, habitat use patterns (Gibeau et al. 2002, Nellemann et al. 2007, Elfström et al. 2013, Steyaert et al. 2013) and den selection patterns (Elfström and Swenson 2009). This suggests that bears exist in a human-defined "landscape of fear", a term which describes effects of predation risk that affect species and their behavior beyond the predation effect, such as altered habitat use (Laundré et al. 2001). Although this most often is used to describe predator-prey relationships, evidence suggests that carnivores can be affected by humans in a similar way (Valeix et al. 2012, Wam et al. 2012). Disturbance can be considered akin to predation risk (Frid and Dill 2002, Beale and Monaghan 2004b), and our results suggests that this relationship also occurs between bears and humans in Scandinavia (Ordiz et al. 2011, Ordiz et al. 2012) and Papers II, III, IV). Females with cubs, particularly cubs of the year, exhibited the strongest immediate reactions to disturbance, by moving greater distances following disturbance (Paper III). The long-term effects of disturbance we documented were unrelated to sex and age (Paper IV). All bears reacted more strongly, in both immediate reactions and longer lasting effects, when there was denser vegetation at the initial site (Papers III, IV). Although denser habitats appear to provide refuge, they can also limit the bears' ability to fully assess the situation, which is expressed in stronger reactions to disturbance. After the initial responses, bears became more nocturnal for several days (Paper IV). There is therefore increased energy expenditure associated with flight responses, but also in potentially lost foraging opportunities that carry over for several days (Papers II-IV), which might affect energy budgets (White et al. 1999). Disturbances that occur during the hyperphagic period, which coincides with the hunting season, could therefore come at a considerable cost to the bears, which must build fat stores for the coming winter.

Human activities during the bear hunting season affect bear movements and diurnal behavior (Ordiz et al. 2012), and hunting activity may be responsible for the high den abandonment rates we documented in October/November. Human disturbance is involved in the majority of documented den abandonments (Swenson et al. 1997, Linnell et al. 2000), and this is therefore a likely explanation, although interspecific competition and social factors may be important as well (Libal et al. 2011). Males are more likely to abandon their dens (Paper V), perhaps because their greater body size better allows them to cope with the costs associated with relocation (Beale and Monaghan 2004a). The costs early in the season are likely to be smaller which may affect the propensity to leave more often in this period than during midwinter, also documented in North America (Reynolds et al. 1976). Bears that abandon their dens during midwinter are likely to incur greater costs in terms of energy expenditure, as relocation to a new den site can take several days and involve many intermediate bed sites (Paper VI). New dens are typically of lesser quality in terms of bed material and insulation, which could require greater energy expenditure to maintain the hibernating state.

Human activity has considerable effects on bears at small and large scales. Increasing encounters between humans and bears will therefore not only affect us humans, but the effects on the bear population are also likely to increase in significance, and could ultimately affect reproduction rates (Swenson et al. 1997). This should be taken into consideration when management plans or actions are devised.

#### Management perspectives

Management authorities require a wide variety of information about a species in order to manage it effectively (Decker and Purdy 1988). In the management of large carnivore-human conflicts information about large carnivore behavior can be used to develop

recommendations targeted at minimizing conflict, and to inform stakeholders and the public to improve knowledge of the species in question. This study provides information on the normal behavior of bears when encountering humans and identifies factors involved when injuries to humans occur and period of increased risk. This information can be used to direct management action to decrease the risk of injuries to humans, as well as develop information material to be distributed to the public.

The den entry period was identified as a very sensitive time for the bear, and a period of increased risk of human injury from bear attacks (Papers I, IV). Although there were variables that related to timing of den entry that had the potential of predictors, the large variations in timing within and between years makes them impractical to use in a management context. Moose hunting is the main activity related to injuries in this period, but implementing hunting restrictions spanning over the den entry period would not only be unpopular, but could also interfere with moose management objectives.

Management success is largely dependent on public acceptance of management measures and tolerance of the species in question, which in turn is linked to the level of knowledge and experience a person has of that species, as well as fear and perceptions of risk (Gore et al. 2009, Thornton and Quinn 2010, Lescureux et al. 2011, Glikman et al. 2012). Providing information about a species and its behavior to increase the level of knowledge and reduce fear has the potential of generating positive outcomes regarding tolerance and acceptance of the species, and therefore management actions. However, tolerance is not only affected by what a person knows, but also what he or she feels, and changing emotions may be more effective than increasing knowledge to improve tolerance (Glikman et al. 2012). Fear is also influenced by many factors, such as gender, geography or education (Røskaft et al. 2003, Sandström and Ericsson 2009, Blekesaune and Rønningen 2010), but also emotions, perceptions of self, and perception of risk (Prokop and Fancovicová 2010, Thornton and

Quinn 2010, Johansson and Karlsson 2011, Johansson et al. 2012). Managers should therefore consider the underlying factors of fear and attitudes, as well as consider the objective, i.e. the desired outcome, when designing information campaigns, and evaluate if the campaigns were successful in order to improve communication (Gore et al. 2006, Dunn et al. 2008, Gore et al. 2009).

In Scandinavia, many different organizations and government authorities are involved in large carnivore-human conflict management, depending on the nature of the conflict. Management would benefit from a greater degree of cooperation to establish common terminology in dealing with wildlife-human conflicts (Hopkins III et al. 2010) and what is considered to be normal or acceptable wild animal behavior. The results from this study can provide useful information for such a process in bear management.

Our results show that the normal behavior of bears is to avoid confrontations with humans. There are therefore some general recommendations for recreational forest users who want to avoid encountering bears: Avoid dense habitat, make noise, and consider the wind direction when choosing where to go. This will help the forest users to avoid disturbing bears that are resting in daybeds, and ensure that they are aware of the person well in advance. Such recommendations are not useful to hunters, who are also the group exposed to the greatest risk of injury. We documented a decrease in injuries, which may have been a result of a communication and hunter education campaign. Based on this, we suggest that this campaign continues and is further developed using the results from this study. Some have called for the possibility of using pepper spray to deter bear attacks, as is done effectively in North America (Smith et al. 2008). Availability of pepper spray in Sweden is subject to quite strict licensing laws, however, and our results indicate that it may not be necessary.

#### Future research perspectives

When you cannot say it better yourself, use a quote. Thus, I include one of my favorite quotes by Richard P. Feynman (1999:144):

"The same thrill, the same awe and mystery, come again and again when we look at any problem deeply enough. With more knowledge comes deeper, more wonderful mystery, luring one on to penetrate deeper still. Never concerned that the answer may prove disappointing, but with pleasure and confidence, we turn over each new stone to find unimagined strangeness leading on to more wonderful questions and mysteries – certainly a grand adventure!"

We stumbled over many questions and fascinating details during the course of this study, and I will mention a couple of them here.

*Denning physiology*. Our analysis of activity data in Paper V showed changes in activity independent of arrival at den sites. Lines of evidence suggest that there are molecular genetic mechanisms that trigger the onset of hibernation (Carey et al. 2003), and analysis of physiological parameters could determine if denning behavior triggers physiological changes, or if physiological changes trigger denning behavior. Data on physiological parameters will also enable better calculations of costs of den disturbance, and bring further clarity in the question of increased risk of injury during the den entry period.

*Physiology, behavior and defensive responses.* We touched upon it briefly in Paper V, but there are many aspects of behavior that links to physiology. Studies on ectotherms have linked lower body temperature to an increasing likelihood of aggressive defensive responses (Herrel et al. 2007, Cury de Barros et al. 2010). Bears are certainly not ectotherms, but their body temperatures during hibernation do decrease (Nelson et al. 1983). Some aspects of their physiology, and its effect on behavior, may therefore be similar. Muscle function is affected by temperature in many taxa, which provides one area of investigation (Bennett 1984, Bennett 1990, Ackerman et al. 2004). Defensive flight or fight responses are also regulated by regions in the brain, such as the amygdala, hypothalamus and the midbrain periaqueductal grey, which is also involved in autonomic regulation, i.e. body temperature, heart rate etc (Behbehani 1995, Misslin 2003, Siegel et al. 2010). It could therefore be interesting to investigate potential effects of brain chemistry linked to the onset of hibernation, and how this affects bear behavior.

*Will our results make a difference?* As outlined under management perspectives, the efficiency of communication campaigns to alleviate fear and increase tolerance of management actions may not only depend on the message communicated, but also <u>how</u> this message is communicated. Current research is providing interesting insights on the building blocks of fear (Røskaft et al. 2003, Berger 2007, Prokop and Fancovicová 2010, Johansson and Karlsson 2011, Lescureux et al. 2011, Johansson et al. 2012), and thus what aspects should be targeted in order to achieve communication objectives. One should therefore test different ways of conveying desired messages, and asses if they have managed to achieve the desired objectives, perhaps using information from this study, or studies like it.

*The use of weapons as a deterrent against bear attacks.* Many hunters who were injured by attacking bears had fired shots at the bear before the injury occurred. We did not assess whether this resulted in more aggression from the bear, or whether it affected the severity of sustained injuries or prolonged the attacks. As wounded bears are considered the most dangerous, such information would be useful to assess best practice when faced with a possible bear attack.

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**Compilation of papers** 

# **P**APER I

### Human injuries and fatalities caused by brown bears in Scandinavia 1977-2012

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#### ABSTRACT

Human injuries and fatalities caused by large carnivores increase public opposition to conservation efforts. We analyzed the pattern of human injuries (including fatalities) caused by brown bears *Ursus arctos* during the past 36 years in Scandinavia, which has the largest population of bears in Western Europe and where no fatalities had occurred for more than a century prior to our study. We verified 2 killed and 31 injured people, all men, in 32 incidents from 1977 to 2012. The number of incidents was positively related to number of hunter-killed bears and the estimated bear population size in Sweden, but this only applied to armed people, who suffered 80% of the injuries or fatalities. Incidents peaked during the fall hunting season and dogs were involved in 80% of the incidents involving armed people. This indicates that the population increase of bears has not elevated the general risk for injuries to people using or living in bear areas, but that the risk is linked to their outdoor activities, with a higher risk when hunting with dogs. Information campaigns targeted at hunters have probably reduced the number of incidents recently. To avoid bears, outdoor hikers and other nonhunters should avoid dense vegetation or make noise when entering such areas.

#### **KEYWORDS**

Bear-human interactions, human injury, hunting, large carnivores, mauling

#### INTRODUCTION

Many large carnivores can be dangerous to humans, resulting in both injury and death (Middaugh 1987, Herrero 2002, Rasool et al. 2010, Packer et al. 2011). These losses of human lives contribute to public opposition against the conservation of large carnivores (Packer et al. 2005). Increased opposition against large carnivores due to human and livestock losses occurs throughout the world, involving many large carnivore species (Löe and Röskaft 2004). In some places the number of attacks is increasing, likely due to habitat encroachment and depletion of natural prey, e.g. Packer et al. (2005). In Europe and North America, attacks may be increasing because of human expansion into large carnivore areas, but also because of increasing and expanding populations of some large carnivores into humanized areas (Enserink and Vogel 2006, Bruskotter and Shelby 2010). This can undermine large-carnivore protection efforts and population recovery, constituting a major conservation controversy and management challenges.

This is illustrated by the brown bear *Ursus arctos*, one of the largest and most widely distributed terrestrial carnivores in the Northern Hemisphere. Human recreational use has expanded into bear habitat in many places, but in some areas brown bear populations also have expanded into areas with dense human populations (Zedrosser et al. 2001), leading to more attacks on people, e.g. (Middaugh 1987, Herrero 2002).

The Scandinavian brown bear population has expanded its range and increased rapidly after a severe bottleneck that almost brought it to extinction around 1930 (Swenson et al. 1995). The population reached ~3300 bears in 2008 (Kindberg et al. 2011), and has been hunted with fall hunting quotas since 1981 in Sweden and 2006 in Norway.

European brown bears are less aggressive than those in North America (Swenson et al. 1996), and Scandinavian brown bears avoid humans both in space and time (Nellemann et al. 2007, Ordiz et al. 2011, Ordiz et al. 2012). An experimental study in Scandinavia showed that

brown bears avoid meeting humans, even when approached at a distance of 50 m (Moen et al. 2012). Nevertheless, bears recently have killed people in Scandinavia, after a fatality-free period of >100 years (since 1902 in Sweden and 1906 in Norway; Swenson et al. (1999)). Such incidences cause fear among inhabitants within the bear population range (Røskaft et al. 2003), and undermine efforts to conserve and manage the brown bear population in Scandinavia. For example, acceptance for the bear in Sweden, which encompasses the majority of the Scandinavian bear range and where most injuries have occurred, is decreasing (Sandström and Ericsson 2009). The most important variables explaining negative attitudes towards bears in Norway are people's concern for their and their families' safety (Røskaft et al. 2007).

Swenson et al. (1999) reviewed the Scandinavian literature from 1750-1962 and analyzed instances of bear-caused human injuries during 1976-1995. They concluded that the most dangerous situations involved a wounded bear, and that wounded bears may have been more common in the 19<sup>th</sup> century due to ineffective hunting techniques, which may have contributed to the apparently higher levels of fatalities then. They also identified several situations that contributed to increased risk of bears behaving aggressively, which were, in decreasing importance, the presence of cubs, proximity to a carcass, proximity to a den, and the presence of a dog (Swenson et al. 1999). Since 1995, the bear population in Sweden has increased threefold (Kindberg and Swenson 2010, Kindberg et al. 2011), whereas the number of bears killed annually by hunters has increased ninefold and an increasing number of people has been injured or killed by bears (data on bears killed during the bear hunting season was obtained from the Swedish National Veterinary Institute's (SNVI) database).

In order to reduce the incidences of bears injuring and killing people in Scandinavia, it is important to know why this occurs and why the number of injuries has increased. In this paper

we analyze the factors involved in all incidents where people were injured or killed by brown bears in Scandinavia from 1977-2012.

#### METHODS

#### The brown bear in Scandinavia

Brown bears reach landscape-wide densities up to 30 bears per 1,000 km<sup>2</sup> in Scandinavia (Bellemain et al. 2005), whereas the human density within their distribution is ~ 4 to 7 habitants/km<sup>2</sup> (StatisticsSweden 2008). Intensively managed coniferous forests cover the rolling landscapes in the south and central areas of the bear range, whereas more mountainous terrain in national parks and adjacent forested areas occur in the north (Zedrosser et al. 2006, Elfström et al. 2008). Logging, berry picking, fishing, and hunting are common human activities in the forest, and reindeer husbandry takes place in the central and northern portions of the bear range.

Brown bears leave their winter dens in spring and the mating season takes place in May-June (Dahle and Swenson 2003). From mid-July to den entry in October, bears accumulate fat during the hyperphagia season (Moe et al. 2007). In Scandinavia, female bears enter their dens in October (Friebe et al. 2001) and males can still be active until mid-November (Manchi and Swenson 2005). Bear hunting starts in late August and bears are hunted during daytime until the quotas are filled, usually after ~2 months (Ordiz et al. 2012). Small-game hunting starts at the end of August and moose *Alces alces* hunting starts in September and continues after the onset of bear winter denning. Thus, bears still encounter moose hunters after the quotas have been filled and bear hunting stops.

#### Humans injured or killed by brown bears in Scandinavia

We extracted information about people injured or killed by bears in Scandinavia from 1977 to 2012 from a careful review of scientific articles, books, hunting magazines, newspapers, police reports, and official records. All but one of the injured people were still alive when we conducted this study and were interviewed to confirm or supplement the information extracted from the written sources. Throughout this paper, we use the term "casualty" as one person injured (i.e. received medical treatment) or killed by a bear, and the term "incident" as a situation where one bear caused one or more casualties.

For each incident we recorded and analyzed the following variables: date, time, month, year, location of incident, number of casualties, gender and age of the persons involved, activity of the persons when the incident happened, whether or not the persons were carrying firearms, whether or not the persons shot at the bear before being injured or killed, the shooting distance, distance to bear when the persons first observed the bear, visibility of the habitat (estimated subjectively in meters by the persons interviewed), bear age and sex, if the bear had been wounded prior to the incident, the presence of bear cubs, the presence of a carcass, the presence of a bear den, and the presence of dogs and their behavior. We only counted dogs as present if they had been in the vicinity of the incidents when they occurred and therefore could have affected the bear's behavior. Some incidents occurred while the dogs were elsewhere, and we therefore concluded that the dogs had not affected the bear's behavior.

#### **Statistics**

We used generalized linear models in R (R Development Core Team 2012) to test for the effects of the number of brown bears shot during ordinary bear hunting and the estimated

brown bear population size in Sweden on the number of incidents. We used two methods to obtain annual estimates of the number of bears in Sweden during 1977-2012:

- Estimates from the literature for specific years (1976: Bjärvall et al. (1990); 1991: Swenson et al. (1994); 1993: Swenson et al. (1995); 1994: Kindberg and Swenson (2010); 1996: SOU (1999); 2000: Kindberg and Swenson (2010); 2005: Kindberg and Swenson (2006); 2008: Kindberg et al. (2011)), corrected for methods used. The estimates for 1991, 1993, and 1996 were based on helicopter counting and were therefore corrected for underestimation by adding 24.6% to the estimate given (Solberg et al. 2006).
- 2. Growth curve calculations: For estimating the bear population in years without an estimate given in the literature, we used a standard exponential growth curve equation and calculated the number based on the estimates given for the closest years before and after, e.g. the estimate for 1977 was based on a standard exponential growth curve between the estimate given for 1976 and the estimate given for 1990. The estimates after 2008 were based on a standard exponential growth curve with a 4.5% annual increase (Kindberg et al. 2011).

Initial analyses revealed that a majority of incidents involved armed people; therefore, we also conducted the analyses separately for incidents involving armed and unarmed people, using a Poisson link for incidents involving armed people and a binomial link for incidents involving unarmed people, because a maximum of one incident involving unarmed people occurred during a year.

#### RESULTS

In a total of 34 incidents, bears injured 34 and killed 2 people in Scandinavia from 1977 to 2012. Two of these incidents involved anesthetized bears that became conscious unexpectedly

and mauled a total of 3 researchers. We excluded these two incidents from further analyses. Thus, we documented that 33 people (casualties), all of them male (age 12-75), were injured (n=31) or killed (n=2) by brown bears in 32 incidents from 1977 to 2012. Most casualties occurred in October (n = 9), September (n = 8), and November (n = 6), comprising 69% of all incidents. Half of the incidents in October and all incidents from November to March were in the vicinity of a den, comprising 41% of all incidents (Fig. 1). The number of casualties has been low during the last 4 years (2009-2012), with one unarmed person and 3 hunters being injured. This is in contrast to the preceding 5 years, when 11 hunters were injured (Fig. 2).

The number of incidents in Scandinavia involving armed men was statistically and positively related to both number of bears shot by hunters and the estimated bear population in Sweden (Table 1, Fig. 2). However, the number of incidents with unarmed men was not statistically related to either the number of bears shot or the population size (Table 1, Fig. 2). In most of the 32 incidents, the people were hunting and thus armed (n=24). In one incident, 2 moose hunters were injured by the same bear, resulting in 2 casualties in the same incident. Nonhunters included 7 unarmed men and 2 armed men, who reported that they were not hunting, but examining their hunting grounds and visiting their livestock on open range (Fig. 3).

In 18 incidents the armed men shot at the bear before being injured. These men first saw the bear on average  $14\pm15$  m (mean  $\pm$  SD) away, and the first shot was fired at  $9 \pm 12$  m. In 6 incidents armed men did not shoot before being injured; they first saw the bear on average 22  $\pm 33$  m away. In 6 incidents unarmed men discovered the bear for the first time at  $9 \pm 10$  m.

One or several of the previously identified aggravating factors that increased the risk of a bear reacting aggressively to an encounter with a human, i.e. a wounded bear, presence of cubs, proximity to a carcass, proximity to a den, and presence of dogs (Swenson et al. 1999), were present in all the 32 incidents (Table 2). Dogs were present in 69% of the incidents and

were the most frequent factor involved when armed men were injured or killed (80%), whereas presence of cubs was the most frequent factor involved in incidents with unarmed men (67%; Table 2). More than one factor was present in 66% of the incidents and three factors were involved in 16% (Table 2). In 19 of the 21 incidents with dogs present, the dog was chasing or barking at the bear prior to the injury. In one of the 19 incidents, the dog was on a leash, but was released during the incident, whereas in the two remaining cases the dog owner was killed (one armed, one unarmed), hence the behavior of the dog during the incident was unknown (Table 2).

#### DISCUSSION

The number of people injured and killed annually by brown bears in Scandinavia increased with the increasing number of hunter-killed bears and with the increasing bear population size in Sweden, but this was true only for armed people, who were primarily hunting bears and moose. We found no relationship with the size of the brown bear population and the number of injured and killed unarmed people. Forestry is a major industry and outdoor activities are very popular in Scandinavia, including hiking, berry and mushroom picking, camping, hunting, and fishing. Hunters are thus a minority of the people using the forest and they hunt during a relatively short proportion of the time when bears are active. Nevertheless, hunting was still the major activity involved in the incidents with bear-caused injury or fatality, as reported earlier by Swenson et al.(1999). This indicates that the recent increase in the bear population in Scandinavia has not increased the general risk of bear-caused injuries or death among people using or living in areas inhabited by bears, but rather that the risk is linked to the type of outdoor activity people are involved in.

Increased bear hunting quotas in the last decade have led to more interactions between hunters and bears. Bears are shot by specialised bear hunters and moose hunters, who use the

same dogs and hunting techniques for both species (Bischof et al. 2008). Loose dogs bark to keep the animal at the site while the hunter approaches the dog quietly, using cover to come close enough to shoot the hunted animal kept at bay by the dog. Brown bears are crepuscularnocturnal in Europe (Kaczensky et al. 2006, Moe et al. 2007), and Scandinavian bears become even more nocturnal when the bear hunting season starts (Ordiz et al. 2012). Bears select dense vegetation cover around their daybeds, even more so during fall when hunting takes place, most likely to avoid detection (Ordiz et al. 2011). The short distance to the bear when first seen and the short visibility in the forest in all incidents  $(24 \pm 24 \text{ m})$ , indicates that bearcaused injuries occurred primarily when bears were surprised in dense vegetation, or when shot at very close distances. The high percentage of incidents involving armed people (78%) and the percentage of dogs present in those incidents (80%) are thus related to hunting and the way it is performed. Studies on other large carnivore attacks have also found that mostly men were affected (e.g. Gurung et al. 2008), and that they often were hunting, e.g.(Treves and Naughton-Treves 1999). In this context, it is interesting to note that fear tends to be higher among women than men (Prokop and Fancovicová 2010, Thornton and Quinn 2010), also in Norway (Røskaft et al. 2003, Blekesaune and Rønningen 2010), even though no women have been injured by bears in Scandinavia since accurate records began.

The order of factors involved in incidents that we documented was different from that reported earlier, with dogs being the most frequent factor involved. We suggest that the increase of bear hunting quotas and the extensive use of dogs during hunting is a reasonable explanation for the currently larger prevalence of dogs involved in the incidents than in the study by Swenson et al. (1999).

Most of the attacks occurred in September, October and November (71%), which includes the start of the annual moose hunting season (in September) and the period with the highest hunting effort for moose in Sweden (Fig. 4). By mid-November most bears have denned
(Manchi and Swenson 2005), which may make it easier to get close to the bear when hunting dogs or hunters approach the den. Escaping from a den while a baying dog is present is likely to be a stressful situation where the bear has limited ability to escape, which may increase the risk of an aggressive defensive response. However, the risk of injury increases before most bears have entered their dens, and there is evidence to suggest the bears undergo activity reductions, probably associated with physiological changes, that may make them less able to evade approaching threats even before they have settled into their dens (Sahlén et al. in prep.-a). Such changes may make flight a less effective defensive response. Thus, in situations where the bear experiences reduced physiological activity or has already entered its den, the risk of aggressive defensive responses may be higher, particularly when baying hunting dogs are involved. Higher human presence and hunting activity appears to be important factors also elsewhere, as a review on bear attacks in Alaska between 1900 and 1985 found that most attacks occurred during summer months and during the fall hunting season (Middaugh 1987).

Rasool et al. (2010) recorded 417 cases of human injuries and deaths caused by Asiatic black bears *Ursus thibetanus* and documented a low mortality rate (2.4%), which they attributed to the defensive nature of the attacks; 93% occurred after sudden encounters in close proximity and 97% occurred during daytime, when people entered bear habitat (Rasool et al. 2010). The incidents in Scandinavia resembled this pattern, where most casualties were hunters out during the day, when bears rest in concealed spots (Ordiz et al. 2011). In clear contrast, predatory attacks performed by "man-eating" large carnivores usually occur at night, e.g. (Packer et al. 2011). In agreement with our results, bear attacks in Europe do not reflect predatory behavior, but rather show bears defending themselves and their cubs (Swenson et al. 2000, De Giorgio et al. 2007). Indeed, the presence of cubs was the most frequent factor involved in incidents with unarmed people (67%; Table 2), and none of these incidents (n=5) involved a fatality. However, there was one such fatality in Finland in 2006, where a male

11

jogger was killed by a female accompanied by a cub (De Giorgio et al. 2007). Brown bear females with cubs are also commonly involved in defensive attacks elsewhere and usually after sudden encounters, e.g. (Herrero and Higgins 1999, 2003).

Large carnivore attacks are increasing in some areas and decreasing in others, sometimes in relation to increases and decreases of large-carnivore populations (Packer et al. 2005, Gurung et al. 2008, Inskip and Zimmermann 2009). The number of brown bear-caused human injuries and fatalities in Alaska apparently increased during the last century, because of humans encroaching into bear habitat and an increasing human use of the outback (Middaugh 1987, Miller and Tutterrow 1999). This pattern is consistent throughout North America, with most of the injuries/fatalities occurring inside national parks and with increasing number of visitors (Herrero 2002). Herrero et al. (2011) also reported increasing numbers of injuries/fatalities caused by American black bears Ursus americanus throughout their range between 1900 and 2009, with 86% of the fatalities occurring after 1960, and a positive relation between the number of injuries/fatalities and human population density. After managers prevented black and brown bear access to human-derived food in North American national parks, most injuries/fatalities have been related to sudden encounters with visitors, and not to food-conditioned bears (Gniadek and Kendall 1998, Herrero 2002). As in Scandinavia, most people injured by brown bears outside national parks in North America are hunters, e.g. (Herrero and Higgins 1999). Wounding a bear also increases the risk of suffering an attack and injury elsewhere, e.g. Turkey (Ambarli and Bilgin 2008). Many of the incidents in Scandinavia involved moose hunters that were not out to hunt bears. Many of them also reported that they thought they were approaching a moose, not a bear, and that they fired their weapon in defense before the injury occurred. A review of bear-caused injuries in Alaska involving firearms revealed that the use of firearms failed to stop an aggressive encounter in

the majority of cases and that the injury rates were not affected by whether or not a firearm had been used (Smith et al. 2012).

The number of people injured in Scandinavia seemed to have decreased during the last 4 years, after a peak in 2004-2008. This may be, at least in part, because hunters are becoming aware of the increasing likelihood of sneaking up on a bear instead of a moose, and are therefore more cautious when approaching their dogs that are holding an animal at bay. The increasing awareness is likely a combination of experience and the intensification of an information effort since 2007/2008 conducted by the Scandinavian Brown Bear Research Project (SBBRP) and the Swedish Association for Hunting and Wildlife Management (SAHWM). Hunters tend to perceive changes in game populations accurately, but with a delay compared to the actual documented change, because the accumulation of experience over time (Swenson and Sandegren 1996). The bear population has increased, but it may have taken time for hunters to experience and therefore perceive the change. As their risk perception has changed, so may the behavior that predisposes them to risk. In addition, the SBBRP has written several scientific reports and popular articles and held numerous lectures on these issues, and the SAHWM has conducted educational programs to inform Swedish hunters about the dangers of hunting bears. The recent decrease in number of hunters injured by bears, in spite of the increasing bear population and number of bears shot annually, suggests that the information campaigns, educational programs as well as the hunters' own experiences, might have increased awareness and contributed to reduce the number of hunters injured or killed by bears.

# **Management implications**

Although more people are killed by dogs, horses or cattle, all-terrain vehicles, or snake bites than by bears (Middaugh 1987, Swenson et al. 1999), the attitudes of people towards

13

bears and other large carnivores reflect their concerns about personal safety (Røskaft et al. 2007), in spite of the relatively low risk they pose to humans. However, fear may be elevated for situations that have a low probability of occurring, but have potentially severe consequences when they do (Decker et al. 2002). In addition, when incidents with large carnivores do occur, they tend to generate much media attention, which can influence people's attitudes (Wahlberg and Sjoberg 2000). How people perceive risk affects the tolerance they have for management decisions (Gore et al. 2009). Therefore, bear attacks have an impact on bear conservation (Servheen et al. 1999, Swenson et al. 2000) and it is essential to provide managers and the general public with accurate and correct information regarding the risks that bears pose to people and how these risks can be reduced. Such information is now available from more than 300 encounters at a distance of approximately 50 m between bears and simulated hikers that have been conducted in Sweden (Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. in prep.-b). None of the bears involved reacted aggressively toward the researchers; rather they ran away and/or hid in more dense vegetation (Ackerman et al. 2004, Moen et al. 2012, Ordiz et al. 2013, Sahlén et al. 2013,

As the nature of bear attacks in Scandinavia is defensive, and the injury rate of armed men was positively correlated to the harvest quotas and population size, hunting requires specific management attention and education effort in order to reduce the number of casualties caused by bears. Continually providing information to the hunters on the risks of encountering bears during moose hunting and how bears behave during such situations must be a prioritized task for managers and hunting associations. Such information campaigns and education schemes may already have contributed to a reduction in the number of bear-caused injuries/fatalities among hunters in the last 4 years.

Bears rely on dense cover to avoid interactions with people during daytime and use areas with low accessibility for people (e.g. steep and rugged terrain (Nellemann et al. 2007, Martin

14

et al. 2010). In order to avoid bears, outdoor hikers and berry pickers should avoid dense vegetation or make noise (talk loud) when entering patches of forest with low visibility to warn bears of their presence, as a safety measure for both bears and people (Ordiz et al. 2011, Ordiz et al. 2013). However, fear also depends on people's perception about uncertainties about their own reactions (Johansson et al. 2012), and educational or information efforts aimed at increasing tolerance for the species and for management actions should therefore address both aspects. Such efforts may be more effective if they contain experiential elements, or if the informant has direct experience themselves (Wahlberg and Sjoberg 2000). One should also consider special communication efforts directed to women, as they typically experience more fear of large carnivores than men (Røskaft et al. 2003, Blekesaune and Rønningen 2010, Prokop and Fancovicová 2010, Thornton and Quinn 2010).

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# TABLES AND FIGURES

Table 1: Generalized linear models for the effects of numbers of brown bears shot during ordinary bear hunting in Sweden (Bears shot) and estimated brown bear population size in Sweden (Bear pop.) on the number of incidents (n=32) where brown bears injured or killed armed or unarmed people in Scandinavia 1977-2012.

Incidents	Parameters	β	Std.Error	d.f.	Z	р
All	Bears shot	0.004	0.002	35	2.477	0.01
	Bear pop.	0.000	0.000	35	3.291	< 0.01
Armed people	Bears shot	0.004	0.002	35	2.122	0.03
	Bear pop.	0.000	0.000	35	2.975	< 0.01
Unarmed people	Bears shot	0.006	0.005	35	1.411	0.16
	Bear pop.	0.000	0.000	35	1.561	0.12

Table 2: The factors: Dog (the presence of a dog), Den (den observed at the site), Wounded bear (bear wounded prior to the incident), Carcass (carcass observed at the site) and Mother w/cubs (the bear was a female with cubs), present during incidents (n=32) when brown bears wounded or killed people in Scandinavia 1977-2012.

				No. of
Armed	Factor 1	Factor 2	Factor 3	incidents
Yes	Dog	Den	Mother w/cubs	1
	Dog	Wounded bear	Carcass	3
	Dog	Den		7*
	Dog	Wounded bear		4
	Dog**	Carcass		1
	Dog	Mother w/cubs		2
	Dog			2
	Den			2
	Carcass			1
	Mother w/cubs			2
No	Dog	Den	Mother w/cubs	1
	Dog	Carcass		1*
	Den	Mother w/cubs		1
	Den			1
	Mother w/cubs			3

\* One person killed \*\* Dog in leash



Figure 1: Number of people injured or killed (casualties) by brown bears by month in Scandinavia, 1977-2012.



Figure 2: Numbers of incidents (n=32) where armed and unarmed men were wounded or killed by brown bears in Scandinavia, in relation to the number of bears shot during ordinary brown bear hunting and the estimated population size in Sweden, 1977-2012. An incident is a situation where one or more people were injured or killed.





# **P**APER II

# Behaviour of Solitary Adult Scandinavian Brown Bears (*Ursus arctos*) when Approached by Humans on Foot

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#### Abstract

Successful management has brought the Scandinavian brown bear (*Ursus arctos* L.) back from the brink of extinction, but as the population grows and expands the probability of bear-human encounters increases. More people express concerns about spending time in the forest, because of the possibility of encountering bears, and acceptance for the bear is decreasing. In this context, reliable information about the bear's normal behaviour during bear-human encounters is important. Here we describe the behaviour of brown bears when encountering humans on foot. During 2006–2009, we approached 30 adult (21 females, 9 males) GPS-collared bears 169 times during midday, using 1-minute positioning before, during and after the approach. Observer movements were registered with a handheld GPS. The approaches started  $869\pm348$  m from the bears, with the wind towards the bear when passing it at approximately 50 m. The bears were detected in 15% of the approaches, and none of the bears displayed any aggressive behaviour. Most bears (80%) left the initial site during the approach, going away from the observers, whereas some remained at the initial site after being approached (20%). Young bears left more often than older bears, possibly due to differences in experience, but the difference between ages decreased during the berry season compared to the pre-berry season. The flight initiation distance was longer for active bears (115 $\pm$ 94 m) than passive bears (69 $\pm$ 47 m), and was further affected by horizontal vegetation cover and the bear's age. Our findings show that bears try to avoid confrontations with humans on foot, and support the conclusions of earlier studies that the Scandinavian brown bear is normally not aggressive during encounters with humans.

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#### Introduction

Human disturbance can influence wildlife negatively by e.g. preventing successful breeding [1,2], causing animals to avoid quality foraging areas or quality habitats [3–6], altering activity patterns [7,8], or distribution patterns [9,10], or even causing increased mortality [11]. Carnivores often present a special challenge to managers, due to the negative attitudes associated with carnivore-human conflicts, e.g. killing livestock, threats to human life and challenges regarding reintroduction [12–15]. Bears (Ursus spp.) are commonly associated with undisturbed areas away from high human densities. Human disturbance can cause grizzly bears (Ursus arctos L.) to use less productive habitats [16-18] and habitats with low levels of human use [19]. The Scandinavian brown bear tends to avoid habitats close to forest roads, cabin resorts, and towns [20,21] and brown bears in Finland have been displaced from previously used habitat by large-scale mechanised forestry [22].

The introduction of bounties in Sweden (1647) and Norway (1733), and the subsequent intensive hunting [23,24], reduced the Scandinavian brown bear population from 4,000–5,000 individuals in the 1850's to approximately 130 animals around 1930 [25]. Brown bears received protection in Sweden in 1927 and in

Norway in 1973, however the Norwegian population was functionally extinct by 1931 [25]. After a slow recovery, the Scandinavian population consisted of around 700 individuals in 1995 [25]. The latest estimates are about 3,300 individuals in Sweden [26] and a minimum of 166 individuals in Norway [27]. Whereas the brown bear population has increased in size and distribution, the areas undisturbed by humans have decreased rapidly. An expanding bear population and extending human activities into the remaining habitats will most likely lead to more frequent bear-human encounters. In fact, there has been an increase in bear-caused human injuries since 1977, especially for hunters, and two people have been killed (O.-G. Støen et al. unpublished). In 2006, a bear-caused human fatality was documented in Finland, the first one since 1936 [28]. The incidents in Sweden have received high media attention and may have contributed to a documented reduction in Swedish people's tolerance towards bears [29]. This reduction in tolerance is more prominent in counties with carnivore presence than the rest of the country. People in Norway are also more afraid of brown bears and wolves (Canis lupus L.) than of the two other large carnivores in the country, Eurasian lynx (Lynx lynx L.) and wolverine (Gulo gulo L.) [30]. However, bear aggressiveness varies geographically and the brown bear in Scandinavia appears to be less aggressive than

those in Russia and North America, and only truly dangerous when wounded [31].

The management challenges of the increasing brown bear population include not only people's fear of carnivores in general, but also fear of the unknown [32]. Informing people about the biology and normal behaviour of large carnivores is a good management strategy to reduce people's fear [33] and increase public acceptance. This is essential to maintain sufficient population sizes in areas where carnivores already are present, as well as a requirement for a successful reintroduction of bears [34]. Although most of the bear-injured people were hunters, there are many more hikers and other recreational users in Scandinavian forests, where the public has the right of trespass on private lands. With increased numbers of bear-injured people and declining acceptance of bears, it is important to document how brown bears normally behave when approached by humans.

In this study, we have used technology that allowed us to determine the behaviour of the bears when encountering humans on foot without observing the bears in the field. Our main goals in this study are 1) to describe how solitary adult bears react to human approaches and 2) to identify factors affecting how bears react to human encounters. This knowledge can help managers when giving advice about what people in Scandinavia can expect when walking in areas with brown bears.

#### **Materials and Methods**

#### Study area

This study was conducted in the southernmost reproduction area of the Scandinavian brown bear population in Sweden (61°N, 14°E). The area consists of gently rolling hills, and most of the area (>90%) lies below the timberline ( $\sim$ 750 m a.s.l.) [35]. The forest is heavily managed and dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* H. Karst). About 8% of the forested areas are clear-cuts, and about 40% of the forest is younger than 35 years [36]. The area is sparsely populated by humans, but there is an extensive road system, consisting of small gravel roads and paved public roads [21]. The bear population in the area is hunted and the density is about 30 individuals per 1000 km<sup>2</sup> [37,38].

#### The bears

We approached 21 female and 9 male radio-collared solitary adult bears; 4 to 19 years old. Of these, 14 females and 3 males were approached in more than one year. The bears were equipped with GPS Plus-3 or GPS Pro-4 neck collars (VECTRONIC Aerospace GmbH, Berlin, Germany), and a VHF transmitter implant (IMP 400L) (Telonics, USA). Methods used for marking and capturing bears have been described earlier [39,40]. All the bears used in this study were captured and handled in March -May the year of their respective approaches, i.e. 1-4 months prior to the start of the approach experiments. Bears can be captured for the first time both as adults and subadults, and older bears have therefore not necessarily been handled more often than younger bears. Bears in the study area reach 90% of their adult size at 4.1 years of age, and we defined the bears as adult when 4 years or older [41]. If the bear was not followed from birth, the age was determined by counting annuli of a cross-section of one of the premolar roots [42]. The bears were approached a maximum of six times each year, and we waited at least fourteen days between each approach of the same individual. The Scandinavian brown bear population is hunted, and the annual brown bear hunting season in Sweden starts on 21 August and ends on 15 October or when quotas are filled. The capturing of the bears were approved by the Swedish Environmental Protection Agency (permit Dnr 412-7327-09 Nv) and the approaches were approved by the appropriate ethical committee i.e. Djuretiska nämnden in Uppsala, Sweden (permit C 47/9).

#### The approaches

We conducted 169 approaches; 19 in 2006 (29 June to 14 August), 61 in 2007 (7 June to 4 October), 76 in 2008 (6 June to 24 October), and 13 in 2009 (13 August to 10 October). We divided the field seasons into a pre-berry season (spring/early summer) and a berry season (summer/autumn), because the bears could potentially change behaviour after entering the period of hyperphagia in late summer. We used the date when we first observed fresh berries in the scats to separate the seasons; 20 July in 2006, 13 July in 2007, 14 July in 2008. In 2009, all the approaches were conducted in the berry season. Before an approach, we programmed the collars to register a GPS position every minute for three hours. Programming of the collars was made via a web-based SMS scheduling service approximately a week before the approach. Of the theoretical maximum of 181 GPS positions per bear per approach, we received  $66\pm21$  (mean  $\pm$  SD) positions (37 $\pm$ 12% of theoretical maximum) in 2006,  $89\pm30$  positions (47±16%) in 2007, 145±43 positions (80±24%) in 2008, and  $177\pm3$  positions (98±1%) in 2009. The increasing proportion of the theoretical maximum of positions received over the years was probably due to improved quality of the GPS collars, with increased position accuracy and fewer erroneous positions (Robert Schulte, Vectronic GmbH, pers.comm). The positions were stored, sent to a base station via SMS, and downloaded to a computer. The approaches started after one hour of 1-minute positions, between 11:00 hrs and 16:00 hrs local time. This time of the day was chosen because the bears are usually inactive in a resting site at this time [43], and because this is the time when most people are in the forest.

Prior to the approach, the bears were located using triangulations of the VHF signals from the radio collar and/or the implant using a portable receiver, a roof-mounted omni-directional antenna, and a hand-held yagi-antenna. One to four people, hereafter referred to as the observers, conducted the approaches. During the approach, the bear was monitored with VHF-tracking equipment, which enabled the observers to monitor the bear's movements while passing close by. The approaches started  $869 \pm 348$  m (n = 154) from the bear, and were directed so that the observers would pass the bear upwind of it, with the wind coming at a  $90^{\circ}$  angle, and at a distance of approximately 50 m. The wind strength was measured when passing the initial site using the Beaufort Wind Scale (scale from 1 (1–3 mph) to 12 (73+ mph)). The observers continued for 500 m, and then walked back to the starting point with a minimum distance of 500 m from the bear's original location. The observers talked with each other and kept a normal hiking pace of 3.4±0.6 km/h (minimum 2.1 km/h, maximum 5.1 km/h). When just one observer approached the bear, this person talked to him- or herself. During the approach, the track of the observers was registered with a hand-held GPS receiver (Garmin GPSMAP 60CSx (Garmin Ltd., USA) or Magellan SporTrack Color (Thales, Santa Clara, California, USA)) that was programmed to record positions every 10 m. After the approach, the observer's tracklog was downloaded into the computer.

#### Passive and active bears

Based on the GPS positions from the start of the 1-minute positioning to the start of the approach, hereafter referred to as the control period, we could recognise two behaviours, passive and active. The bear was regarded as passive if it remained within a limited area that had a diameter between the outer GPS positions  $<70 \text{ m} (30 \text{ m}\pm13 \text{ m}, \text{minimum 8 m}, \text{maximum 69 m})$ , hereafter referred to as a cluster. Passive bears were usually resting, and we usually found daybeds in the cluster. The bear was regarded as active if the positions indicated movement. The distance between the two outermost positions were on average  $411\pm327 \text{ m}$  (minimum 85 m, maximum 1092 m), and active bears were usually foraging. Depending on behaviour, as described above, the bears were grouped into passive and active for analysis. Most bears were either active or passive during the whole period, but 14 bears were active during the control period and became passive just before the approach started and were therefore analysed as passive bears. Eight bears were therefore analysed as active bears.

#### Habitat description

One to 41 days (median 4 days) after the approach, field personnel visited the clusters and described the vegetation where the bear had stayed during the control period, hereafter referred to as the initial site, and the cluster where the bear settled down after being disturbed, hereafter referred to as the second site. In cases where the bear was active during the control period, the last GPS position from the bear during the control period was defined as the initial site. We searched for daybeds, excrements, and other bear signs at the sites. In 2006, the horizontal vegetation cover in the initial and the second site was measured with an umbrella that was 95 cm in diameter and divided into eight equal sectors. The horizontal vegetation cover was measured at 10 m in every cardinal direction, and the sectors were scored for visibility (0 = 0 - 1)33% visibility, 0.5 = 33-66% visibility and 1 = 66-100%) with a maximum score of 32 if fully visible. The sums of the scores were used in the analyses. In 2007 to 2009, we measured the horizontal vegetation cover in the initial and at the second site as the sighting distance with a cylinder; 60 cm tall and 30 cm in diameter. This cylinder was divided into 2 colours, a red upper part and a white lower part [44]. We placed the cylinder in the bed, or in the midpoint of the initial site/second site when no bed was found, and walked in the cardinal directions until we no longer could see the cvlinder.

To use the horizontal vegetation cover data from 2006, we estimated the comparability of the two sampling methods by using both the umbrella and the cylinder in 53 plots in 2007. The sum of the umbrella score in all cardinal directions (Sum<sub>UMBRELLA</sub>) was regressed on the average of the distances in the four cardinal directions using the cylinder sighting distance (Average<sub>CYLINDER</sub>). The linear equation was Average<sub>CYLINDER</sub> = 10.7+(0.73\*Sum<sub>UM-BRELLA</sub>). The regression analyses showed a linear relationship ( $R^2$ adj = 53.7\%, n = 53, p<0.000). For the analyses, we used the estimated sighting distance from this equation for 2006, and the observed sighting distance for 2007, 2008 and 2009.

#### Data analysis

We did not find any difference in the maximum distance bears moved between the first and the second hour of 1-minute positions for bears that had been scheduled for an approach, but were not approached (two-tailed t-test:  $t_{21} = 0.28$ , p = 0.78, n = 22). Hence, we assumed that the bears would behave similarly in the control period and the following hour if they had not been disturbed. We calculated the speed between two successive positions (m/min), and transformed the data by (log(speed\*100)) to normalise the residual distribution. Using statistical quality control, we estimated an upper control limit (UCL) [45] for the speed between two positions for passive and active bears during

the control period. Only data from bears that stayed passive or active during the entire control period were used in the calculations of UCL. Based on UCL, we judged that passive and active bears had been disturbed once they reached speeds above 33.5 m/min (2.01 km/h) and 101.3 m/min (6.08 km/h), respectively.

If the bear remained in its initial site while being approached, we defined the tolerance distance as the shortest distance to the passing observers. When the speed between two positions exceeded the behaviour-specific UCL, we used  $\mathrm{ESRI}^{\textcircled{B}}\operatorname{ArcMap}^{\mathrm{TM}}$ 9.2 [46] to determine if this reaction occurred before or after the observers passed the bear. The distance to the observer at the time of the reaction was defined as the flight initiation distance (FID) [47–52]. When calculating FID, we did not include approaches where more than one GPS position from the bear was missing around the time of disturbance. The GPS position prior to the GPS position exceeding UCL was defined as the FID, and hence used for the calculation of the distances to the observers. In 15 approaches, the bears left the initial site, but the speed in the movement did not exceed UCL and we could therefore not determine FID. In four approaches, the bears left the site after the observers had ended their approach, and FIDs were not determined.

After leaving the initial site, some of the bears settled in a second site before the 1-minute positioning period was over. The distance between the coordinates of the beds in the initial and the second site was defined as the distance moved. At sites where a bed was found, but no coordinates were registered by field personnel, the midpoint of the cluster was used as the position of the site (n = 27). For active bears, we used the GPS position of FID as the start to determine the distance moved. We defined the time the bear spent active after disturbance as the time interval in minutes from the GPS position of FID to the first position in the second site.

We used generalised linear mixed models to determine if various variables were related to whether the bears remained or moved (using binomial link function), and linear mixed models for the analysis of the FID. The initial models consisted of the following variables and interactions: Age of the bear; Sex of the bear; Cover (sighting distance in the initial site); Activity of the bear (passive = 0; active = 1); Season (pre-berry = 0; berry = 1); Minimum distance between observer and initial site (only in the binomial model); Carcass present at initial site; Wind strength near bear; Number of observers; Age of the bear\*Cover; Age of the bear\*Activity of the bear; Age of the bear\*Season; Sex of the bear\*Cover; Sex of the bear\*Activity of the bear; Sex of the bear\*Season; Cover\* Activity of the bear; Cover\*Season. An AICbased backward elimination was performed on these models and the final models were selected based on the lowest value of AIC [53] (Table S1). We chose mixed models in order to account for the random effect of each individual bear using Bear ID as a random effect in the models, and thereby avoid biases caused by pseudoreplication. We used the statistical programming language and environment R version 2.8.1 [54], and the lmer (lme4 library) package.

#### Results

We passed the bears' initial sites at an average of  $54\pm 61 \text{ m}$  (n = 131), which was further than the average sighting distance in the initial sites (18 $\pm$ 7 m, n = 120). There was significantly less cover in initial sites (25 $\pm$ 10 m, n = 21) than second sites (17 $\pm$ 8 m, n=21) for active bears (two-tailed paired t-test:  $t_{31}$ =2.88, p=0.007), but no difference between the initial sites (17 $\pm$ 8 m,

n = 99) and second sites (16±6 m, n = 95) for passive bears (twotailed paired t-test:  $t_{183} = 1.07$ , p = 0.29). The initial site of active bears had significantly less cover than those of passive bears (two-tailed t-test:  $t_{22} = -3.80$ , p = 0.001), but there was no difference in cover in the second sites of passive and active bears (two-tailed paired t-test:  $t_{29} = -0.65$ , p = 0.52).

#### Detection of the bears

None of the bears displayed any aggressive behaviour towards the observers, and none of the observers reported feeling threatened during any of the approaches. Bears were detected in 15% of the approaches (n=154); 17 bears were seen, we heard movements from five bears, and during one approach we heard vocalization and movements. The detection rate did not vary with the sex of the bear (chi-squared test:  $\chi^2 = 0.82$ , df=1, p=0.36), or the season (chi-squared test:  $\chi^2 = 0.38$ , df=1, p=0.54). Most of the 17 bears were first seen while standing still, and after the initial observation, all of the bears walked or ran away. We observed a fresh carcass in eight of the initial sites.

#### Remaining or moving

The bears left the initial site and moved away from the observers in 80% of the approaches (n = 148); the bears that remained had a tolerance distance of  $84\pm64$  m (median 62 m, minimum 23 m, maximum 313 m, n = 30). The older bears remained more often than the younger bears, but this difference decreased during the berry season (Table 1). We also found a tendency for the bears to leave more often with increasing number of observers (Table 1). The other variables were not related to whether the bears remained or left their initial site (Table 1).

#### Flight initiation distance (FID)

Passive bears that left before we passed the initial site had an average FID of  $69\pm47$  m (median 59.6 m, minimum 13 m, maximum 309 m, n = 65). Nine passive bears that remained at their initial site when we passed them at an average distance of  $68\pm68$  m (median 159 m, minimum 27 m, maximum 248 m) left when the observers were on average  $326\pm356$  m (minimum 68 m,

**Table 1.** Results from the generalised linear mixed model for remaining or leaving the initial site.

Explanatory variables	β	SE	Z	Р
Age of the bear	-0.558	0.223	-2.503	0.012
Sex of the bear (male = 0, female = 1)	-2.769	1.769	-1.536	0.125
Cover (sighting distance at the initial site)	0.204	0.215	0.945	0.345
Season (pre-berry = 0, berry = 1)	0.860	1.866	0.461	0.645
Wind strength near bear	-0.313	0.277	-1.128	0.259
Number of observers	0.843	0.488	1.727	0.084
Age of the bear * Season	0.304	0.130	2.338	0.019
Sex of the bear * Cover	0.128	0.099	1.288	0.198
Cover * Season	-0.139	0.108	-1.292	0.197

Results from the generalised linear mixed model (binomial link function) explaining whether brown bears remained (0) or left (1) their initial site when approached by humans on foot in central Sweden in 2006–2009 (n = 148). Test statistics are given for the model with the lowest value of AIC. The parameter  $\beta$  is the slope, SE denotes the standard error, Z denotes the z-value, and P denotes the p-value for the test.

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Explanatory variables	β	SE	т
Age of the bear	-0.039	0.013	-3.038
Cover (Sighting distance at the initial site)	0.018	0.007	2.655
Activity of the bear (passive = 0, active = 1)	0.410	0.187	2.189

Results from the linear mixed model (Gaussian link function) explaining the flight initiation distance (FID) for brown bears when approached by humans on foot in central Sweden in 2006–2009 (n = 78). Test statistics are given for the model with the lowest value of AIC. The parameter  $\beta$  is the slope, SE denotes the standard error and T denotes the t-value. doi:10.1371/journal.pone.0031699.t002

maximum 1221 m) away. Active bears that left before we passed them had an average FID of  $115\pm94$  m (median 82.3 m, minimum 22 m, maximum 324 m, n=13). The bears that left before we passed the initial site left at a shorter distance when there was more horizontal vegetative cover at the initial site (Table 2, Fig. 1). Younger bears left at a longer distance than older bears, and passive bears left at a shorter distance than active bears (Table 2, Figs. 1 and 2). The other variables did not seem to affect FID.

#### Distance moved and time spent active

The bears that settled at a new site after leaving their initial site before the schedule with 1-minute positions ended were active for  $24\pm23$  min (minimum 2 min, maximum 101 min, n=78), and moved on average  $1,173\pm1,094$  m (minimum 99 m, maximum 6,291 m, n=92) before they settled at the second site. Neither activity behaviour, age of the bear, season, the closest distance between observer and bear, nor sex of the bear was related to the



Sighting distance at initial site (m)

Figure 1. Flight initiation distance (FID) in relation to sighting distance at the initial site. Distribution of flight initiation distance (FID) for passive (circles and full line) and active (triangles and broken line) Scandinavian brown bears approached by humans on foot in central Sweden in 2006–2009 (n = 78), in relation to sighting distance at the initial site (shorter sighting distance indicates more horizontal vegetation cover).

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Figure 2. Flight initiation distance (FID) in relation to age of the **bear**. Distribution of flight initiation distance (FID) for passive (circles and full line) and active (triangles and broken line) Scandinavian brown bears approached by humans on foot in central Sweden in 2006–2009 (n = 78), in relation to the age of the bear. doi:10.1371/journal.pone.0031699.g002

time they spent active or the distance they moved (all p-values>0.22).

#### Discussion

#### Detection of the bears

None of the approached bears showed any form of aggressive behaviour, which is consistent with the view that the Scandinavian brown bear is less aggressive than brown bears in Asia and North America [31]. This may be a result of the extermination attempt during the 1600-1800's, when bold animals may have been removed selectively [25,31]. The few brown bears that survived in Sweden around the 1930s were reported to be wary [55]. The present population may contain more bold individuals because the population is larger; however hunting might take out some of the bolder individuals first [56]. The Scandinavian brown bear can act aggressively if wounded, when with cubs of the year, when surprised at carcasses, or if hunting dogs are involved in the encounter [31]. However, the bears we approached near carcasses did not show any aggressive behaviour. Most bears were standing still when first observed and changed behaviour after being detected; by walking or running away. This strengthens our conclusion that the bears wanted to avoid confrontations with humans.

We detected the bears in only 15% of the approaches. This is a low proportion considering that the observers knew the direction and the approximate distance to the bear. This clearly indicates that most encounters between hikers and bears go unnoticed by humans. This could be because bears tend to use densely vegetated sites as their daybed sites [43]. After the encounters, both active and passive bears settled in densely vegetated sites, perhaps to avoid exposing themselves to humans. The fact that there was no difference in sighting distances between initial and second sites of passive bears shows that the bears always select quite dense resting areas. Active bears were disturbed in areas that are more open and sought cover in sites with similar sighting distance as passive bears after being disturbed.

#### How did the bears behave when approached?

The bears showed a varied set of behaviours when approached. The majority of the bears left before we passed them, although some bears left and then came back towards the observers before leaving the area. Others remained until we passed before leaving, or simply remained in the area even after the approach. None of these behaviours should be considered abnormal.

We found that the younger bears moved away more often when approached than older, but this difference decreased during the berry season (Table 1). A previous study found that bears chose daybeds with more horizontal vegetation cover during the berry season than the pre-berry season [57]. This might indicate that the bears respond to the increased human activity during autumn (berry pickers, hunters etc) by choosing sites with more cover, and our results show that the bears are more easily disturbed during the berry season.

Grizzly bears' (also *U. arctos*) level of reaction to people has previously been found to not be influenced by distance (closer or further away than 150 m) when in cover [17]. We usually came closer to the bear than 150 m, but also did not find that the distance to the bear influenced whether the bear left or not.

One way to identify disturbance is using a flight response [58], i.e. as a quantitative measurement of a response defined as "the distance to which a person can approach a wild animal without causing it to flee" [59]. Our finding that the bears left at a greater distance from the observers when there was less cover in the initial site (Table 2, Fig. 1), suggests that the bears made a contextdependent decision of when to leave [58]. Escape theory predicts that prey will determine their behaviour based on the behaviour of the predator, and a change in behaviour of the prey will occur when the risk of remaining exceeds the cost of leaving [60,61]. The cost connected to leaving when approached by humans includes the loss of benefits achieved by continued foraging or resting, the energetic cost caused by leaving the site, and the cost of being detected. If the animal regards itself as well hidden, the benefit of leaving will occur at a shorter distance to the observer than if the animal is in open habitat, hence the animal should leave sooner in an open habitat [60]. Similar results to ours have also been documented in Eurasian lynx [62] and grizzly bears [16,63].

Another explanation for why bears remained longer at initial sites with more horizontal vegetation cover could be that the cover concealed scents to a certain degree and reduced noise from the observers, and hence delayed the bear's detection of the observers. Bears have an excellent sense of smell [64], and during our approaches, we made sure that the wind blew  $90^{\circ}$  in relation to our track, i.e. from us towards the bear when we passed it. We simulated hikers by behaving like them during the approaches, regarding the speed of the approach, and the noises we made.

We also found that active bears had a longer FID than passive bears (Table 2, Fig. 2). It is possible that active bears are more vigilant than passive bears, and when the bears already were active, the inclination to change behaviour and start moving away from the observers was probably higher than when the bears were passive. This pattern has been reported in desert bighorn sheep (*Ovis canadensis* Shaw), which were more likely to flee from human disturbance when moving or standing, than when feeding or bedding [65].

Younger bears left the initial site more often than older bears (Table 1), and the younger bears left at a greater distance from the observers than older individuals (Table 2, Fig. 2). We suggest that this could be because young bears are less experienced. Though adult female grizzly bears have been found to be the most risk-averse category and female grizzly bears were normally found further from vehicles, noise, and paved roads than males [18], we

did not detect any difference between the sexes in any of our analyses. These findings do not necessarily contradict each other. As mentioned earlier, hunting can cause individuals to become more wary by removing bold animals. As there is no hunting selection for sex in Sweden [66], we suggest that the sexes experience risk from humans in the same way. Hence, there is no difference in wariness and behaviour towards human encounters, even though females might choose habitats further from vehicles, roads and noise when they have the opportunity to choose. We approached the bears in habitats where they were usually not close to humans, hence the exposure to humans was not chosen by the bear itself and the reaction towards a human encounter could be based on the amount of previous experience. We did not detect animals of either sex more often, stressing that boldness did not vary by sex.

It is important to note that FID does not necessarily reflect the entire impact of human disturbance [67]. If a disturbance is great enough, it can cause an extra cost that can influence growth, health, and reproductive fitness [68]. An animal might detect a predator long before it decides to leave [60], and the bears probably reacted internally before reacting in a way that we could record by a change in GPS positions, making it hard to detect when the animal actually reacted initially [69]. A more accurate way to measure the reaction might be by using physiological measurements, such as heart rate [68,58]. Heart rates of kittiwakes (Rissa tridactyla L.) and European shag (Phalacrocorax aristotelis L.) increased by 50% when exposed to potentially threatening stimulus, indicating that the birds could be distressed even when there were no visible changes in behaviour [58].

#### Management implications

Our findings support an earlier conclusion that the Scandinavian brown bear normally is not aggressive [31]. Human fear can negatively affect the acceptance of bears and other carnivores, and it is important that people receive information about the bears' normal behaviour in order to feel safe when using the outdoors. Our results can contribute to educational material where people

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can obtain information about the normal behaviour of solitary adult bears, how to behave if they encounter them, and what generally to expect when hiking in bear habitat. Such information would be useful both in areas with an established brown bear population, and in areas where the bears are re-establishing.

Our findings document how solitary adult Scandinavian brown bears normally behave towards humans on foot in the forest. The probability that people will encounter a bear in Scandinavia is small, because the bears occur in low densities, the daytime habitat they choose is normally too dense for hiking, and because the bears normally are wary and avoid confrontations with humans if possible. Even though there seems to be great variation in the bears' reactions towards human disturbance at close range, most bears left the area before the observers passed the bear's initial site. Crucially, none of the bears behaved aggressively towards the observers.

#### **Supporting Information**

Table S1 List of candidate and selected models (lowest AIC value) for remaining or leaving the initial site, and the flight initiation distance (FID) for brown bears when approached by humans on foot in central Sweden in 2006-2009, respectively. We show AIC values, differences in AIC values between the selected model and each candidate model ( $\Delta AIC$ ), and AIC weights (Wi). (DOCX)

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#### **Author Contributions**

Conceived and designed the experiments: OGS JES. Performed the experiments: GKM OGS VS. Analyzed the data: GKM OGS VS. Wrote the paper: GKM. Edited the manuscript: OGS VS JES.

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# **P**APER III

# Behavioral differences between females with dependent young and single Scandinavian brown bears when experimentally approached by humans

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# ABSTRACT

Carnivore-human encounters have increased in areas with increasing and expanding large carnivore populations. Females with cubs (FC) are often involved when humans are injured by brown bears *Ursus arctos*, and in Scandinavia this is particularly true for unarmed recreational forest users, such as berry-pickers. A better understanding of possible behavioral differences between single bears and FC is important to minimize the risk of injuries to recreational forest users. This has management and conservation implications for bear populations.

We documented the reactions of GPS-collared FC and single brown bears to experimental approaches by humans within 50 m of the bear on 42 and 108 occasions, respectively. None of the bears displayed any aggressive behaviors. FC were seen or heard in 26 % and single bears in 14 % of the approaches. The majority of FC (95%) and single bears (89 %) left when approached. Bears that left were passed at a shorter distance and were in more open areas than those that stayed. FC and single bears had similar flight initiation distances (FID), which was longer for bears that were active at the time of the disturbance. FC selected more open habitat than single bears, which was true also for the new site they selected following disturbance. FC, particularly active females with cubs of the year, also showed the greatest reactions to disturbance by moving greater distances and spending more time active following the approach.

FC did not behave more aggressively than single bears, but their tendency to select more open habitat may predispose them to encountering people that are not involved in hunting activities, which may be the primary explanation why this category of bear is often involved when unarmed people are injured in Scandinavia.

### **KEY WORDS**

Conflict prevention, conservation, disturbance, flight initiation distance, human-carnivore interactions, wildlife management

## INTRODUCTION

Large carnivores present a particular conservation and management challenge, as they are often in direct or indirect conflict with humans over damages to livestock and/or property, as well as the fear they cause due to the potential risk they pose to humans (Clark et al. 1996, Packer et al. 2005, Gurung et al. 2008, Herrero et al. 2011). Management strategies in the past were therefore aimed at eliminating these threats, resulting in major population declines among large carnivores in both Europe and North America (Linnell et al. 2001). A change to a more conservation-oriented management has resulted in increases of large carnivore populations in both Europe (Enserink and Vogel 2006) and North America (Packer et al. 2009, Wydeven et al. 2009, Smith et al. 2010). Brown bears *Ursus arctos* are one such example, with increased legal protection and management targeted at recovery leading to population increases in some areas (e.g. (Swenson et al. 1995, Kendall et al. 2009)). Recovery, although a success, means that new challenges arise (Swenson et al. 1998). Increasing large carnivore populations, expanding human populations, and increasing backcountry use also increases the chance of large carnivore- human encounters, which involves bears and other species (Goodrich and Berger 1994, White et al. 1999, Smith and Johnson 2004, Ordiz et al. 2011, Ordiz et al. 2013) and affects humans, e.g. (Miller and Tutterrow 1999).

The brown bear population in Scandinavia has increased in recent decades (Kindberg et al. 2011) and there has been a concomitant increase in human injuries caused by brown bears in Scandinavia in recent years, with two fatalities during the 2000s (Sahlén et al. in prep.). One result is that the acceptance for the bear is decreasing in Scandinavia (Sandström and Ericsson 2009). The increase in bear-caused human injuries has occurred mainly among armed men involved in hunting activities, whereas no such increase can be detected for unarmed people (Sahlén et al. in prep.). The majority of those injured are hunters, and the presence of dogs, wounded bears, and vicinity of a den are the main secondary factors involved. For unarmed people, the greatest risk factor is encountering females with cubs (Sahlén et al. in prep.). Although the frequencies of the factors involved have changed, this is largely in agreement with previous findings (Swenson et al. 1999). Encounters between humans and

bears not only affect humans, but are also a source of disturbance that displaces bears (Moen et al. 2012), which may also have fitness consequences (White et al. 1999).

Brown bears generally avoid people and human activities throughout their range, both spatially and temporally (Nellemann et al. 2007, Ordiz et al. 2011, Ordiz et al. 2012). Experimental approaches on single brown bears in Scandinavia have also shown that they avoid confrontation with people (Moen et al. 2012). Even when the observers passed the bears at quite close distances (~ 50 m), none of the bears displayed any aggressive behavior, nor did the observers feel threatened. The majority of the bears, which were either active or resting in a day bed, left their location as the observers passed them and moved to a new location, where they hid in denser habitat. The bears' responses to the disturbance were immediate and pronounced and the effects on their movement patterns lasted several days (Ordiz et al. 2013). The effects of disturbance on animals could be similar to that of predation risk. Thus, disturbance studies may benefit from using this framework when generating hypotheses about responses to disturbance (Frid and Dill 2002). Indeed, bears adjust their behavior to avoid human encounters in a way similar to prey avoiding their predators (Ordiz et al. 2011, Ordiz et al. 2012), which has also been documented in lions and wolves (Valeix et al. 2012, Wam et al. 2012). In this study, we experimentally approached females with cubs (FC) to document differences in the behavior of FC and single bears that could explain why FC are more frequently involved in incidents when unarmed people are injured. This study is interesting from; 1) a behavioral perspective, to document the reaction of FC, whose survival rates are important for population trends (Schwartz et al. 2006) and are protected from hunting in Scandinavia, where bears are harvested based on annual quotas (Bischof et al. 2008); and 2) from a management perspective, because FC are often involved in attacks on unarmed people. This is of interest to the general public and management agencies.

The risk-disturbance hypothesis in the context of parental investment predicts that the response to disturbance should be greater in individuals with dependent offspring, which could cause abandonment of the young if they are unable to follow the mother (Frid and Dill 2002). However, bear cubs, and particularly yearlings, are quite mobile during summer and fall. The presence of cubs may therefore not keep a female from leaving due to human disturbance, even if the move may incur energetic costs for the cubs. Further, female bears often "tree" their cubs as a response to threats (i.e.

the cubs climb high up a tree where they are harder to reach), which is dependent on the presence of taller trees (Herrero 1972, Jordan 1976, Herrero 1983). We therefore predicted that FC would respond to approaching humans by leaving more often and earlier than single bears and that they would respond to disturbance by moving farther and remaining active for longer.

# **METHODS**

# Study area

The study area is located in south-central Sweden (Dalarna and Gävleborg counties), which is part of the core reproductive area of the southern Scandinavian brown bear population (61°N, 14°E). The topography is varied, with gently rolling hills, and >90 % of the area is below the timberline (~750 m a.s.l.) (Dahle and Swenson 2003). The forestry industry manages the area intensively, resulting in a large proportion of young forest and interspersed clear-cuts (Swenson et al. 1999a). Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* H. Karst) dominate the landscape, with some deciduous trees, consisting mainly of birch (*Betula pendula* and *B. pubescens*), mountain ash (*Sorbus aucuparia*) and willows (*Salix* spp.) (Sahlén et al. 2011). Forestry practices have also created an extensive road network of gravel roads of varying sizes and paved public roads (Nellemann et al. 2007). The area is popular for berry pickers and other recreational users, including hunters.

# The bears and approaches

# Approach method

All bears we studied, except dependent young, were equipped with a GPS Plus-3 or GPS Pro-4 collar (VECTRONIC Aerospace GmbH, Berlin, Germany), and a VHF transmitter implant (IMP400L) (Telonics, USA). All yearlings were equipped with a VHF transmitter implant. The GPS-collars were programmed via the GSM network to fix a location every minute for a 3-hour period, during which the approach was conducted; one hour before the approach started (control period), one hour during, and one hour after the approach. Approaches were conducted by 2 observers (median, range: 1 - 6)

between 9:00 - 14:00 hrs local time (GMT+2). The data were delivered via the GSM network to our database and any omitted positions were later physically downloaded from the collar, once it had been retrieved.

Prior to the approach start, observers located FC using a combination of triangulation of the VHF signal and last received GPS positions sent directly to the observers' cell phones. We standardized the experiment and aimed to pass the bears at a distance of 50 m with the wind direction toward the bear at the time of passing, so it would be able to catch wind of us as we passed. Observers talked with each other in a normal speaking voice during the approach, or to him/herself if he/she was alone. The observers' track was recorded using a hand-held GPS receiver (Garmin GPSMAP 60CSx (Garmin Ltd, USA) which was programmed to record one position every 10 m.

The majority of single bears left after being disturbed (Moen et al. 2012); thus, for ethical reasons we did not approach FC during the main breeding season in early summer, as their displacement could expose the cubs to increased risk of infanticide. Infanticide is a prominent cause of death for subadult bears in Scandinavia, particularly during the mating season, (Swenson et al. 2001, Steyaert 2012), and all approaches were therefore conducted from the second half of July until mid-October.

## Females with cubs (FC)

We conducted 42 approaches on FC (19 on females with cubs of the year (FCOY) and 23 on females with yearlings (FY)) in 2008 - 2011 (2008, 9; 2009, 15; 2010, 12; and 2011, 6). Two FC were approached in more than one year, so the number of individual females was12. We waited a minimum of 21 days between approaches for FC. Each FC was approached on average 3 occasions per year (range 1 – 5), and each FC was approached on average 3.5 times in total during the study (range 1 – 7). Females were 6 – 16 years old and were accompanied by 1– 3 cubs.

We received  $93.3 \pm 15.1 \%$  (mean  $\pm$  SD) of the theoretical maximum of GPS positions (181 per approach). The observers started the approaches  $1013.0 \pm 995.6$  m from the family group and walked at a normal hiking pace ( $3.5 \pm 1.5 \text{ km/h}$ ).

# Single bears

We approached 23 female and 8 male single bears on 108 occasions (76 on females and 32 on males) in 2006 – 2009 (2006, 10; 2007, 40; 2008, 48; and 2009, 10). Single bears were approached throughout the full season and on average 3.5 occasions per individual per year (range 1 - 6), but we used only data from the equivalent period of time as FC. We received on average 66 % of the theoretical maximum of GPS positions each year, but this improved greatly between 2006 (37 ± 12 %) and 2009 (98 ± 1 %), mainly due to improvements in technology (Moen et al. 2012). The approaches started at 869 ± 348 m from the bears and observers kept a normal hiking pace of  $3.4 \pm 0.6$  km/h.

# Passive and active bears

We classified FC as either passive or active during the approach control period, using the definition of Moen et al. (2012). FC that were either active or passive during the entire control period were used to calculate an upper control limit (UCL) for speed (m/min) using statistical quality control (Montgomery 2005), against which we could measure potential reactions to disturbance in terms of flight initiation distance (FID).

Initial analyses of average speed revealed a difference in speed between FC and the single bear dataset, so we tested the differences using Welch's t-test to account for unequal variances and sample sizes, after log-transforming the speed to normalize the residuals (log(speed\*100)). Active FC had significantly higher speed than active single bears ( $t_{\alpha=0.05,df=2222.097}$ =8.2664, *p* <0.001), but there was no significant difference between passive FC and passive single bears ( $t_{\alpha=0.05,df=1837.976}$ =-6.3696, *p* = 0.239). We therefore calculated a new UCL for active FC and pooled the passive FC and passive single bears approaches to calculate a new UCL for passive bears. UCL was estimated to 41.5 m/min for passive bears, against which passive FC were assessed and 127.4 m/min for active FC, against which active FC were assessed. The single bears were assessed against the UCL previously established for active and passive single bears (see (Moen et al. 2012)).

The position immediately preceding the first point at which UCL was exceeded was considered the bear's flight initiation point, and the distance between this point and the temporally corresponding observer location was considered the FID. We did not estimate FID if there had been more than one minute between the point at which UCL had been exceeded and the immediately preceding point. We checked the accuracy of the method by visual inspection of the dataset using ArcGIS 10.x (ESRI, 2010). There were two factors that made an approach unsuitable for FID analyses; 1) the bear did not exceed UCL during the approach, or 2) the bear exceeding UCL was delayed (i.e. FID occurred later than the movement suggested). Where bears did not exceed UCL, we could not determine whether they left as a result of our disturbance, so they were removed from all further analyses pertaining to reaction to disturbance. Approaches where bears exceeded UCL some minutes after leaving the initial site could potentially distort analyses of FID. These approaches were excluded from analyses involving FID, but as the bears were considered to have responded to our disturbance, they were included in analyses that were not dependent on FID. We were able to determine FID for 36 family groups and 62 single bears.

We classified the bears as passive or active based on their activity during the control period until the start of the approach. This resulted in 12 active and 30 passive FC and 23 active and 84 passive single bears. We examined whether bears stayed or left, the FID for those that left, and visited the sites that the bear had been prior to the approach (initial site, IS) and the new sites where the bears settled after being approached (second sites, SS) to estimate the horizontal vegetation cover. We used sighting distance (SD) as a way to measure horizontal vegetation cover; the more vegetation cover, the lower the SD. We placed a two-colored cylinder at IS and SS and measured the maximum distance in each cardinal direction from which the cylinder could still be seen, and averaged this distance to obtain the SD (Ordiz et al. 2009, Moen et al. 2012). We also recorded the habitat type at IS and SS using forestry habitat classification ((Karlsson et al. 1991, Esseen et al. 2003), Table 1).

# Data analysis

We assessed the factors affecting SD, whether bears stayed or left, their FID, time spent active, and distance moved after the approach (Table 2) using generalized linear mixed models (GLMMs) in the lmer/glmer package (lme4 library, R Development Core Team 2011), with bear ID as a random variable to account for the repeated sampling of individuals. For the analyses, we set candidate models with potential explanatory variables and interactions between variables based on previous findings (Moen et al. 2012), and what we found biologically and behaviorally reasonable (Table 2). We included only interactions in the models if initial data exploration revealed it as warranted. Sex was not a significant factor in Moen et al. (2012) or in Ordiz et al. (2013), and all single bears were therefore grouped together. Initial data exploration did not show any great differences between females with cubs of the year (FCOY) and females with yearlings (FY), and these were grouped together as FC in the analyses (variable Reproductive category (Rep Cat); FC or single (S)). There was one exception; we analyzed them as separate categories (here Family status (Fam stat): FCOY, FY or S) for the behavior after the approach (distance moved and time spent active following the approach).

To identify the best candidate models, we used model dredging (Hegyi and Garamszegi 2011, Symonds and Moussalli 2011) with the model.dredge package (MuMIn library, R Development Core Team 2011) and model selection using the Akaike's Information Criterion (AIC). Model selection using AIC typically identifies the model with the lowest AIC as the top model (Burnham and Anderson 2002). However, models that do not differ from the top model by more than 2 AIC units (i.e  $\Delta$ AIC <2) are likely to be equally good (Burnham and Anderson 2002). Therefore, rather than select one best model based on the lowest AIC value, we calculated AIC weights for the candidate models with  $\Delta$ AIC < 2, as well as for the variables included in the models (Wagenmakers and Farrell 2004). Variable weights provide information on how often an explanatory variable has been included in the selected candidate models (i.e. a variable that is included in all candidate models will have a variable weight of 1), which gives the relative importance of each variable (Symonds and Moussalli 2011).

# RESULTS

We passed the bears' initial sites at 50.6 ± 53.7 m (n = 146, mean ± SD). We heard or saw FC in 11 of 42 (26 %) approaches (6 FCOY, 5 FY) and single bears in 15 of 108 approaches (14 %) (10 females, 5 males). This difference was not statistically significant, but indicates a trend for FC to be more easily detected than single bears (Chi-square test of association, with Yates' Correction for Continuity ( $\chi^2_{(1, N = 150)} = 3.00, p < 0.10$ ). None of the bears showed any aggression toward the observers and none of the observers reported feeling threatened.

Both IS and SS had longer SD (less cover) for FC than single bears, regardless of habitat type (Fig. 1). SD was longer for active bears than passive bears, longer in IS than SS, and differed among habitat types (Table 2a).

Whether the bears stayed or left was affected by passing distance and SD at the IS and, to a lesser extent, (as indicated by lower variable weights) reproductive category, age and activity (Table 2b). Bears that decided to leave were passed at a shorter distance and were in more open areas (shorter SD) than those that stayed. There was a tendency for FC to be more likely to leave than single bears, and for younger bears to be more likely to leave than older bears. The FID was primarily affected by the bears' activity and to a lesser extent age (as indicated by lower variable weight), with longer FID for active and younger bears than passive and older bears (Table 2c).

Bears that had been active at the start of the approach moved farther than those that had been passive and FC moved farther than single bears, particularly active FCOY (Fig. 2). Bears, irrespective of family status, tended to move shorter distances when the SD at the IS was longer (i.e. less cover). There were only small differences in time spent active after the approach, but time spent active tended to be longer for FCOY than single bears and FY, and for active bears (Table 2e).

### DISCUSSION

Reaffirming the results of previous studies (Moen et al. 2012, Ordiz et al. 2013) none of the bears, whether FC or singles, reacted aggressively to the observers. This is an essential message for managers and forest users. Rather, the vast majority of bears (95 % of FC and 88 % of single bears)
left following disturbance. The decision to leave was primarily affected by the proximity of the disturbers and the density of the surrounding vegetation, indicating that the risk of being discovered was a primary driver to leave the location. Although the vegetation cover influenced whether bears stayed or left their IS, it did not appear to affect the bear's FID, which differs from what has been previously found for this study population (Moen et al. 2012). We are unsure why this would be, but the effect of cover on FID can differ between and within species (Stankowich 2008).

The effect of reproductive status on FID was small, lending no support to our prediction that FC would leave earlier than single bears, as has been documented for family units in ungulates (e.g. (Ciuti et al. 2008, Stankowich 2008)). This may be because bear cubs have alternative defensive responses other than fleeing available to them when faced by threats, such as climbing a tree. However, both FC and single bears left at greater distances when active than passive, and activity at the time of the disturbance appeared to be the greatest determinant of the distance a bear decided to leave, as previously documented (Moen et al. 2012). Active individuals may have been more likely to react to human disturbance by leaving at longer distances because they already were active, but also because they may have been better positioned to detect and assess potential threats (Papouchis et al. 2001, Moen et al. 2012).

Although FID was unrelated to SD, there were notable differences in the habitats used by the bears. FC were in more open habitat than single bears prior to the approach, which was true for both active and passive bears regardless of the habitat type (see Fig 2). There was also little difference in the SD at IS of passive FC and active single bears. Females with dependent offspring select more open habitat at the landscape scale during the mating season than either lone females or adult males, as a potential counter-strategy to SSI, but the difference in habitat selection was not as pronounced after the end of the mating season (Steyaert et al. 2013). It is possible, however, that the difference in vegetation cover we documented here between single bears and FC at small habitat scales, is attributable to such social factors. More open habitat may be used by FC, because it is less preferred by other categories of bears that may pose a risk to the cubs, but also because more open habitat facilitates detection of potential threats. An adult bear without dependent young typically has little to fear from other bears within its own home range; in fact, much of a single adult bear's habitat selection at small and large scales

appears to be directed at avoiding human activity and structures (Nellemann et al. 2007, Ordiz et al. 2011). However, FC must take the threat of conspecifics into account, at least during the mating season, and evidence suggests that humans in this context may be the "lesser of two evils" (Nevin and Gilbert 2005b, a, Steyaert et al. 2013). An alternative explanation to the use of open habitats by FC is the greater berry abundance associated with more open habitats (Nielsen et al. 2007). Berries are a primary source of food for Scandinavian brown bears at this time of year (Dahle et al. 1998, Persson et al. 2001), and females may have to select feeding areas that will have enough food for both herself and her offspring, thus forgoing the shelter available in less open habitat.

The choice of more open habitat may also explain the trend of detecting FC more often than single bears during the approaches. Despite this, none of the FC displayed any aggressive behavior towards the observers, and all of the visually observed FC fled the site after detection. After disturbance, active and passive FC and active single bears settled into denser habitats, which has also been documented in ungulates ((Stankowich 2008), and references therein). However, passive single bears showed no difference in cover between IS and SS. Moen et al. (2012) proposed that the lack in difference in cover between IS and SS for single passive bears was because they already had selected a protected site to rest. Passive FC did not show this pattern, which further strengthens our conclusion that FC had to take other factors than humans into account when selecting a daybed. The selection of a denser site following disturbance may indicate that FC, once exposed to an approaching human, take the human threat more into account in the selection of the habitat they retreated to.

The bears' reactions to human disturbance, in terms of distance moved and the time spent active, also differed clearly between FC and single bears; this was even noticeable between FCOY and FY. Active FCOY displayed the greatest reactions to disturbance, which is consistent with the predictions from the predation-risk hypothesis framework of Frid and Dill (2002), indicating that bears do perceive humans as a threat. Female bears with dependent offspring may have to compromise in terms of habitat selection to take threats from both humans and conspecifics into account, but this does not lessen the impact approaching people have on them.

Less dense vegetation at the IS reduced the strength of the responses in both FC and single bears. Ordiz et al. (2013) documented a similar effect of vegetation cover on the strength of the responses to the approach, particularly when the bears detected humans at short distances. This may be because an animal's response to disturbance is likely to be context dependent (Beale 2007, Moen et al. 2012), largely based on the behavior of the approaching threat and associated costs with behavioral responses (Ydenberg and Dill 1986, Cooper 2008). More open habitat may provide bears with a better overview of the approaching threat, enabling them to fully assess the threat and the best course of action. This may mitigate the effect of the disturbance and diminish the strength of the bears' responses. However, this also highlights the importance of dense cover for bears, which rely on dense locations for resting during the day (Ordiz et al. 2011)

# Are females with cubs more aggressive than solitary bears?

Aggressive defense of dependent offspring is a form of parental investment evident in several species (e.g. merlins *Falco columbaris* (Wiklund 1990), bank voles *Clethrionomys glaerolus* (Koskela et al. 2000) and Eurasian magpies *Pica pica* (Redondo and Carranza 1989). Increasing maternal aggression during the more sensitive offspring developmental stages has been suggested to improve protection of offspring against threats from conspecifics or predators (Maestripieri 1992). Attacks on humans from females accompanied by dependent young has been documented in e.g. cougars *Felis concolor* (Beier 1991), sloth bears *Melursus ursinus* (Bargali et al. 2005), and ungulates (Conover 2002, Hubbard and Nielsen 2009), but these incidents are not more frequent when compared to attacks from single animals of the same species.

Human injury rates and statistics confirm why female black *U. americanus* and brown bears with dependent young have a reputation for being more aggressive than their solitary conspecifics (Herrero 1976, Herrero and Higgins 2003); however, our results do not support this. FC tended to be more likely to leave when disturbed and they did so at similar distances to single bears. Nor did any of the females display any aggressive behavior directed at the observers, despite the presence of cubs. FC reacted to the approaching humans to a greater extent than even single bears. The reaction goes beyond the immediate flight response, with behavioral effects lasting for several days (Ordiz et al. 2013).

Nothing in our results suggests that FC were more aggressive or more prone to defend themselves or their offspring more aggressively than other bears. Rather, our results suggest that underlying behavioral patterns moderated by social factors better explained the greater risk of injury to unarmed recreational forest users. This is because FC often occupy areas closer to humans and human activity, and alter their active periods to overlap more with human active periods (Nevin and Gilbert 2005b, a, Nellemann et al. 2007, Ordiz et al. 2007, Ordiz et al. 2012), perhaps to avoid other categories of bears that may pose a threat to their young. This, and the fact that FC use more open habitat than single bears regardless of habitat type, makes them more likely to encounter humans that are in the forest for recreational purposes, such as berry or mushroom picking or hiking. Our results clearly show that if a bear is aware of an approaching human, they do everything to avoid an encounter. The results of Moen et al. (2012) also made it evident that the habitat that single bears tend to select as a resting habitat during the day is so dense that people that are in the forest for recreational purposes are unlikely to walk in such areas. On the other hand, the habitat selection of FC may make them the most likely bear category that recreational forest users would encounter. Thus, when a recreational forest user surprises a bear at a short distance, it is more likely to be a FC than a single bear.

Such incidents occur infrequently (Sahlén et al. in prep.), and in Scandinavia no fatalities have resulted from aggressive encounters with FC for over 100 years, since accurate records have been kept (although one such outcome has been documented in Finland (De Giorgio et al. 2007)). However, our study was not designed to assess any differences between single bears and FC who have been surprised at close distances, as we approached bears with the wind toward them (see methods).

## Management implications

Incidents where humans have been injured or killed can lead to decreased acceptance for large carnivores, including bears (Sandström and Ericsson 2009), and it is therefore in the interest of management and conservation of bear populations to minimize the risk of injury to people. There is a link between having knowledge of a species and the willingness to protect it (Vaske and Donnelly 2007), but knowledge that pertains to a person's feelings about that species is more likely to shape the

person's tolerance of certain management or conservation actions than the person's cognitive beliefs (Glikman et al. 2012). The perception of risk has a major influence on the attitudes and behavior of the public and wildlife managers (Kellert 1985, Gore et al. 2009), and fear is related both to a person's uncertainty about their own responses to an encounter, as well as the perceived unpredictability of the animal (Johansson and Karlsson 2011, Johansson et al. 2012). Information that can provide recommendations for how people should behave to minimize risk, as well as provide them with knowledge that reduces animals' perceived unpredictability, have the potential to alter risk perceptions and reduce fear and is likely to be the most effective tool in increasing tolerance for the species, or management action, in question. No differences in level of aggression appeared to explain why FC are more often involved than single bears in incidents with unarmed people. Therefore, the best way for nonhunters to avoid encountering a bear, regardless of its reproductive category, is to make noise while walking in the forest, to talk with each other or to oneself if alone, and to pay attention to wind direction, especially if approaching patches of denser vegetation where bears usually rest during daytime.

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# TABLES AND FIGURES

**Table 1** Forestry habitat classifications used in the description of initial and second sites of Scandinavian brown bearsapproached by humans on foot (in alphabetical order by code)

Habitat type	Description
G - Mid-aged forest	Refers to G1/G2 in Karlsson & Westman (1991). Medium tree <sup>3</sup> 10 cm diameter at breast height
R - Pre-commercial thinning	Refers to R1 and R2 in Karlsson & Westman (1991).Young forest; primary, non-commercial thinning. Tree sizes range from planting stage until medium tree is >1.3 m but < 10 cm in diameter at breast height
RD - Road	Road (irrespective of size, type or condition)
S - Mature forest	Refers to S1 in Karlsson & Westman (1991). Mature forest at the age when ca 10 years remain before the final harvest, and older (in our area an S1 forest is 80-90 years and above)
SF - Swamp forest	Swamp forest – a waterlogged ground (not on peat), often with broadleaf grasses and herbs and sedges, with trees. Contrary to the bog, in a "swamp" there is in- and outflow of groundwater that adds to the productivity, and a "swamp" often has some herbs that demand high productivity.
TRB - Tree rich bog	Like a bog (very wet ground, on peat ground with low productivity and no in-or out flow of ground water, with no or very few trees) but more rich in trees.

 
 Table 2
 List of original and resulting candidate models for factors affecting Scandinavian brown bears' behavior when
 approached by humans on foot, in terms of a) sighting distance (SD), b) staying or leaving at the initial site when approached and c) flight initiation distance (FID), d) distance moved after disturbance, and e) time spent active after disturbance. Original models prior to model dredging are provided, where \* is an interaction term and + includes the variable without interactions. We show AIC<sub>c</sub> values, differences in AIC<sub>c</sub> values ( $\Delta$ AIC<sub>c</sub>) and AIC<sub>c</sub> weights for models (W<sub>i(M)</sub>) and variables (W<sub>i(V)</sub>). A plus symbol (+) indicates that a categorical variable is included in the model, whereas the inclusion of numerical variables are indicated by values (positive or negative depending on relationship with the response variable). Age = age of the GPS collared bear and Pass Dist = observer passing distance. The categorical variables are described in footnotes.

a) Response variable: Sighting distance (m) Original model: Rep $\operatorname{cat}^{1*}$ Activity <sup>2</sup> * Site type <sup>3</sup> + Habitat type <sup>4</sup>								ΔAIC <sub>c</sub>	<b>W</b> <sub>i(M)</sub>
Oliginali	nouei.	Nep cat	Activity	Site typ		lat type			
Model ID	(Int)	Activity	Habitat	Site type	Rep Cat	Activity : Rep cat			
1	3.38	+	+	+	+		316.5	0.00	0.70
2	3.45	+	+	+	+	+	318.2	1.72	0.30
$W_{i(V)}$		1	1	1	1	0.30			

<ul> <li>b) Response variable: Staying or leaving (binomial, 0 and 1)</li> <li>Original model: logAge * Activity<sup>2</sup> * Rep cat<sup>1</sup> + logSD * logPass Dist</li> </ul>										ΔAIC <sub>c</sub>	W <sub>i(M)</sub>
Model ID	(Int)	Activity	Age	Pass Dist	SD	Rep cat	Age:Rep cat	Pass Dist:SD			
1	1.51			-2.65	1.85				87.1	0.00	0.24
2	2.28			-2.71	2.02	+			87.9	0.80	0.16
3	3.39		-0.69	-2.88	1.82				87.9	0.86	0.16
4	5.09		-0.97	-2.95	1.87	+			88.1	1.06	0.14
5	2.98	+		-2.78	1.63				88.5	1.44	0.12
6	16.88		-5.63	-2.93	1.83	+	+		89.0	1.95	0.09
7	-1.57			-0.88	2.97			-0.64	89.1	1.98	0.09
$W_{i(V)}$		0.12	0.39	1.00	1.00	0.40	0.09	0.09			

c) Respo Original r	nse va nodel:	riable: Fli Rep cat <sup>1</sup>	ght initiati * Activity <sup>2</sup>	on distance (m) AIC <sub>c</sub> * logAge * logSD	ΔAIC <sub>c</sub>	<b>W</b> <sub>i(M)</sub>
Model ID	(Int)	Activity	Age			
1	4.52	+		164.6	0.00	0.53
2	5.11	+	-0.27	164.9	0.24	0.47
$W_{i(V)}$		1	0.47			

d) Response variable: Distance moved after disturbance (m) Original model: Activity <sup>2</sup> * Fam stat <sup>5</sup> * logSD * logPass Dist + Age									∆AIC <sub>c</sub>	W <sub>i(M)</sub>
Model ID	(Int)	Activity	Fam stat	Pass Dist	SD	Activity:Fam stat	Pass Dist:SD			
1	72.09	+	+		-7.79	+		811.1	0.00	0.54
2	69.37	+	+	0.34	-7.73	+		812.7	1.61	0.24
3	88.26	+	+	-1.90	-14.17	+	0.79	812.8	1.75	0.22
$W_{i(V)}$		1.00	1.00	0.46	1.00	1.00	0.22			

e) Response variable: Time spent active after disturbance (min) Original model: Activity <sup>2</sup> * Fam stat <sup>5</sup> * logSD + logPass Dist						<b>W</b> <sub>i(M)</sub>
Model ID	(Int)	Activity	Fam stat			
1	2.84			266.1	0.00	0.41
2	3.37		+	267.0	0.93	0.26
3	3.07	+		267.9	1.83	0.17
4	3.58	+	+	268.0	1.87	0.16
$W_{i(V)}$		0.33	0.42			

Rep cat = Single (S) or female with cubs (FC) 1)

2) Activity = Active (A) or passive (P)

Site type = Intitial site (IS) or second site (SS)
 Habitat type = See Table 1 for habitat type

5) Fam stat = Single (S), female with cubs of the year (FCOY) and female with yearlings (FY)



**Fig. 1** Average sighting distance in initial sites (IS) and second sites (SS) for approached Scandinavian brown bear females with cubs (FC) and single bears (S) in different habitat types (see Table 1 for habitat type definitions), in order of habitat type (e.g. G-FC = mid-aged forest, females with cubs). Longer sighting distance indicates less horizontal vegetation cover (i.e. more open habitat). The error bars show the standard error of the mean.



**Fig.2** Mean distance moved (m) after disturbance for active (A) and passive (P) Scandinavian brown bears in relation to family status (Fam Stat) with the categories: females with yearlings (FY), females with cubs of the year (FCOY) and single bears (S).

# **P**APER IV

# Lasting behavioural responses of brown bears to experimental encounters with humans

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## Summary

1. Some large carnivore populations are increasing in Europe and North America, and minimizing interactions between people and carnivores is a major management task. Analysing the effects of human disturbance on wildlife from a predator–prey perspective is also of conservation interest, because individual behavioural responses to the perceived risk of predation may ultimately influence population distribution and demography.

**2.** The Scandinavian brown bear population provides a good model to study the interactions between an expanding large carnivore population, and people who use forests extensively for professional and recreational activities. We experimentally approached 52 GPS-collared brown bears (293 approaches on foot) from 2006 to 2011, to document the reaction of bears and quantify the effect of disturbance on bear movements.

**3.** None of the bears reacted aggressively to the observers. Although the location of the animals was known, bears were usually in quite concealed spots and were physically detected in only 16% of the approaches (seen in 42 approaches; heard in 6). However, the bears altered their daily movement patterns after the approaches. Bears increased movement at night-time and moved less at daytime, which was most visible in days 1 and 2 after the approaches, altering their foraging and resting routines.

4. Synthesis and applications. We provide experimental evidence on the effect of human disturbance on a large carnivore. The lack of aggressive reactions to approaching observers reinforces the idea that European brown bears generally avoid people, although bears can respond aggressively if they feel threatened (e.g. when wounded). However, the movement patterns of the bears changed after disturbance. Separating large carnivores and people temporally and spatially is an important goal for conservation and management. Conserving the shrub cover that provides concealment to the carnivores and keeping people away from the most densely vegetated spots in the forests is a way to avoid encounters between carnivores and people, therefore promoting human safety and carnivore conservation.

**Key-words:** behaviour, conservation, experimental disturbance, human-wildlife interactions, large carnivores, management, people, time allocation, *Ursus arctos* 

#### Introduction

Most studies on human-wildlife 'conflict' report damages caused by animals, from small birds to the largest mammals, to human property, safety or valuable resources (Peterson *et al.* 2010). In turn, human–wildlife interactions cause a large proportion of wildlife mortality and behavioural responses that can imply demographic costs (e.g. Moore & Seigel 2006 for reptiles; Müllner, Linsenmair & Wikelski 2004 for birds; Harrington & Veitch 1992 for mammals). Behavioural responses to human disturbance are indeed of conservation and management concern, because they can be even more important for population

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dynamics than direct demographic effects (Pauli & Buskirk 2007).

The study of animal behaviour in recent decades has helped understand ecological patterns (Sih et al. 2012). An animal's perceived risk of predation influences its foraging, reproduction, hiding and fleeing behaviours (Lima & Dill 1990), and such responses are adaptive traits that influence population dynamics (Valdovinos et al. 2010). Given that adaptive behaviours are likely to have arisen after a long coexistence between predators and prey, disturbance stimuli could be analogous to predation risk from an evolutionary perspective (Frid & Dill 2002). Behavioural responses such as the modification of movement patterns or habitat use are often the first reaction that animals show to environmental changes and help determine the capacity of a species to cope with human-induced changes (Tuomainen & Candolin 2011). This predator-prey framework can be useful to study how large carnivores (e.g. wolves Canis lupus, brown bears Ursus arctos, lions Panthera leo; Linnaeus 1758) behave in a human-altered environment (Rode, Farley & Robbins 2006; Ordiz et al. 2011, 2012). Large carnivores are elusive animals, which stresses the need of understanding the effects of human activities on their behaviour, as cautious species are more susceptible to human disturbance and to exhibit declining populations than bolder ones (Sih et al. 2012).

Predation on livestock and occasional attacks to people are the most conflict-causing interactions between large carnivores and humans (Graham, Beckerman & Thirgood 2005). In turn, humans cause the majority of large carnivore mortality and have caused severe population reductions and extirpations worldwide (Woodroffe & Ginsberg 1998). However, some large carnivore populations are now increasing and some people living in recolonizing areas oppose their recovery. This is a major concern for the conservation and management of these species, whose large spatial requirements and use of multiple-use landscapes increase their contact with people, and this is occurring now in Europe (Enserink & Vogel 2006) and North America (Bruskotter & Shelby 2010).

Brown bears in Scandinavia provide a model to analyse the interactions between an expanding large carnivore population and people. This bear population was almost extinct by 1930, but recovered and reached c. 3300 bears in 2008 (Kindberg *et al.* 2011). GPS-collared bears were approached by Moen *et al.* (2012) to document their reactions when meeting people in Scandinavian forests. Most bears (80%) ran away and none behaved aggressively towards the observers, reinforcing the idea that European bears are generally not aggressive to people (Moen *et al.* 2012). Likewise, Karlson, Eriksson & Liberg (2005) approached Scandinavian wolves, which always fled from the observers.

Large carnivores often respond behaviourally to reduce encounters with humans. Bears select resting sites in denser vegetation with an increasing human activity (Ordiz *et al.* 2011); lions avoid the vicinity of cattle posts (Valeix

et al. 2012); and selection of breeding sites by wolves is influenced by villages and roads (Theuerkauf, Rouys & Jedrzejewski 2003). Yet, beyond the evaluation of the animals' fear (i.e. perceived risk, Stankovich & Blumstein 2005) and immediate reactions, it is important to document experimentally how long the effects last after the carnivores encounter people. Long-term effects of human disturbance on individual behaviour can have implications at population and community levels, and human activity can constrain the ecological role that carnivores play in ecosystems (Ritchie & Johnson 2009), thus justifying attention by management agencies (e.g. Cline, Sexton & Stewart 2007). For example, interactions of bears with human activities can have effects at the population level. Black bears Ursus americanus (Pallas 1780) accessing garbage near human settlements were heavier than their wildland conspecifics and had higher densities and fecundity; ultimately, there was a human-induced redistribution of the population in the landscape (Beckmann & Berger 2003). Often, large carnivore displacement due to disturbance occurs in the opposite direction, avoiding human settlements (e.g. Hebblewhite et al. 2005). Beyond the direction of displacement, consequences can arise at the individual level (e.g. 'problem bears'; Elfström et al. 2013), population level (e.g. population redistribution; Beckmann & Berger 2003) and ecosystem level, after altering interactions between species (Hebblewhite et al. 2005).

We conducted approaches on foot to brown bears and analysed daily bear movement patterns before and after the approaches. Our hypothesis was that bears would become more nocturnal after encountering people, modifying their circadian foraging and resting periods. In the long term, these behavioural responses to disturbance may have consequences at population level. This requires management attention to keep large carnivores and humans separated, reducing interactions as much as possible.

#### Material and methods

#### STUDY AREA

The study area was in south-central Sweden. Elevations range from c. 200 to c. 1000 m above sea level, with most of the area below the timberline (c. 750 m). The hilly landscape is mostly covered with intensively managed forest, dominated by Scots pine *Pinus silvestris* and Norway spruce *Picea abies*. Heather, grasses and berry-producing shrubs dominate the understorey layer. Human density ranges from 4 to 7 habitants km<sup>-2</sup>. Logging, berry picking, fishing and hunting, including bear hunting, are common in the forest.

#### APPROACHES TO RADIO-COLLARED BROWN BEARS

From 2006 to 2011, we approached 33 female and 19 male radiocollared adult bears, 4–19 years old. Twelve of the female bears had dependent cubs in some years of the study. The bears were equipped with GPS–GSM neck collars (VECTRONIC Aerospace

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#### 308 A. Ordiz et al.

GmbH, Berlin, Germany) and a VHF transmitter implant (IMP 400L, Telonics, USA). All details on marking and capturing are available in Arnemo, Evans & Fahlman (2011). The bears were approached  $\leq 6$  times each year, with  $\geq 14$  days between each approach on the same bear. Before each approach, the collar was programmed to register a GPS position every minute for 3 h. In the field, the observers (1.9  $\pm$  0.7) tracked the bear by VHF triangulation, started the approach several hundred metres away and aimed to pass the bear at c. 50 m, with the wind towards it (downwind). The observers continued walking for 500 m and returned to the starting point, but keeping  $\geq 500$  m distance to the original bear location. They walked together at a normal hiking pace, talking at a normal level. When only one observer approached a bear, he/she talked to him/herself. We registered the track of the observers during the approach with a hand-held GPS receiver that recorded positions every 10 m. We conducted 293 approaches (28 in 2006, 74 in 2007, 101 in 2008, 58 in 2009, 15 in 2010, and 17 in 2011), between 11:26  $\pm$  59 min and 12:41  $\pm$  68 min, that is, around noon, when bears are at resting sites (Moe et al. 2007) and when most human activity in the forest occurs.

#### PRE-BERRY AND BERRY SEASONS IN RELATION WITH BEAR BEHAVIOUR AND HUMAN ACTIVITIES

The first period of brown bear activity after leaving the den in spring includes the mating season. The foraging season or hyperphagia, when bears eat primarily berries to accumulate fat for hibernation is from mid-July to den entry in October (Friebe, Swenson & Sandegren 2001). Seasonal differences in bear behaviour also appear related to changing levels of human activity (Ordiz *et al.* 2011). Therefore, we divided the field seasons into a pre-berry season (<15 July, n = 215 approaches) and a berry season (>15 July, n = 78 approaches), with 15 July being the mean date of first observing fresh berries in the scats.

#### STATISTICAL ANALYSES

We used the GPS positions recorded by the collars every 30 min to construct daily bear movement patterns, calculating the distance travelled by the bears every 30 min during 24 h. Using all the positions recorded up to 6 days before the approach, we built a baseline movement pattern, with which we compared the 30-min distances travelled by the bears after the experimental approaches. We chose a Bayesian model formulation with estimation using Markov chain Monte Carlo methods (MCMC) to analyse the data. This approach can easily handle missing values that occur due to lack of GSM coverage (some missing GPS positions prevented us from calculating distance travelled for a given time interval). Further, the Bayesian model makes it straightforward to account for dependencies in the data, such as temporal correlations and repeated measurements of individual bears.

We used a linear model for the response variable y (square root of distance travelled every 30 min):

$$y_{ijklm} = \lambda_{ij} + \alpha_k + \gamma_l + \eta_m + \beta_{1j} x_{day} + \beta_2 x_{age}$$
  
+  $\beta_{3j} x_{app} + \beta_{4j} x_{dist} + \beta_{5j} x_{vis} + \epsilon_{ijklm}$  eqn 1

The time interval from 6 days before to 7 days after each approach was divided into 14 periods (i = 1, ..., 14) defined relative to the day of approach as follows: periods 1-6 = (day -6 to -1), 7 = (day of the approach), 8 = (day +1), etc., up to

period 14 = (day +7). The model parameter  $\lambda_{ij}$  is the effect of daily half-hour interval j (j = 1, ..., 48) within temporal period i. Further,  $\alpha_k$  (k = 1, ..., 52) is the random effect of bear k assumed to be distributed as  $N(0, \sigma_b^2)$ ,  $\gamma_l$  (l = 1,2) is the effect of pre-berry or berry season, and  $\eta_m$  (m = 1,2,3) is the sex-class effect (male, female or female with cubs). Several continuous covariates were also included: number of daylight hours  $(x_{day})$  with regression coefficients  $\beta_{1j}$ , assumed to be dependent on the daily time interval j, age of the individual  $(x_{age})$  with coefficient  $\beta_2$ , number of observers  $(x_{app})$  with time-dependent coefficients  $\beta_{3j}$ , minimum distance from the observers to the bear  $(x_{dist})$  with timedependent coefficients  $\beta_{4i}$  and visibility around the site where the bear was approached  $(x_{vis})$  with time-dependent coefficients  $\beta_{5j}$ . Visibility was measured as sighting distance (in metres) from the bear site and was used as a proxy of vegetation cover (see Ordiz et al. 2011 for further details). The noise term  $\in_{ijklm}$  accounting for unexplained variation was assumed to be distributed as  $N(0, \sigma_i^2)$ ; that is, the noise variance was also assumed to be dependent on daily time interval. The temporal correlation was included by assuming that the effect of a given time interval depended on the previous time interval within the same period. Specifically, we assumed

$$\lambda_{11} \sim N(0, 1000) (\text{vague prior distribution})$$
  

$$\lambda_{ij} = \nu \cdot \lambda_{i(j-1)} + \varepsilon_{ij} \text{for } j = 2, \dots, 48 \qquad \text{eqn } 2$$
  

$$\lambda_{i1} = \nu \cdot \lambda_{(i-1)48} + \varepsilon_{i1} \text{for } i = 2, \dots, 9$$

where v is an autoregressive coefficient, and  $\varepsilon$  is assumed to be distributed as  $N(0, \tau^2)$ . The variance parameter  $\tau^2$  controls the level of smoothing of the time effect. A large value induces minimal smoothing, whereas a small variance gives heavy smoothing. The sensitivity analysis of  $\tau^2$  indicated that the model parameter estimates were minimally sensitive to the choice of value for  $\tau^2$ , apart from the smoothness of  $\overline{\lambda}_{ij}$ . In the final model fit, we used  $\tau^2 = 1/5$  based on comparisons of the deviance information criterion (DIC) (Spiegelhalter *et al.* 2002) for different smoothing levels.

For all regression coefficients of continuous effects and for the parameter v, vague normal distributions N (0, 1000) were assumed *a priori*. Next, for the categorical variables season and sex class, the first level was set to zero (baseline), whereas vague normal priors were assumed for the remaining levels. To complete the Bayesian formulation of the model, the inverse of all variance components (the precisions) were given gamma priors *Ga* (0.001, 0.001), a commonly used vague prior for precisions.

The unknown model parameters were estimated by Bayesian posterior means using MCMC methods, implemented in Open-BUGS (Lunn et al. 2000). Due to the large number of observations, convergence was relatively fast and assessed by visual inspection of runs with differing starting values. The convergence was fastest for low levels of smoothing, but usually about 10 000 iterations were sufficient. Upon burn-in, a subsequent set of 10 000 iterations was used for parameter estimation (see Appendix S1 in Supporting Information for the OpenBUGS code). The estimated posterior distributions for the model parameters provided point estimates (mean) and credible intervals (lower 2.5% and upper 97.5% percentiles of the estimated distribution). We considered effects as statistically significant if the credible intervals of the corresponding parameters did not contain zero. The MCMC approach for parameter estimation is an iterative process allowing the missing values

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to be predicted by the given model and the current estimates of the unknown model parameters (data augmentation). With the MCMC estimation method, it is also straightforward to obtain posterior mean estimates and credible intervals for any combination of the main model parameters. We used this possibility to study derived parameters defined as the time-dependent differences in the effect of the approaches.

The differences of interest are those between each of the periods 7–14 and the average effect of period 1–6; thus, posterior means and uncertainty intervals were computed for difference parameters defined by

$$\delta_{ij} = \lambda_{ij} - \lambda_j$$
 eqn 3

for i = 7,..., 14 and j = 1,..., 48, and where  $\overline{\lambda}_j$  is the average effect of time *j* across periods 1 to 6. A significant positive difference implied increased movement after disturbance for the given time interval, and a negative difference implied reduced movement. We assessed the goodness of fit of the linear model with the coefficient of determination  $\mathbb{R}^2$ , based on all nonmissing observations and computed as  $\mathbb{R}^2 = cor(y, \hat{y})^2$  where  $\hat{y}$  are the fitted values from the estimated model.

# Results

None of the bears reacted aggressively to the observers in any approach (n = 293). Bears were seen (n = 42) or heard in the vegetation (n = 6) in 16% of the approaches. The minimum distance between observers and bears was  $89 \pm 68$  m ( $\geq 50$  m in 74% of the approaches; mean  $\pm$  SD). The visibility around the initial site where the bears were approached was  $21 \pm 11$  m.

Regarding bear movements, initial model estimations showed that the effects of both age and sex class were nonsignificant; thus, these factors were removed from the model. The final model  $R^2$  was 0.23. Based on the estimated time effects from each time period, the bears moved mostly during crepuscular and some nocturnal hours during the week prior to the approaches, with two distinct resting periods around midday and during the darkest hours around midnight (Fig. 1a). Approached bears initially moved away from their daybed and then reduced movements, which was reflected in the estimated pattern of distance travelled the day of the approach (Fig. 1b). However, the effect of the approaches on the bears lasted beyond their initial reaction. Compared to the previous week, significant periods of an increased movement at night and reduced movement during daytime were visible in the days following the approach, with a U-shaped pattern in difference from pre-approach levels most visible for days 1 and 2 (Fig. 2). Differences in movement patterns throughout the season may have occurred due to changes in day length, so the effect of day length on movement was estimated. Shortening day length had a positive effect on movement during the day and a negative effect during the night (Fig. 3). Bear movements increased in the berry season (0.491  $\pm$  0.067; 95% CI = 0.37 - 0.62). However, the main result was that

16 (a) 4 Square root meters 4 9 ω 9 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 ό 2 å 5 4 6 Time 16 (b) 4 Square root meters ⊵ 9 ø 6 2 7 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 å 4 5 6 8 Time

Fig. 1. (a) Estimated time effect (every 30 min during the 24 h day) on daily activity pattern of brown bears in south-central Sweden during the week before the experimental approach. The Figure shows the main resting period during midday and the second around midnight. (b) Estimated time effect on daily activity pattern of bears on the day of the approach, showing the initial escape after the disturbance event, followed by a reduction in movement. Vertical lines show the range of time when most approaches were conducted (start at  $11:26 \pm 59$  min, end at 12:41  $\pm$  68 min). The curves represent the mean of the distance travelled and the 95% credible intervals.

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#### 310 A. Ordiz et al.

encounters with people consistently caused an increase of bear movements at night and a reduction during daytime, which persisted after correcting for daylight, berry season and random bear effects. The number of observers was quite consistent  $(1.9 \pm 0.7)$  and had no significant effect on bear movements. A time-of-day-dependent effect showed that bears were most disturbed (movement pattern more altered) when vegetation cover around bear sites was denser and when observers-bear distances were shorter (Fig. 4).

# Discussion

In areas where large carnivores and human populations are increasing and expanding, people often become more afraid of potential encounters with carnivores and tolerance decreases. This is occurring in Scandinavia (Moen *et al.* 2012) and elsewhere (e.g. Gurung *et al.* 2008). The most dramatic consequences of human–carnivore interactions, that is, human fatalities and retaliatory killing of animals, receive most attention, but documenting the behavioural reactions of carnivores that encounter people is also important from a management perspective, to reduce encounters and their effects for both people and carnivores of conservation concern.

The fact that none of the bears reacted aggressively to the observers and that bears were not even seen or heard in 84% of the approaches show that bears clearly avoid any confrontation with people. The outcome can be different when the encounters are perceived by carnivores as more threatening, which may explain why most people injured by bears in Scandinavia are hunters (Moen *et al.* 2012). The minimum distance between observers and bears (89  $\pm$  68 m.) was almost double the planned 50 m., and 4 times larger than the visibility (21  $\pm$  11 m.) around the initial bears' sites, because the bears were in concealed places and generally moved away before the observers could get closer. However, the approaches affected the daily movement patterns of the bears. The immediate reaction after the encounters caused an average 26% increase in distance travelled by the bears compared to the same time of the day during the week prior to the approaches, immediately followed by a 10% reduction in movement (Fig. 2). Bears moved 11% and 8% more, respectively, during the darkest part of the 2 nights following an approach and for periods lasting  $\geq 4$  h 30 min, that is, when they previously had rested. During daytime, movement reduction was as intense in the 2 days following the encounters (10% and 11%) as in the day of approach (10%; Fig. 2). It is interesting to note that bears already had a marked resting period in the middle of the day before the approaches (Fig. 1a). As a reaction to the encounters, the bears lengthened the period of inactivity during daytime, probably relying on cover to avoid detection and the costs and risks of fleeing from people (Ordiz et al. 2011). The shorter the distance between observers and bear and the denser the cover, the stronger the effect of the approach on bear movements (Fig. 4). That is, bear behaviour was especially disrupted where the bear detected humans at short distance and in the highly concealed spots where bears hide and rest during the day (Ordiz et al. 2011; Moen et al. 2012).

Bears were expected to become more active during daytime as days became shorter (Fig. 3) and during the berry season, which has been reported before for this bear population (Fig. 1 in Moe *et al.* 2007) and elsewhere (Stemlock & Dean 1986). However, the expected trend towards more diurnal behaviour was disrupted by the encounters with people. This strengthens previous findings, because Ordiz *et al.* (2012) also found that bear movements



Fig. 2. Estimated differences in distance travelled by brown bears in south-central Sweden, every 30 minutes during the 24 h day, comparing the post-disturbance movement pattern of the bears, after they were experimentally approached, with the pre-disturbance movement pattern of the previous week. Two continuous vertical lines show the range of time when most approaches were conducted. The average percentage of bears' movement variation at night (+) and daytime (-) after the approaches is indicated for all significant time periods with duration  $\geq 1$  h 30 min. Differences at 30-min intervals were considered significant when the mean and the 95% credible intervals were all above or below zero.

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Fig. 3. According to the expectation from the Bayesian model, bears would increase movements during daytime caused by shortening of the days as the autumn season advanced. The curves represent the estimated daylight effect on the distance travelled and the 95% credible intervals.



Fig. 4. Time-dependent effect of (a) sighting distance (cover) and (b) minimum distance between observers and bears. Bears approached in more open areas (larger sighting distance) and detecting the observers further away altered movement patterns less than bears approached closer and in denser spots. The curves represent the estimated effect on the distance travelled and the 95% credible intervals.

increased during night-time and decreased during daytime after the start of the bear hunting season. Moen *et al.* (2012) found that younger bears left their initial site following an encounter more often than older bears, but the difference decreased in the berry season, when human activity in the area increased. In our case, the pattern of disturbance during the days after the approach was consistent for all bears, regardless of age or sex. The effect of age also tended to be negative in our study  $(-0.028 \pm 0.021)$ , but not significantly so. The same result was reported on bear resting site selection, thus

reinforcing that bears consistently hide from people (Ordiz *et al.* 2011).

Many studies of the effects of human activities on wildlife utilise short-term measures, such as flight initiation distance (FID) and/or composite metrics including FID and alert distance; however, more systematic research is needed to evaluate long-term effects of disturbance (Stankowich 2008). Short-term measures may not even reflect the effects of disturbance, if animals do not have alternative places to flee to (Gill, Norris & Sutherland 2001). For brown bears, Moen *et al.* (2012) showed the

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initial effects of encounters in terms of FID, and our analyses highlight the duration of the reaction and the changes in time allocation for resting and foraging.

Behavioural responses induced by human activity may not necessarily have negative effects on fitness (Gill, Norris & Sutherland 2001). However, fitness costs of human disturbance are reported for a variety of species and can negatively affect population size (Mallord et al. 2007) and viability (Kerbiriou et al. 2009). The lasting changes in bears' resting and foraging routines after disturbance deserve attention, because changes in time allocation after human disturbance may also have fitness consequences (Li et al. 2011). Sixty-seven percent of abandoned winter dens of Scandinavian bears had evidence of human activity within 100 m, and 3 of 5 pregnant females that abandoned dens lost cubs, compared to just 6% of 36 females that did not move (Swenson et al. 1997). This suggests that brown bear reproduction is affected by disturbance in addition to environmental and intraspecific factors (Ordiz et al. 2008). Disturbance during hyperphagia may also affect fitness, due to the strong correlation between bears' condition in the autumn and subsequent hibernation and reproductive success, which highlights the importance of storing fat during hyperphagia (e.g. Welch et al. 1997). The body mass of Scandinavian bears increases dramatically from spring to the onset of hibernation: c. 65% for females, c. 35% for males (Swenson et al. 2007). During hyperphagia, most bear populations rely on berries and/or nuts. Berries represent c. 81% of the annual digestible energy in central Scandinavia (Dahle et al. 1998). However, bears fattening on fruits ingest seven times less digestible energy per hour than salmonfeeding bears (Robbins et al. 2007). Fluctuations in berry availability and efficiency in eating berries pose additional constraints. Consequently, bears move constantly for many hours a day, as shown by our model expectation of an increased movement during the berry season, feeding at sites with the highest berry densities, and choosing the most visible berry clusters to maintain high intake rates (Welch et al. 1997). Good visibility should favour foraging on berries during daylight hours (MacHutchon et al. 1998). However, following approaches, bears reduced their activity during daytime and increased movement during the darkest part of the night. Thus, disturbance would affect energy gain by altering optimal foraging and resting, and also because responses to threats impose energetic costs (Preisser, Bolnick & Benard 2005).

The current scenario of global warming poses an extra concern. With the unique exception of some coastal populations with access to spawning salmon, all boreal populations of brown bears rely on berries during hyperphagia. Bokhorst *et al.* (2008) showed experimentally that even short warming episodes (1 week) cause a virtual elimination of fruit production in *Vaccinium* spp., which are essential berries for bears (e.g. Dahle *et al.* 1998). The entire European brown bear distribution falls within the area of highest increase in

temperature at the global scale in recent decades (see Fig. 1a in Walther *et al.* 2002). Brown bears at the southernmost edge of the distribution of bilberry *Vaccinium myrtillus* in Europe are now consuming fewer bilberries than a few years ago, which was linked to climate change (Rodriguez *et al.* 2007). Our results document that human disturbance can impede animals from exhibiting optimal activity patterns, for example foraging when it is most efficient, thus amplifying the broad effects of global warming on conservation.

Also at the population level, repeated encounters with humans may help explain the distribution of large carnivores in the landscape, with adults often living further away from human settlements than juveniles (e.g. Nellemann et al. 2007). The observed behavioural responses of bears to people (e.g. Moen et al. 2012; Ordiz et al. 2011, 2012; this study) may also help explain why bears (and other carnivores) are mainly diurnal in remote areas of North America, active for up to 17-18 h day<sup>-1</sup> and feeding c. 80% of the time (Welch et al. 1997), whereas in the more populated Europe bears are active only c. 12 h day<sup>-1</sup>, with a marked period of inactivity at midday (e.g. Moe et al. 2007). Zedrosser et al. (2011) argued that the ultimate reasons for transcontinental differences in life history parameters are related to the more extended persecution of large carnivores in Europe. The nocturnal activity pattern is definitely more marked after the start of hunting seasons (Ordiz et al. 2012) and after our approaches. This may reflect the level of bear elusiveness due to experienced risk of human encounters and helps reveal the importance of behavioural responses as a trait involved in population resilience to human-induced environmental changes (see Introduction).

# CONCLUDING REMARKS AND MANAGEMENT RECOMMENDATIONS

Brown bears avoided the approaching observers, which delivers a reassuring message for forest users and managers. However, the behavioural reaction of the bears after disturbance is of conservation concern. Large carnivores can play key ecological roles in the ecosystems they inhabit, but they themselves live in a landscape of fear instilled by human persecution (Ordiz *et al.* 2011; Valeix *et al.* 2012), which can constrain their apex role (Ritchie & Johnson 2009).

Nonlethal effects of predation risk are receiving increasing attention and appear essential to understand predatorprey interactions and population dynamics (e.g. Peckarsky *et al.* 2008). Nonlethal effects are costly and can be particularly strong in large-bodied, long-lived species (Heithaus *et al.* 2008) and in cautious animals (Sih *et al.* 2012). All of these features characterize large carnivores. The effects of human activities on carnivore dynamics should be studied from not only a demographic perspective, but also by accounting for nonlethal effects that can cause behavioural Nonlethal effects of nonconsumptive human activities can also be strong (Kerbiriou *et al.* 2009). We did not use dogs to chase the bears, that is, we simulated hiking or berry picking, not hunting and the clear alteration of brown bears' daily activity patterns responding to mere human presence is a strong indicator of the magnitude of disturbance effects. We talked during our on-foot approaches, which presumably alerted the bears of our presence. Other parameters, for example stress levels and foraging efficiency, may help quantify the disturbance. Experimental approaches to other species have shown that on-foot observers induce a stronger response than vehicles and that talking observers lengthened FID compared to silent observers (Wolf & Croft 2010).

Prevention of problems between carnivores and people through temporal and spatial separation (Treves & Karanth 2003) and minimizing carnivore displacement by human activity (Rode, Farley & Robbins 2006) are major management issues. Management should secure the protection of cover where large carnivore populations persist, and the restoration of cover in areas where current carnivore recoveries are to succeed. At the same time, people should be kept away from areas with shrub cover that provide concealment for resting carnivores during daytime, when people are outdoors. Our call to the protection of cover is important because the shrub layer is often destroyed, considered unproductive and/or to reduce fire risk, to increase pasture for cattle or even to promote conservation of endangered species (e.g. Revilla, Palomares & Fernández 2001). Preserving cover and avoiding the most densely vegetated spots in the forests is a simple, but reliable way to avoid encounters with carnivores, which would ultimately benefit both human safety and carnivore conservation.

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#### 314 A. Ordiz et al.

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### **Supporting Information**

Additional Supporting Information may be found in the online version of this article.

Appendix S1. OpenBUGS code for the statistical model

# **P**APER V

# Den entry behavior in Scandinavian brown bears *Ursus arctos*; implications for preventing human injuries.

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# ABSTRACT

Encounters between Scandinavian brown bears *Ursus arctos* and humans that result in human injuries and fatalities typically coincide with den entry in October/November, and commonly occur in the presence of a den. Our aim was to determine when bears arrive at their dens, identify potential predictors of the timing, and document behavior and activity associated with this period and how this might explain the increased risk of bear-caused human injuries documented in this period. We analyzed GPS location and activity data from brown bears in south-central Sweden, using generalized linear mixed models, statistical process control, and activity analyses.

Bears arrived at their den sites from 6 October until 1 December. Timing varied with reproductive category and bear age, and between years. Half of all bears reduced their activity significantly on average 2169 m from and 1.8 days before arriving at the den area. The other half reduced their activity after arriving at the den area. The latter bears took longer time to reach hibernation activity levels, but there was no difference in start of hibernation activity between the two groups. Bears also appeared to be more sensitive to disturbance in this period, with higher den abandonment rates than later in winter, particularly for males and bears that had not visited their den sites before den entry.

Den entry occurred over a long period, with high variability and poor predictability of its timing. Restrictions on hunting or other recreation activities that may disturb bears and expose people to greater risk of injury by bears therefore would probably be both impractical and ineffective. Our findings can be used to educate hunters about bear behavior at this time of year. Many associate dens with increased risk of a bear responding aggressively to disturbance, but our results indicate that other behavioral and possibly physiological changes in this period also may be involved.

### **KEY WORDS**

Activity, bear-human conflict, bear management, body temperature, defensive behavior, predenning

# INTRODUCTION

The Scandinavian brown bear *Ursus arctos* population is a conservation and management success story. Protection and careful management enabled recovery from the few individuals that survived persecution at the end of the 19<sup>th</sup> Century to a population that now exceeds 3000 individuals (Swenson et al. 1995, Kindberg et al. 2011). The bear has enjoyed more support from the general public than other large carnivores in Sweden (i.e. gray wolves *Canis lupus* and wolverine *Gulo gulo*) (Sandström and Ericsson 2009), possibly due to relatively low conflict levels in terms of damages to livestock and its status as a game species. However, encounters between bears and humans resulting in human injury and death do occur in Scandinavia (Swenson et al. 1999b). Such incidents have increased with the increasing population levels, or perhaps more importantly, with increasing hunting quotas and harvest (Sahlén et al. in prep.), and have resulted in decreasing public support for the bear (Sandström and Ericsson 2009). People in Norway are also most negative to bears and wolves (Røskaft et al. 2007). It is therefore important for managers to know which factors are involved when bear-human encounters lead to human injury, primarily to minimize the risk of human injury and fatalities from bear encounters, but also to maintain public support for the bear population.

Sahlén et al. (in prep.) recently reviewed all known bear-human encounters resulting in human injury or death in Scandinavia since 1977 and documented that the risk of injury from an attacking bear is greatest during the end of September until mid-November, and that the vast majority of injured people were armed hunters. During October/November, a large proportion of the incidents occurred at or near a winter den.

The period of increased risk of injury coincides both with brown bear den entry (Friebe et al. 2001, Manchi and Swenson 2005), and the moose *Alces alces* hunting season, when large numbers of hunters are present in the forest. Experimental approaches in the study area by researchers simulating hikers have documented that the majority of bears leave when approached by humans (Moen et al. 2012). However, the stalking, quiet behavior of hunters probably makes them more likely to surprise wildlife at close range than other groups of recreational forest users, exposing them to increased risk of attack and injury. Yet there is a similar concentration of hunters during the early part of the bear hunting season, which begins on 21 August and lasts until 15 October, unless quotas fill earlier. Despite this, very few incidents occur during bear hunting season (Sahlén et al. in prep.). Part of the explanation might therefore lie in changes in the bears' behavior during their behavioral and physiological preparation for winter near and at the den site.

Winter is associated with an abrupt decrease in available food resources for brown bears, and the majority of brown bear populations respond to this by hibernating in dens (Friebe et al. 2001, Haroldson et al. 2002, Ciarniello et al. 2005, Manchi and Swenson 2005, Baldwin and Bender 2010), although some exceptions have been documented (Nores et al. 2010). Hibernating bears survive on the energy stores accumulated during the fall hyperphagic period, and disturbance resulting in abandonment of a den site and subsequent movement to a new site comes with energetic costs that can have fitness consequences (Swenson et al. 1997, Linnell et al. 2000). In the southern SBBRP study area, most den abandonments appear to be the result of disturbance from human activity (Swenson et al. 1997). Evidence from both Scandinavia and North America suggests that bears select den sites that will reduce such risks of disturbance (Ciarniello et al. 2005, Elfström et al. 2008, Elfström and Swenson 2009, Goldstein et al. 2010). However, social factors may influence this selection and force some age/sex categories closer to human activity (Elfström and Swenson 2009, Libal et al. 2011), with compensatory selection in terms of small-scale habitat (Sahlén et al. 2011).

The denning period in Scandinavia spans from October until May, the duration varying due to factors such as reproductive status and latitude (Friebe et al. 2001, Manchi and Swenson 2005). Timing of den entry is influenced by factors such as sex, reproductive status, and environmental conditions (e.g. first snowfall), as well as age and/or body size (Friebe et al. 2001, Manchi and Swenson 2005). A recent study of American black bears (*Ursus americanus*) in Alaska has shown that proximity to human activity, and precipitation in early summer also may affect the timing of den entry (Baldwin and Bender 2010).

Most previous research on brown bear denning chronology was based on VHF data, but the use of GPS data provides information on a much finer scale, both temporally and spatially. The higher-resolution data allowed us to ascertain den locations, date of entry, duration, and potential den abandonments with greater certainty than previously. This is particularly true when the GPS data are

complemented with activity data from activity sensors measuring acceleration fitted into the GPS collars.

In this study, we used GPS and activity data from bears with confirmed and visited den locations to describe changes in bear activity levels, movement around the den site, and variables that may influence such movement. Our goal was to determine how brown bear movement and activity before and during den entry might explain the increased probability of aggressive behavior in encounters with humans documented during this period of time. In addition, we wanted to determine whether it was possible to predict when these aggressive encounters are most likely to occur. If so, managers could use this information to inform the appropriate public.

## MATERIALS & METHODS

# Study area

We conducted this study in the Scandinavian brown bear population's southern reproduction area in Sweden (61°N, 14°E). The area consists of gently rolling hills, and most of the area (>90 %) lies below the timberline (~750 m a.s.l.) (Dahle and Swenson 2003). The area is within the northern boreal forest zone and dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* H. Karst). The forest is a patchwork of tree monocultures and large clear-cuts (ca. 8 % of the forested areas) due to intense forestry management, and about 40% of the forest is younger than 35 years (Swenson et al. 1999a). The area is sparsely populated by humans and limited to a few villages and single cabins, many of which are only seasonally inhabited. Forestry practices have generated an extensive road system of varying size and quality, from unmaintained gravel roads to the paved national main road E45 (highway), which provides the main inland connection between north and south of Sweden (Nellemann et al. 2007).

# The bears

The Scandinavian Brown Bear Research Project (SBBRP) captured and handled bears during March – May using the methods for marking and capturing described earlier (Arnemo et al. 2011, Fahlman et al. 2011). The SBBRP captured offspring of already marked females, as well as previously unmarked, adult, and subadult bears. If the bear had not been followed from birth, age was determined by Matson Laboratory LLC, Miltown, Montana, USA by counting the annuli in a cross-section of a premolar root . The bears in this study were equipped with GPS Plus-3 or GPS Pro-4 neck collars, which were fitted with dual-axes motion sensors (activity sensors), VHF-transmitters, and a GSM modem (VECTRONIC Aerospace GmbH, Berlin, Germany). The capturing of the bears was approved by the Swedish Environmental Protection Agency (permit Dnr 412-7327-09 Nv) and Uppsala's Ethical Committee on Animal Experiments (Djuretiska nämnden i Uppsala), approval number C47/9.

The southern SBBRP study area is situated on the border of two counties, where the bear population density is about 30 individuals per 1000 km<sup>2</sup> (Bellemain et al. 2005, Solberg et al. 2006). Hunting of brown bears is permitted in Sweden and quotas are set at the county level by the County Administration Boards. The area is popular for bear hunting, with a large number of guest hunters present during the first week of hunting, and quotas are typically filled within the first two weeks of the hunting season. Moose hunting is permitted in some parts of the area from the first Monday in September until the end of September, with a two-week break for the rut, and then in the entire area from the first Monday in October until the end of February. The highest hunting activity for moose is during the period before the break.

# **Data collection**

The GPS collars were programmed to collect GPS location fixes at 30-min intervals during the period 1 August until 30 November (except for 2004 and 2005, when they were programmed at 3-hr intervals in this period), and once per day (at noon) from 1<sup>st</sup> December until 30 March. The activity sensors measured true acceleration in 2 orthogonal directions 6–8 times per second. The acceleration

values were then accumulated and averaged for each direction during the time interval between two successive activity fixes over a recording interval of 5 min. Activity counters in the GPS collars are an individual-based method to measure animal activity levels. The acceleration value measured by the sensor can be affected by several factors, such as collar placement and how tight the collar is on the neck. Therefore, activity levels can differ between bears or even for the same bear in the case of long-term recordings (Moen et al. 1996, Gervasi et al. 2006) as body weight, and consequently neck size, differ between seasons and individuals (Swenson et al. 2007). We selected data from bears for which we had GPS location data and activity measurements before, during, and after hibernation (August until mid-June) in each year. We used the full data set to identify denning sites and den abandonments, to ensure that we identified all potential dens used during the hibernation period for field verification. Potential den sites were identified using matched activity and GPS data (i.e. locations where the bear collar showed low activity and stationary behavior) and later confirmed with field visits. For the analyses related to den entry, we selected the data from 1 August until at least 31 December for the bears whose dens we had visited.

This left us with 90 den observations from 45 individuals (16 males ( $n_{obs}$ =29), 29 females ( $n_{obs}$ =61)) aged 2 – 18 years (median = 6 years) during 7 winters in 2004 - 2011. Based on the den entry date, as defined by the activity data (see below), we designated one "first den" per individual per season, and used only these in the analysis, resulting in 70 observations of den entry (see Table 1 for a summary). One female in 2004/2005, whose collar recorded very low activity levels throughout the season, and one male in 2009/2010, who denned outside the area for which we have digitalized road maps, were excluded from further analysis.

# Definitions

# GPS data

We used a 50-m radius around the den to assess the habitat in the near vicinity of the den, and to record bear activity that may relate to predenning behavior. An initial visual assessment of the GPS location data in ArcGIS 10 (ESRI Inc. 2010) showed that the GPS positions around each den site

rarely exceeded this area, and we therefore defined movement within a 50-m radius of the den site as movement at the den, i.e. the 'den site'. As our primary purpose with this study was to assess how bears' behavior around the time of denning could explain increased risk of human injury, we were also interested in how bears moved around the den area prior to entering the den. Experimental approaches on individuals from this study population have revealed that bears react to humans approaching at distances greater than 50 m; if the bear was active they tended to leave when observers were on average 115 m away from the bear, and on average 67 m if the bear was passive (Moen et al. 2012). To account for this, as well as a potentially greater sensitivity during the den entry period, we noted how much time the bear spent within 150 m of the den site prior to hibernation and defined this as the 'den area'. Bears approached their dens directly or gradually and we therefore made a distinction between arriving at the den site or den area to stay for hibernation and visit (bears entered the den site/area and then left again). If the bear arrived at the den site or den area for any period of time and then left and stayed away for a minimum of 24 consecutive hours, it was considered a visit. Because GPS data can tell us if a bear is at a den site, but not if it has entered the den, we use the term arrival. This is similar to the definition of den entry in other studies, e.g. (Friebe et al. 2001, Manchi and Swenson 2005), and we therefore use den entry when discussing arrival in more general terms. Arrival date was considered as the first GPS location within the den area after which the bear did not leave the area for more than 24 hours. We calculated the duration of each stay as the temporal difference between the first and last GPS location of that stay, and added the duration of all stays together for the total duration. Visits consisting of only one GPS-location were counted as 29 minutes in duration. For each den site, we calculated straight-line distances to the nearest road (divided into classes) and settlement (divided into classes). All definitions and road and settlement class divisions are listed in Table 2.

GPS location data are subject to primarily two types of error; missing location fixes and location error (D'Eon et al. 2002), which are influenced by habitat, terrain, topography, fix intervals, and animal behavior (e.g. (Cain et al. 2005, Heard et al. 2008) and references therein). Missing location fixes in our data set were recorded as "0-positions", and therefore easily discovered and removed, but location errors were difficult to filter out, unless the errors were very large (i.e. for our GPS data we
used a maximum speed threshold to filter out unlikely positions). The consequence of minor location error is that an animal may appear to be moving despite being stationary. In addition, bears tend to select denser habitats for their resting sites, e.g. (Moe et al. 2007, Ordiz et al. 2011), which is a combination of cover and behavior that can decrease GPS fix rates (Heard et al. 2008). This is likely to be an even greater problem at den sites, as many den sites are under ground or under very dense cover. The fix rates in our data subset confirmed this, as the proportion of 0-positions increased during the den entry period. In fact, in the absence of activity data, the proportion of 0-positions can be a very effective tool in determining the timing of den entry from GPS data. However, as our interest lay in the bear's behavior before it becomes inactive in its den, we used the GPS data to define arrival at a den site and used the activity data to determine when a bear had reached an inactive state indicative of hibernation.

# Activity data

#### Defining hibernation activity levels (HA)

We created individual activity indices by summing the acceleration values on the orthogonal axes (ranging from 0 to a maximum of 510) for each 5-minute interval. The bear was defined as physically active when its activity index was higher than 22.9 during a recording interval of 5 minutes. This threshold value is based on the first tests of the Vectronics dual-accelerated motion sensors (Gervasi et al. 2006). We defined the start of hibernation as the first day in autumn when activity dropped below 1 hour per day (= less than twelve 5-minutes activity recordings > 22.9 per day) (Laske et al. 2011).

#### Defining when activity levels are below normal activity

In order to quantify the time of change in activity, we adopted a statistical approach known as statistical process control (SPC), which is much used for controlling industrial processes (Shewhart 1931). The basic steps of SPC are firstly to identify an "in control" or normal behavioral process,

which here will refer to the activity patterns of a bear before denning. Based on the normal behavioral data, a mean trend is fitted and residual variance is estimated. Usually control borders around the mean are set as the interval defined by the mean  $\pm 2$  or 3 standard deviations. The process is then allowed to run beyond the range of the normal behavioral data, and if the process (here the activity levels) cross the control borders, then the process is said to be "out of control". For our purpose, a reduced activity level below a certain control limit indicated a lower than normal activity level, indicating the start of predenning activity (PDA).

# Statistical analyses

# Predenning activity (PDA)

Bears generally have a bimodal daily activity pattern with two activity peaks (early morning and late evening) and two activity lows (midday and middle of the night) (Moe et al. 2007), and the amplitude and duration of the high and low periods change with the time of year. The initial plotting of the activity data revealed a reduction in activity and increase in duration of the daily low activity periods throughout the fall leading up to hibernation, but the bimodal activity pattern persisted. This daily activity pattern can complicate the determination of when activity levels are reduced compared to normal activity. The mean trend in the bear activity data before denning could be estimated by a so-called moving average estimate. However, the low-activity periods within the high-activity period would make this impractical. Because we were most interested in the high-activity levels, we estimated a moving upper 90 percentile of the activity data, rather than a moving average. We set the width of the moving window to 150 data points. This gave a quite ragged curve, so we used an extra LOWESS smoother (Cleveland, 1979) to produce a final activity pattern curve. Two examples of such smoothed activity curves are provided in Figure 1a and b.

Activity curves from 67 bears were used as input to SPC. As a first step, a period of in control (normal behavior) observations was defined for each individual. This period was set to well before denning was expected to start. Then the normal behavior data for all 67 bears were used as observed

responses in a linear mixed model. Let  $Y_{ij}$  denote the j'th observation of the in control activity data (smoothed curve) for bear number i. Further, let  $x_{ij}$  be the time point corresponding to the observed response and  $a_i$  the random intercept term associated with bear number i (for i=1,..., 24). The random terms were assumed to be normally distributed with zero mean and variance  $\sigma_a^2$ , hence we assume  $a_i \sim N(0, \sigma_a^2)$ . Further, another random term was defined as the random effect of time for each bear, with the assumption  $b_i \sim N(0, \sigma_b^2)$ . The model assumed for the data was:

$$Y_{ij} = (\alpha + a_i) + (\beta + b_i)x_{ij} + \epsilon_{ij}$$

where  $\alpha$  and  $\beta$  are the intercept and slope parameters common for all bears and  $\epsilon_{ij} \sim N(0, \sigma^2)$  is the noise term. The fixed/random parameters were estimated/predicted using the nlme-package in R, based on the REML method for estimation. In lay words, this fits a bear-specific linear model to the normal behavior data, but the noise variance  $\sigma^2$ , which is of particular interest, was estimated based on all 67 bears. Upon estimation of the linear model and the noise variance, a lower control limit was defined for bear *j* as:

$$LCL = (\hat{\alpha} + \hat{a}_i) + (\hat{\beta} + \hat{b}_i)x - 2 \cdot \hat{\sigma}$$

That is the fitted linear model for the individual bear minus 2 estimated standard deviations. The time point of start of PDA was finally set as the first time the activity curve dropped below the *LCL* in the expected den entry period. The fitted *LCL* for two bears are shown in Figure 1.

We were unable to identify behavioral changes in two bears, due to generally low activity levels and such a gradual change in activity that the method could not identify a definite point in time where the bears had changed their behavior. The dates were uncertain for one bear and highly uncertain for the other. On one occasion, the PDA date occurred after the HA date. These three bears had prior potential den attempts before reaching the HA, but the dens could not be confirmed during field visits, or the dens were confirmed, but the bear switched dens before reaching HA (the location therefore did not qualify as a den). These three observations were excluded from further analysis.

We compared the PDA date to arrival dates and HA dates to determine when a bear began PDA in relation to arrival at the den site and the beginning of HA. Bears began PDA before arriving at the den

area (PDAB) or after arriving at the den area (PDAA). We therefore compared arrival date in the den area, PDA date, HA date, and time between PDA and HA between PDAA and PDAB using Welch's tests (accounting for uneven sample sizes and variances) on transformed variables (log- or square root to normalize residuals) or Wilcoxon rank-sum tests (for variables whose residuals could not be effectively normalized). We tested if males or females were more likely to begin their PDA before or after arrival at the den site using a Chi-square test of association with Yates' correction for continuity.

#### Movement at and near den sites

Because of the high number of potential explanatory variables that we wanted to include in relation to the relatively low number of observations, our models risked nonconvergence and false convergence (overspecification of the model). Therefore, we first ran a principal component analysis (PCA), using the statistical programming language and environment R version 2.14.1, and the PCA package (FactoMineR library, R Development Core Team 2011), where we included all continuous variables to evaluate whether there was any clustering of the variables. Because the PCA is sensitive to non-normality, all continuous variables with a non-normal distribution were log-transformed to normalize the data (see Table 3 for details). Variables that could not be normalized were excluded from the PCA. We selected variables from the resulting dimensions and included those seen as relevant in the subsequent generalized linear mixed models (GLMMs) using the lmer/glmer package (lme4 library, R Development Core Team 2011). In all models, the individual was included as a random variable to account for repeat sampling of individuals. We used the model.dredge package (MuMIn library, R Development Core Team 2011) to identify the best candidate models. Model dredging has been criticized as a "fishing expedition", which can produce spurious results (Burnham and Anderson 2002); however, such an approach can be useful for observational studies where there are a high number of potential explanatory variables (e.g. Hegyi and Garamszegi 2011, Symonds and Moussali 2011). When using an information-theoretic approach, it is in any case important to select explanatory variables with care, as the results of such an approach must always be considered in relative terms, i.e. selection of variables with little biological relevance could still generate a "best

model". For our models, we selected potential explanatory variables based on what has been previously substantiated in other studies on den entry and den selection (e.g. Baldwin and Bender 2010, Elfström and Swenson 2009, Elfström et al. 2008, Friebe et al. 2001, Manchi and Swenson 2005). Because all variables have a biological rationale, support from previous research, or both, we are confident of their biological/ecological relevance, which further reduces the risk of finding nonsensical candidate models.

Model selection is often based on the calculation of Akaike's Information Criterion (AIC) value, where the model with the lowest AIC is typically considered the "best model" and the difference between the AIC value of the top model and other candidate models is known as the  $\Delta$ AIC (Burnham and Anderson 2002). Candidate models with  $\Delta$ AIC < 2 are generally considered as equally good, whereas models with a  $\Delta$ AIC < 6 should not be discounted (Burnham and Anderson 2002, Richards 2005). In the case of small sample sizes this is accounted for by calculating corrected AIC (AIC<sub>C</sub>) values, which was the case in our analyses. Therefore, candidate models with a  $\Delta$ AIC<sub>C</sub> < 6 were selected from the model dredging results, and were used to calculate model and variable weights. AIC weights can be interpreted as the probability of a given model to be the best approximating model (Symonds and Moussali 2011), and thus we calculated AIC<sub>C</sub> weights for each candidate model, using the formula

$$w_i(AIC) = \frac{exp\{-\frac{1}{2}\Delta_i(AIC)\}}{\sum_{k=1}^{K} exp\{-\frac{1}{2}\Delta_k(AIC)\}} \quad (\text{Wagenmakers and Farrell 2004}).$$

To assess the relative importance of each explanatory variable on each response variable, we summed the weights of the models in which a given variable was included, to obtain variable weights (Symonds and Moussali 2011).

To determine which variables influenced timing of arrival at a den site, we ran a GLMM, with the original model including the variables (transformed where applicable) reproductive category + year + age + previous visits to den area (Y/N) + distance to main roads + distance to main gravel roads + distance to minor gravel roads + distance to settlements type 1&2 + distance to settlements type 3 + distance to the E 45 highway.

To determine which variables influenced how long the bears spent within 150 m of the den (i.e. the den area) prior to reducing activity below the hibernation threshold, we ran a GLMM with the original model including the variables (transformed where applicable) reproductive category + year + age + arrival date at the den site + distance to main roads + distance to main gravel roads + distance to minor gravel roads + distance to settlements type 1&2 + distance to settlements type 3 + distance to the E 45 highway.

To determine factors that may influence den abandonment, we ran a GLMM with a binomial link function. We included the following variables: sex + age + year + arrival date at den site + distance to settlements type 1&2 + distance to settlements type 3 + distance to main roads + distance to main gravel roads + distance to E 45 highway + time spent in the den area + time spent within the den area + previous visits to den area (Y/N). We also included the interactions sex:age and sex:previous visits. The model selection for den abandonment produced many models with  $\Delta AIC_C 2 < 6$  that varied very little in weight from each other, and did not contain any additional variables. We therefore elected to calculate weights based on the candidate models with  $\Delta AIC_C < 2$ .

### RESULTS

# **Predenning activity**

Bears began PDA on 22 October  $\pm$  11 days (mean  $\pm$  SD, median = 23 October). Bears began PDA before arriving at the den area (PDAB) on 35 of 60 occasions (58 %), and after arriving at the den area (PDAA) on 25 occasions (42 %). PDAB bears began PDA on 20 October  $\pm$  10.6 days, median = 20 October) and PDAA bears began PDA on 25 October  $\pm$  10.3 days (median = 23 October).

PDAB bears averaged  $2164 \pm 1690$  m from the den (median = 1662 m, min = 30, max = 7310 m) at the time they began PDA. One observation at a 30 m distance was included, because our arrival definition did not include visits, i.e. if the stays in the den area were separated by more than 24 consecutive hours. All other observations were at distance >250 m. PDA began  $1.8 \pm 1.8$  days (median = 1.3, min = 0.1, max = 7.9 days) before arriving at the den area, and  $5.7 \pm 3.5$  days (median = 5.2 days, min =1.3, max = 16.5 days) before HA. These bears spent  $4.0 \pm 3.4$  days (median: 3.0 days, min

= 0, max = 14.9 days) in the den area before HA, whereof  $3.6 \pm 3$  days (median = 3.0, min = 0, max = 12.4 days) were spent at the den site. Most of PDAB bears (66%) had visited the den area prior to the final arrival (n = 23, average visits:  $2.3 \pm 2.3$  visits, median = 1, min =1, max = 10).

PDAA bears were 175 m  $\pm$  430 m from the den (median 16 m, min = 2 m, max = 1741 m) when PDA began. One observation at 1741 m was included, because our arrival definition allowed for stays outside the buffer area that lasted less than 24 consecutive hours. PDA began 1.5  $\pm$  1.4 days (median: 0.95, min = 0.09 days, max = 5.4 days) after arriving at the den area, and 3.8  $\pm$  3.7 days (median: 3.1, min = 0.01 days, max = 14.1 days) before HA. These bears spent 5.4  $\pm$  4 days (median= 4.8, min = 0.9 days, max = 16.7 days) in the den area before HA, whereof 4.5  $\pm$  3.1 days (median: 4.1, min = 0.9, max = 12.9 days) were spent at the den site, and 72 % had visited the den area prior to final arrival (n = 7, average visits: 2.9  $\pm$  2.1, median: 2, min = 1, max = 7).

PDAB bears were significantly farther from the den than PDAA bears when PDA began (Wilcoxon rank-sum test: W = 51, p < 0.001). There was no difference between the two categories regarding the timing of HA (Welch's t-test t = 0.9797, df = 52.076, p = 0.3); however, there was a trend for PDAB bears to begin PDA earlier than PDAA bears (Welch's t-test, t = 1.7351, df = 52.665, p = 0.09, mean PDAB = 20 October, mean PDAA = 25 October).

There were no significant differences between the two categories in time spent at the den area before HA (PDAB:  $4.0 \pm 3.4$  days, PDAA:  $5.4 \pm 4$  days, Wilcoxon rank-sum test, W=338, p =0.1377); however, PDAB bears had shorter time between PDA and HA than PDAA bears (Wilcoxon rank-sum test, W = 250, p < 0.005). There were no significant differences between PDAB and PDAA bears in number of visits to the den site (Wilcoxon rank-sum test with continuity correction, W = 538, p = 0.13).

Females were more likely than males to be PDAB bears (28/46 females, 7/14 males, Chi square test of association with Yates' correction for continuity,  $\chi^2$  (df=1) = 5.63, p < 0.025.

#### Timing of arrival and movement at and near den sites

Bears arrived at the den area (within 150 m) on 23 October  $\pm$  11.1 days (range = 6 October - 30 November), spending 4.6  $\pm$  3.8 days (max = 16.8 days) in the den area before reaching HA.

In 22 of 68 den entry events, bears did not visit the den area before arriving at the den area to stay. The others visited the den area  $2 \pm 2.2$  times (range = 1 - 10 times), spending in total  $13.8 \pm 22.6$  hours in the area during visits (range= 29 minutes – 4.5 days) prior to their final arrival. Bears arrived at their den sites (within 50 m) on 24 October  $\pm 11.4$  days (mean  $\pm$  SD, range = 6

October – 1 December). They spent  $4.0 \pm 3.2$  days at the den site (max = 14 days) before reaching HA on 28 October  $\pm$  12.5 days (range = 6 October – 15 December). On three occasions, activity levels were already below the HA threshold when the bears arrived at their den sites (i.e. arrival at the den site and entry was set to the same time). These bears had either previous den attempts or smaller clusters that did not fit the den criteria before arriving at the den area and den site. Their activity values before and during hibernation corresponded to that of other bears, thus indicating that the early lowering of activity levels was not an artefact of the activity sensors. As previously mentioned, these three individuals had reduced their activity before arriving at the den sites, indicating that the smaller clusters may have been early den attempts, despite our inability to find dens or partial dens at the locations.

#### Factors affecting timing of arrival at the den site

The model selection resulted in 5 candidate models within  $\Delta AIC_C < 2$ , which included (listed according to the variables' AIC<sub>C</sub> weights) reproductive category, winter season (year), distance to minor gravel roads, distance to settlement type 3, distance to settlement type 1&2, age, whether the den area had/had not been visited between 1 August and final arrival at the den site, and distance to the E45 highway. Model dredging generated 29 candidate models with  $\Delta AICc < 6$ , which also included distance to main gravel road as an explanatory variable. Variable weights indicated year and reproductive category as the main factors deciding the timing of arrival at a den site (Table 4, Figure 2a-b). Timing of arrival at the den site varied among years, with earlier arrivals in 2007 and 2010. Pregnant females (n = 30), single females (n = 11), and females accompanied by cubs of the year (n = 3) arrived at their dens earlier than males (n = 19) and females with yearlings (n = 5). Bears tended to arrive earlier to den sites that were closer to minor gravel roads. We found the opposite relationship for small permanent settlements, as bears tended to arrive later to den sites that

were closer to these settlements. Bears may arrive slightly earlier to den sites closer to hunting cabins and smaller summer dwellings, which typically have a less predictable frequency of use, than den sites further away from such dwellings. Older bears tended to arrive to their den sites earlier than younger bears (Figure 2c). There were very low variable weights for whether the den site had been visited prior to final arrival, and the differences between the two categories (visited/not visited) were small.

#### Time spent in den area (<150 m) before reaching HA

The top model regarding time spent in the den area prior to HA, and the only model within  $\Delta AIC_C$  < 2, included only age as a variable (Figure 3). Models with  $\Delta AIC_C < 6$  also included distance to the E45 highway, distance to settlement type 1 & 2, visits to the den area, distance to settlement type 3, distance to minor gravel roads and distance to main gravel roads (Table 5). Age was by far the most influential variable according to the weights; all other variables had very little effect on time spent in the den area prior to HA.

# **Den abandonment**

Bears abandoned their first dens in 15 of 68 (22 %) denning events. Most den abandonments occurred early in the denning period, with only three abandonments occurring after 15 December (Table 1).

Sex and visits to the den area were the most influential variables (Table 6). Males abandoned their dens more frequently than females (Figure 4a, and bears that had prior visits to the den area abandoned their dens less frequently than bears that did not (Figure 4b). Longer time spent in the den area appeared to increase the likelihood of den abandonment. Distance to the E45 highway, distance to minor gravel roads, distance to settlement type 3, age and den site arrival date had low variable weights, indicating very little effect on whether or not bears abandoned their dens.

#### DISCUSSION

The bears reduced their activity gradually during the course of the autumn, but it was possible to statistically identify activity reductions – PDA – before the bear reached an inactive state and began hibernation. Approximately half of the bears reduced their activity before arriving in their den areas while far away from their dens, whereas the other half arrived in their den areas before reaching PDA. Females tended to be more likely to reach PDA before arriving in their den area, but it is possible that the timing of PDA depends on other factors, such as body size, individual condition, or possibly reproductive status (pregnant, accompanied by cubs, or single). Those that have already began PDA before arriving in the den area reach HA faster than those the beginning PDA after arriving, but there was no difference in the actual timing of HA.

The pattern and timing of arrival at the den we documented was similar to what had been documented previously for our study population, regarding the effects of reproductive category, age, and year (Friebe et al. 2001, Manchi and Swenson 2005). Single females, pregnant females, and FCOY arrived at their den sites earlier than males and females with yearlings. We did not group FCOY and FY as "females with cubs" in our analyses, as they had large differences in the timing of arrival at their den sites, with FY more resembling males in their timing (see Figure 2). Friebe et al. (2001) did not detect an effect of age on entry dates for female brown bears (although denning duration increased with female age), but we detected a tendency for younger bears to arrive at their den sites later than older bears. However, we did not analyze for differences within and between sexes in this respect, and it is possible that age affects male and female timing of arrival differently, as it does for duration of denning (Manchi and Swenson 2005). There were also yearly variations in timing of arrival at the den, which is in agreement with previous findings (Manchi and Swenson 2005). We did not include any weather or environmental variables in our analyses, because of the already high variable-to-observation ratio, but other studies have documented effects of environmental variables (e.g. food availability (Van Daele et al. 1990, Schooley et al. 1994), snowfall, snow cover (Craighead and Craighead 1972, Reynolds et al. 1976, Servheen and Klaver 1983, Manchi and Swenson 2005) on den entry. Although this may be less important for pregnant females (Friebe et al. 2001), interannual variations in the onset of winter are the most likely explanation for the differences we documented. Baldwin and Bender (2010) documented that bears entered their dens earlier when closer to roads and hypothesized that this may be due to increased access to food sources near roads, which allowed them to gain enough fat reserves to den early. We also found some effects of distance to human activity, with bears arriving at their den sites earlier when closer to minor gravel roads and smaller permanent settlements. Elfström and Swenson (2009) documented a tendency for adult males to den further from plowed roads and permanent settlements. In our study, males arrived at their den sites later than other bears, and although we did not analyze for interactions between human infrastructure and reproductive category, it is possible that the effects of distance to roads and settlements we documented may actually be an effect of social organization in den selection, i.e. avoidance of dominant males (Elfström and Swenson 2009). Dumpsites for slaughter remains tend to be associated with minor gravel roads, however, and are typically used by local hunting teams on a yearly basis to dispose of hides and bones from the moose hunt (Sahlén 2006). It could be interesting to document the presence and size of such sites in our study area in detail, to examine any potential effects they may have. How long a bear spent in the den area before HA was mainly related to the age of the bear, with older bears spending less time in the den area than younger bears. This may be an effect of older bears' greater experience and familiarity with their home range. Manchi and Swenson (2005) documented that distance between an individual's dens in successive years was short for adult males and females irrespective of age, indicating that the same general area tended to be used for denning year after year, but that young male bears had long distances between successive years' dens, due to the subadult males' dispersal behavior.

The den abandonment rate we documented (22%) was higher than the 9 % reported previously for our study area, which was based on VHF radiotelemetry (Swenson et al. 1997). However, the greater location accuracy and sampling frequency of the GPS data allowed us to record movements on a finer scale than when using VHF data. Most den abandonments in this study occurred early in the denning season; only 4 % occurred after mid-December. This pattern, although different in effect size, is also in agreement with Swenson et al. (1997). Because of the differences in quality between VHF and GPS data, we were probably less likely to notice these finer location shifts early in the denning season when relying on VHF tracking alone. Thus, we doubt that den abandonment rates have increased. Males, and bears that had not visited their den area before final arrival, regardless of sex, were more likely to abandon their dens. There was also a smaller effect of how much time they spent in the den area before HA; bears that abandoned their dens spent more time in the den area than bears that did not abandon their dens. Given that the majority of documented den abandonments appeared to be the result of human disturbance (Swenson et al. 1997, Linnell et al. 2000), it seems likely that this may be the case here as well. The moose-hunting season starts at the end of September and is most intense during October and beginning of November, and forestry is active all year round in the area. Both activities have great potential for disturbing bears, especially moose hunting, which often involves unleashed baying dogs. Bears that had visited the den area previously may be aware of most of the regular disturbances that occur and are therefore either used to them, or have already selected against such disturbances when choosing their den site. We know from small- and large-scale studies that adult males avoid human activity to a greater extent than other categories of bear (Nellemann et al. 2007, Elfström et al. 2008). Additionally, males are more likely to den in open "nest dens", which could also make them more vulnerable to disturbance (Elfström and Swenson 2009). However, males' greater likelihood of abandonment may also be an effect of males' better ability to bear the cost of abandonment (Beale and Monaghan 2004), due to their greater body size and fat reserves. Abandonment is particularly costly for pregnant females, which are more likely to lose their cubs than pregnant females that did not abandon their dens (Swenson et al. 1997). The cost of abandonment is likely to increase later in the winter season, when the bears are deeper in hibernation and the snow cover makes it difficult to locate new suitable dens (Evans et al. 2012). This, and less human activity in the forests, may explain the lower den abandonment rates documented in late winter.

Longer time spent in the den area before entering hibernation increased the likelihood of abandonment, and the bears that spent more time in the den area tended to be younger. However, even among older bears, longer time spent in the den area could indicate greater uncertainty about the suitability of the selected den area, or of a higher level of disturbance nearby, which could affect the bears' decision to stay or leave.

# What do our results mean for predicting injury risks?

Bears arrive at their dens over the course of several weeks, with great variation in timing both within and between different reproductive categories and between years, making the onset of denning difficult to predict. Most of the human injuries occur during the moose-hunting season, which is concurrent with the den entry period. A high predictability in the timing of den entry could have permitted hunting restrictions during limited times as a useful management tool to reduce the risk of injury to humans and the risk of disturbance to the bears. However, imposing moose-hunting restrictions lasting almost a month is unlikely to be effective in reducing either risk or disturbance and would certainly not be supported by hunters. Reducing the moose hunting period could also interfere with moose management objectives.

One important finding is that bears do not have to be at their den site to begin predenning activity; in fact, half of the bears in our study were often kilometres away from their final den location when their activity levels dropped significantly. This means that many bears were moving in this lowered activity state for almost two days before arriving at their den area. Whether this activity state is only behavioral or also physiological cannot be assessed in this study, but it raises the question of whether bears in this activity state away from their den may respond similarly to meeting a human as a bear in this state near its den.

Studies of rodent species have shown that animals faced with threats respond in a continuum of defensive behaviors, ranging from escape to fight and attack (Blanchard and Blanchard: in (Eilam 2005)). The fight response is typically triggered when there is a limited ability to flee and/or the threat is close to the animal. Bears undergo a series of physiological changes during the hibernation period, including a decrease in body temperature (Nelson et al. 1983). Although the onset of hibernation is associated with environmental cues (Craighead and Craighead 1972, Reynolds et al. 1976, Schooley et al. 1994, Friebe et al. 2001, Manchi and Swenson 2005), brown bears and other mammals tend to begin hibernation even in absence of such cues, suggesting a molecular genetic mechanism (Carey et al. 2003). The reduction in activity we documented in the bears did not depend on having settled into a den, which suggests that physiological changes affecting the bears' behavior may begin before this

time. Studies on ectotherms, such as lizards and snakes, have shown a relationship between decreasing temperatures and increasing use of fight rather than flight as forms of defensive behavior (e.g. (Hertz et al. 1982, Crowley and Pietruszka 1983), but see Keogh and DeSerto (1994)). This is because low body temperature impairs the ability to move, in particular on aspects of speed and endurance (Bennett 1990), but less so on the ability to defend themselves aggressively (Herrel et al. 2007). This may be further affected by body size, as an aggressive response may be ineffective as a defensive strategy in smaller individuals, whose best defense is then still to flee even at diminished capacity (Cury de Barros et al. 2010). Muscle function in both endo- and ectotherms are affected by temperature, often with lowered function associated with low body temperature (Bennett 1984). This could mean that brown bears react more aggressively to disturbance, not because they are defending themselves at or near a den, but because their physiological state prevents them from using escape as an effective defensive mechanism. This could also explain why injury rates increase during the den entry and moose hunting period, and that this physiological state of the bear could be a factor, even without the presence of a den, when humans are injured by bears during the den entry period (Sahlén et al. in prep.). The use of hunting dogs may further affect the bears' behavior, whether restrained physically by being cornered in a den or physiologically by decreased mobility, as dogs can be persistent when they have located their prey and remain baying for hours.

# CONCLUSION

The very long time span over which den entry occurs, and the high variability in its timing, makes it difficult for managers to impose any restrictions on recreation or hunting that could reduce the risk of injury to hunters and disturbance to bears in this sensitive period.

Therefore, we recommend that managers continue with their information efforts to increase the awareness among moose hunters, especially those using unleashed baying dogs, about when the risk of disturbing, and being injured by, a bear is greatest. The growing and expanding bear population means that the risk, or chance, of encountering a bear is increasing. Our results show that half of the bears alter their behavior before they have arrived at their den and that there is a potential that bears are

more likely to respond aggressively to disturbance as a result of a change to prehibernatory behavior rather than the presence of a den. It is therefore important that hunters approach barking dogs that are assumed to be holding a moose at bay with caution until they are certain that the dog has a moose at bay and not a bear. This has dual benefits in terms of reduced risk of injury to the hunter, as well as to the bear.

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# TABLES AND FIGURES

	First se	election	Number	Observations	First dens only	Number	Observations
Individ	duals		45	90		45	70
	Males		16	29	Males	16	20
	Female	es	29	61	Females	29	50
		with cubs of the year	3	3	with cubs of the year	3	3
		with yearlings	4	7	with yearlings	4	5
		single	10	12	single	10	11
		pregnant	21	39	pregnant	21	31
	Age	Min	2		Age Min	2	
		Max	18		Мах	18	
		Mean	7.6		Mean	7.6	
		Median	6		Median	6	
Dens			89*	90		70	70
	Den at	tempts		4			
	First d	ens		70			
	Second	d dens		15			
	Third o	dens		1			
	Den ab	pandonment	17	20	Den abandonment	14	15
		Attempted shifts**	4	4			
		Early shifts	11	13	Early shifts	11	12
		Mid-season shifts	3	3	Mid season shifts	3	3

# Table 1: Description of the data used in the study of denning behavior by Scandinavian brown bears.

\*) One bear used a previous first den as a second den two years later \*\*) See Table 2 for definitions

Variable	Definition
Bear category	Bear reproductive class
Single female	Female unaccompanied by young during den entry, who did not give birth during the following winter
Pregnant female	Female unaccompanied by young during den entry, who gave birth during the following winter
FCOY	Female accompanied by cubs born during the previous winter (cubs of the year)
FY	Female accompanied by cubs born two winters earlier (yearlings)
Male	Males
Den	A location where a bear has been stationary (i.e. not left for more than 24 consecutive hours at a time) for a minimum of five days
attempt	A potential den location according to GPS data, but field investigations did not reveal any den structure, only digging attempts or partial dens, or the bear reached hibernation activity at a subsequent den site
first den	The first den where the bear first reduced its activity below the threshold value
second den	The new den after abandonment of a first den
third den	The new den after abandonment of a second den
Den abandonment	The bear has left the den site and moved to a new location
attempt shift	Abandonment of a den attempt
early shift	Abandonment of a den before 14 December
mid-season shift	Abandonment of a den between 15 December and 14 February
late season shift	Abandonment of a den after 15 February (separated from den exit by the bear selecting a new confirmed den after abandonment
Arrival 150	The first GPS location within 150 m of the den where the bear does not leave for more than 24 consecutive hours prior to arrival within 50 m
Arrival 50	The first GPS location within 50 m of the den, after which the bear is stationary for a minimum of five days, without being away from the site for more than 24 consecutive hours at a time
Entry_activity	The first day in a seven day period where the activity does not go above the hibernation activity threshold (< 22.8)
Visit	Time spent within 150 m of the den which is separated in time from arrival and other visits by at least 24 hours
1st visit	First position within 150 m of the den site
Number of visits	Number of visits within 150 m of the den site
Total duration	Total time spent during visits within 150 m prior to arrival within 150 m
Time within 150 m	Total time spent within 150 m after arrival within 150 m until reaching the hibernation activity threshold
Roads	
E45	Paved main road through the area, the inland connection between south and north of Sweden (state road)
Main roads	Paved main roads within the district. Connects the largest communities (county roads)
Main gravel roads	High standard gravel roads. Connects larger roads and minor communities (county and communal roads)
Medium gravel roads	Gravel roads of good standard with a relatively constant but minor traffic. Typically connecting larger roads, minor communities and recreation sites, or used as a short-cut between larger roads (communal and private roads).
Minor gravel roads	Gravel roads of varying quality. The activities associated with these are occasional and unpredictable e.g. forestry, recreation, berry picking, hunting and fishing (communal and private roads)
Railroad	Low activity railroad, mostly cargo, which runs largely parallell to the E45. Limited tourist traffic during summer
Settlements	
Type 1 & 2	Forest cabins; low and unpredictable activity & summer houses/hunting cabins; varying activity between and within seasons
iype 5	י פווזומויפות שבנעפוויבות נוויסטצווסטר נווב אבמו, שווצוב וויסטצי נס שוומו נסוווווטווונוצי (< סט וווומטונמונג)
Type 4	Larger communities; villages and towns (> 50 inhabitants)

Table 2: Definitions of the variables used in the models to determine factors influencing denning behavior of Scandinavian brown bears.

Table 3:	Variable	transformations	(see	Table	2).
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Variable	Transformation type
Bear age	log
Time spent in den area before HA*	log10
Time spent at den site before HA*	log10
Distance to E45	log
Distance to main road (paved)	log
Distance to main dirt roads	square root
Distance to medium dirt roads	log10
Distance to railroad	log
Distance to town roads	log10
Distance to settlement type 1 & 2	log10
Distance to settlement type 3	log10
Distance to settlement type 4	log 10

Table 4: Factors affecting timing of arrival of Scandinavian brown bears at the den site. Blank cells shows the variable is not included in the candidate model, + indicates that a categorical variable is included in the candidate model, and numbers show the relationship between the intercept and the numerical variable in the candidate model.

Model_ID	Intercept	Cat- egory	Age	E45	Minor gravel roads	Settlement 1 & 2	Settle- ment 3	Main gravel roads	Year	Visited den area	df	logLik	AICc	delta	weight
1	297.2	+	-3.302		5.824	5.856	-6.859		+	+	18	-192.852	435.7	0	0.17
2	295.2	+	-3.239		6.095	6.11	-7.163		+		17	-194.79	435.8	0.16	0.157
3	293.1	+			6.041	6.257	-8.056		+	+	17	-195.639	437.5	1.85	0.067
4	298.3	+	-3.291	-0.101	5.756	5.811	-6.782		+	+	19	-191.844	437.5	1.86	0.067
5	295.6	+	-3.236	-0.03356	6.075	6.092	-7.144		+		18	-193.798	437.6	1.89	0.066
6	291.4	+			6.272	6.471	-8.294		+		16	-197.545	437.8	2.09	0.06
7	308.3	+	-3.571		5.178		-3.535		+	+	17	-196.229	438.7	3.03	0.037
8	305.6	+	-4.491		6.739	3.409	-7.433	0.1162	+	+	19	-192.565	439	3.3	0.033
9	295	+		-0.1858	5.917	6.176	-7.908		+	+	18	-194.614	439.2	3.52	0.029
10	306.3	+	-3.505		5.511		-3.752		+		16	-198.283	439.2	3.57	0.029
11	289.4	+	-4.042		4.886	2.509			+	+	17	-196.522	439.3	3.62	0.028
12	292.6	+		-0.1212	6.198	6.421	-8.21		+		17	-196.541	439.3	3.66	0.027
13	301.5	+	-4.282		7.149	4.075	-7.929	0.1064	+		18	-194.806	439.6	3.91	0.024
14	286.1	+	-3.995		5.194	2.668			+		16	-198.604	439.9	4.21	0.021
15	310.6	+	-3.533	-0.2544	5.01		-3.374		+	+	18	-195.189	440.3	4.67	0.016
16	312.6	+	-3.618			4.331	-5.009		+	+	17	-197.068	440.4	4.71	0.016
17	312.1	+	-4.798		6.52		-5.601	0.1285	+	+	18	-195.214	440.4	4.72	0.016
18	298.4	+	-3.999		4.771				+	+	16	-198.892	440.5	4.79	0.016
19	312.9	+	-4.477	-0.7002	6.296	3.087	-6.96	0.1243	+	+	20	-191.371	440.6	4.95	0.014
20	307.9	+	-3.479	-0.1817	5.401		-3.646		+		17	-197.264	440.8	5.1	0.013
21	294.5	+	-3.945	-0.4737	4.624	2.502			+	+	18	-195.435	440.8	5.17	0.013
22	304.6	+			5.345		-4.589		+	+	16	-199.178	441	5.36	0.012
23	306.9	+	-4.264	-0.5441	6.851	3.853	-7.598	0.1122	+		19	-193.699	441.2	5.57	0.011
24	295.4	+	-3.951		5.102				+		15	-201.007	441.2	5.58	0.01
25	310.2	+	-3.53			4.659	-5.376		+		16	-199.317	441.3	5.64	0.01
26	290.4	+	-3.915	-0.4065	4.986	2.652			+		17	-197.55	441.3	5.68	0.01
27	308.7	+	-4.618		6.969		-5.777	0.1196	+		17	-197.611	441.5	5.8	0.009
28	302.8	+			5.637		-4.762		+		15	-201.194	441.6	5.95	0.009
29	318.5	+	-3.501	-0.7319		4.219	-4.611		+	+	18	-195.844	441.6	5.98	0.009
Variable	_weight	0.999	0.795	0.275	0.964	0.832	0.91	0.107	0.999	0.543					

Table 5: Factors affecting time Scandinavian brown bears spent in the den area (< 150 m) before hibernation activity. Blank cells shows the variable is not included in the candidate model, + indicates that a categorical variable is included in the candidate model, and numbers show the relationship between the intercept and the numerical variable in the candidate model.

				Minor gravel	Settle-	Settle-	Main						
Model ID	(Int)	Age	E45	roads	ment 1&2	ment 3	gravel roads	Visits	df	logLik	AICc	delta	weight
1	0.9824	-0.2587							4	-38.392	85.4	0	0.432
2	0.1414	-0.3017	0.1022						5	-38.374	87.7	2.3	0.137
3	0.4213	-0.2675			0.1653				5	-38.771	88.5	3.09	0.092
4	0.4948								3	-41.096	88.6	3.15	0.09
5	1.025	-0.2408						+	5	-39.151	89.3	3.85	0.063
6	0.9036	-0.2625				0.0235			5	-39.271	89.5	4.09	0.056
7	1.101	-0.2583		-0.0431					5	-39.358	89.7	4.27	0.051
8	0.6458	-0.2685					0.005821		5	-39.782	90.5	5.11	0.034
9	0.6118							+	4	-41.308	91.3	5.83	0.023
10	-0.232	-0.306	0.09692		0.123				6	-38.996	91.4	5.95	0.022
Variable v	veights	0.887	0.159	0.051	0.114	0.063	0.034	0.097					

Table 6: Factors affecting den abandonment of Scandinavian brown bears. Blank cells shows the variable is not included in the candidate model, + indicates that a categorical variable is included in the candidate model, and numbers show the relationship between the intercept and the numerical variable in the candidate model.

Model ID	(Int)	Arrival at den site	Minor gravel roads	Age	E45	Settle- ment 3	Time in den area	Sex	Visited	df	logLik	AICc	delta	weight
1	-1.159							+	+	4	-29.634	67.9	0	0.167
2	-0.551						-1.161	+	+	5	-28.619	68.2	0.3	0.143
3	0.5016		-8.00E-05				-1.473	+	+	6	-27.691	68.8	0.86	0.109
4	-1.969							+		3	-31.361	69.1	1.19	0.092
5	-0.5782		-5.18E-05					+	+	5	-29.162	69.3	1.39	0.083
6	1.613				-0.316			+	+	5	-29.163	69.3	1.39	0.083
7	-1.848			0.3874				+	+	5	-29.4	69.8	1.87	0.066
8	2.066				-0.303		-1.111	+	+	6	-28.208	69.8	1.89	0.065
9	3.403					-1.082	-1.3	+	+	6	-28.211	69.8	1.9	0.065
10	1.426					-0.7216		+	+	5	-29.419	69.8	1.9	0.064
11	-8.362	0.0266					-1.319	+	+	6	-28.229	69.8	1.93	0.063
Variable	e weights	0.063	0.192	0.066	0.148	0.129	0.445	1	0.908					





Figure 1a and b. Examples of pre-denning activity analyses on individual Scandinavian brown bears. The blue line shows the bear-specific linear model to the normal behavior data, and the red line is the LCL. The activity patterns clearly show the gradual reduction, activity variations and hibernation activity levels (HA).



Figure 2a: Arrival at the den site (Julian date) by reproductive category of Scandinavian brown bears. F0 = females with cubs of the year (n = 3), F1 = females with yearlings (n = 5), M = males (n = 19), P = Pregnant females (n = 30) and S = single females (n = 11).



Figure 2b: Arrival at the den site (Julian date) by year (winter season) for Scandinavian brown bears, 2004/05-2010/11.



Figure 2c: Arrival at the den site (Julian date) by age (years) of Scandinavian brown bears.



Figure 3: Time spent (days) in the den area (<150 m) in relation to age (years) of Scandinavian brown bears.



Figure 4a: Den abandonment (yes or no) vs. sex of Scandinavian brown bears (male or female).



Figure 4b: Den abandonment (yes or no) vs. den area previously visited (yes or no) by Scandinavian brown bears.

# **P**APER VI

# Capture, Anesthesia, and Disturbance of Free-Ranging Brown Bears (*Ursus arctos*) during Hibernation

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#### Abstract

We conducted thirteen immobilizations of previously collared hibernating two- to four-year-old brown bears (Ursus arctos) weighing 21-66 kg in central Sweden in winter 2010 and 2011 for comparative physiology research. Here we report, for the first time, an effective protocol for the capture and anesthesia of free-ranging brown bears during hibernation and an assessment of the disturbance the captures caused. Bears were darted in anthill, soil, or uprooted tree dens on eleven occasions, but two bears in rock dens fled and were darted outside the den. We used medetomidine at 0.02-0.06 mg/kg and zolazepam-tiletamine at 0.9-2.8 mg/kg for anesthesia. In addition, ketamine at 1.5 mg/kg was hand-injected intramuscularly in four bears and in six it was included in the dart at 1.1–3.0 mg/kg. Once anesthetized, bears were removed from the dens. In nine bears, arterial blood samples were analyzed immediately with a portable blood gas analyzer. We corrected hypoxemia in seven bears (PaO<sub>2</sub> 57-74 mmHg) with supplemental oxygen. We placed the bears back into the dens and antagonized the effect of medetomidine with atipamezole. Capturing bears in the den significantly increased the risk of den abandonment. One of twelve collared bears that were captured remained at the original den until spring, and eleven, left their dens (mean  $\pm$  standard deviation) 3.2 $\pm$ 3.6 (range 0.5–10.5) days after capture. They used 1.9 $\pm$ 0.9 intermediate resting sites, during 6.2±7.8 days before entering a new permanent den. The eleven new permanent dens were located 730±589 m from the original dens. We documented that it was feasible and safe to capture hibernating brown bears, although they behaved differently than black bears. When doing so, researchers should use 25% of the doses used for helicopter darting during the active period and should consider increased energetic costs associated with den abandonment.

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#### Introduction

Growing interest in hibernation physiology requires development of safe and effective field techniques for immobilizing hibernating bears with the least possible risk to both researchers and bears. Free-ranging brown bears (*Ursus arctos*) in Sweden hibernate six to seven months each year and with fewer disruptions than the three months for brown bears in captivity at the same latitude [1]. Due to a longer hibernation and different physiology [2,3], free-ranging bears are likely to be a better model for human medical research regarding cardiovascular disease, space medicine, bed-ridden patients, and obesity than captive bears. When a Scandinavian brown bear goes into hibernation in the fall it has typically gained 40% in weight most of which is stored fat. For the next half year the bear lies still and plasma cholesterol levels rise to an average of 12 mmol/L [4]. However, when the bear emerges from the den in spring it has remained free from vascular thrombosis, atherosclerosis [5] and heart failure [6] despite these quite dramatic risk factors. Although there are many research projects that can utilize samples from hibernating bears [7,8], research on capture, anesthesia, and disturbance is important to ensure the welfare of the research animals, safety of the capture personnel, and to evaluate the ethics of such research. Evaluation of disturbance and impact of research on free-ranging animals is becoming more valued [9,10]. We developed this capture protocol for hibernating brown bears based on limited reports of immobilization of American and Asiatic black bears (Ursus americanus and U. thibetanus) during winter [11,12,13], immobilization of captive brown bears in wintertime [14], springtime brown bear immobilization protocols in the same study areas [15,16], and knowledge of denning ecology [17,18,19] and hibernation physiology [3,20].

Brown bears select their den sites prior to hibernating [18], typically at least 1-2 km from human activity [17]. Human activity closer than this, particularly closer than 200 m, can cause bears to abandon their dens [17]. Brown bears that abandoned their dens in our study area moved on average 5.1 km before finding a new den, with 56% moving 2 kilometers or less [21]. In a study where 14 denning female American black bears with cubs were captured, none abandoned their dens [22]. However, den abandonment by brown bears as a result of non-research human disturbance has been documented in Scandinavia [21], and den abandonment was therefore considered a possible response to our captures.

In Scandinavia, free-ranging brown bears are immobilized during their active period with a combination of medetomidine and tiletamine-zolazepam, with atipamezole used for antagonism of the effects of medetomidine [15]. In April captures, subadults were given a mean  $\pm$  SD dose of 0.08 $\pm$ 0.02 mg/kg medetomidine combined with 4.1±1.3 mg/kg tiletamine-zolazepam [16]. Recent studies showing hypoxemia correctable with intranasal oxygen resulted in the addition of oxygen supplementation for all bears during spring and summer captures [16,23]. During hibernation, American black bears reduce oxygen consumption by 75% [24], but we do not know how oxygen consumption in bears is affected by anesthesia or what the optimal PaO<sub>2</sub> levels are during anesthesia of hibernating bears. Ketamine has been used in combination with alpha-2 agonists at doses ranging from 1.5-17.1 mg/kg in American black bears [25,26,27], 4.4 mg/kg in Asiatic black bears [27], and 2.0-7.2 mg/kg ketamine in brown bears [25,27]. American black bears (Ursus americanus) are commonly captured during hibernation and when approached quietly, can be localized without disturbing or flushing them and immobilized with a blow dart, jab stick or dart gun [12,13].

In previous studies, brown bears have only been anesthetized during winter in captive situations. One study of non-hibernating brown bears concluded that the ideal dose for oral carfentanil was 12.7  $\mu$ g/kg in the summer and 7.6  $\mu$ g/kg in the winter (60% of summer dose) [14]. Another study mentions, but does not describe, the anesthesia of four captive brown bears with tiletamine-zolazepam during hibernation [6]. In that study, 2 mg/kg tiletamine-zolazepam was used during hibernation and 5 mg/kg during the summer months (personal communication, Nelson, 12/2009).

Our objectives were to develop an effective capture and anesthesia protocol for hibernating free-ranging brown bears, to evaluate arterial oxygenation in order to determine if supplemental oxygen should be administered and to evaluate the disturbance that the captures caused to the bears. Our hypothesis was that a low-dose combination of medetomidine and zolazepam-tiletamine would be effective for capture and anesthesia of hibernating brown bears, and that these captures would cause the bears to abandon their dens.

#### **Materials and Methods**

All captures were approved by the Swedish Ethical Committee on Animal Research (application numbers C212/9 and C47/9) and the Swedish Environmental Protection Agency. Fieldwork was carried out in Dalarna, Sweden during February-March (winter) and in June (summer) 2010 and 2011. We selected six female and six male hibernating brown bears, two to four years old, previously fitted with global positioning system (GPS) collars and very high frequency (VHF) abdominal implants. One female was anesthetized during both years. We only anesthetized subadults to reduce the chance of encountering females with cubs in the dens and to avoid older animals, considered to pose greater risk to the capture team. Snow depth ranged from 80-120 cm with temperatures ranging from  $-15^{\circ}$ C to  $+1^{\circ}$ C.

We located bears using GPS and VHF radio collars/implants (Figure S1 and S2). All dens were between 5 and 20 km from plowed roads, so we used snowmobiles to transport equipment and the field team to within 200-800 m of the den. Once we had located the den entrance and removed the snow (Figure S3), a metal grate was placed over the entrance. Two field personnel held the grate over the entrance using their own body weight and were assisted by up to three more people if necessary to keep the bear in the den. Anesthetic agents were administered by remote darting through the grate (Figure S4) using a flashlight and CO<sub>2</sub> powered rifle (Dan-Inject<sup>®</sup>, Børkop, Denmark) fired from 0.3-3.5 meters distance. Darts were 3 ml with a 2.0×30 mm barbed needle (Dan-Inject®). The bears were anesthetized with a total dose of 0.6-2.5 mg of medetomidine (Domitor® 1 mg/ml, and Zalopine®,10 mg/ml, Orion Pharma Animal Health, Turku, Finland) and 31-125 mg tiletamine-zolazepam (Zoletil®, 500 mg/vial, Virbac, Carros, France). A second dart with a full dose was administered if the bear was mobile after 10 minutes. In four bears, 75-100 mg ketamine (Narketan 10<sup>®</sup>, 100 mg/ml, Chassot, Dublin, Ireland) was hand-injected before handling and for six immobilizations; 37-75 mg of ketamine was included in the initial dart.

Once anesthetized, we took each of the bears out of the den (Figure S5) and placed them on an insulated blanket. We measured temperature, heart rate, and respiratory rate in all bears. We were unable to obtain pulse oximetry readings with a veterinary sensor clip placed on the tongue, lip, ears, or vulva were from the first four bears during February, so we abandoned this for the remaining bears. Blood samples from the femoral artery were collected anerobically in pre-heparinized syringes from ten bears at 15-25 and 65-75 minutes from darting. The samples were immediately analyzed in a portable analyzer (iSTAT 1® Portable Clinical Analyzer, Abbott Laboratories, Abbott Park IL, 60064-6048, USA) with the bear captured both years only sampled during the second year. Blood gas samples and pH were corrected to rectal temperature. Intranasal oxygen was provided from a portable oxygen cylinder to eight bears via a nasal line inserted 10 cm into one nostril with an oxygen flow rate of 0.5-2.0 liters per minute after the first arterial sample was collected.

After sampling, we placed the bears back into the dens and antagonized the effects of medetomidine with atipamezole (Antisedan<sup>®</sup>, 5 mg/ml, Orion Pharma Animal Health, Turku, Finland) given intramuscularly at 5 mg per mg of medetomidine. We covered the entrance with branches and snow and the bears were left to recover undisturbed.

In June we recaptured bears by darting from a helicopter as previously described [16]. Ten bears were captured with 5 mg medetomidine combined with 250 mg zolazepam-tiletamine and one was darted twice for a total of 10 mg medetomidine and 500 mg zolazepam-tiletamine. Two smaller bears (22 and 28 kg) were immobilized with 2.5 mg medetomidine and 125 mg zolazepam-tiletamine. Sampling was conducted as described for February bears, except that a narrower time range was selected for each arterial sample (20–30 minutes and 60–65 minutes from darting).

Hypoxemia was defined as mild ( $PaO_2 60-80 \text{ mmHg}$ ), marked ( $PaO_2 40-60 \text{ mmHg}$ ), or severe ( $PaO_2 < 40 \text{ mmHg}$ ). Acidemia was defined as a pH <7.35, and acidemia was considered marked if pH <7.25. Hypocapnia was defined as a Pa-CO<sub>2</sub><35 mmHg and hypercapnia was defined as mild ( $PaCO_2$  45–60 mmHg) or marked ( $PaCO_2 > 60 \text{ mmHg}$ ). A paired two-

tailed t-test was used to compare the first and second sample at both winter and summer captures, and between winter and summer for both the first and second samples. Bears not receiving oxygen were excluded from comparisons that included a second sample for the variables with direct relation to oxygen ( $PaO_2$ ,  $PaCO_2$ ,  $SaO_2$ ,  $HCO_3$  and pH).

#### Disturbance Data Analysis

Twelve of the thirteen winter-captured bears were fitted with GPS Plus and GPS Plus Pro collars with GSM lateral modems (Vectronic Aerospace GmbH, Berlin, Germany), which allowed collection of GPS and activity data. The GPS collars also had dual-axis motion sensors and VHF transmitters. We programmed the collars to register GPS-position data every ten minutes from the date of capture until at least four days after capture. The collars registered only one GPS-position per day (at noon) until 31 March, and from 1 April reverted to the standard programming of one GPS-position per 30 minutes. GPS position data were stored in the collar and sent to a base station in packages of seven positions per text message, via the GSM (Global System for Mobile Communications) network. We retrieved collars during captures in June and downloaded GPS data in order to obtain any data not sent via text messaging.

The collars recorded activity data at 5-minute intervals, based on the average of 4–8 measurements per second for five minutes immediately preceding the time of recording. Activity level was measured in two orthogonal directions, yielding two numeric activity values ranging from 0–255. The average of these two values indicated whether a bear is active ( $\geq$ 50) or passive (<50) [28]. Activity data were not sent via mobile network text messages, but were stored in the collar and downloaded after we retrieved the collar.

GPS data documented the time and distance of movements following immobilization. We defined a cluster of positions (hereafter called a cluster) as the equivalent of six GPS positions within 50 m, with a 30-minute position interval. We divided clusters into dens and beds, i.e. outside dens, based on follow-up visits to the sites during May and June. The activity data identified activity changes associated with movements. We considered a bear to have remained at a den or bed (a temporarily used aboveground site) until the time of the last inactive measurement before movement. We defined arrival at a bed or den as the first GPS location within the cluster, and we considered bed or den use to have begun at the time of the first inactive measurement following arrival.

We considered a new permanent den as the location where the bear remained for the majority of the remaining denning period. We defined resumed inactivity at the new permanent den as the first inactive measurement during five consecutive days where less than 5% of the daily activity measurements were active. We defined den emergence as the time of the last GPS position within 50 meters of the den. Data for all variables are presented as mean  $\pm$  standard deviation (range). We used a subsample of marked bears in the study area that were not captured in the den, for which activity data, GPS data and den location data were available for 76 denning events in 2004-2011. We conducted a chi-squared test of association with Yates' Correction for Continuity to compare the den abandonment rate of bears captured in the den with that of bears that were not. We have no information on other non-research related human disturbance around the dens, and thus could not compare the effects of different types of human disturbance on den abandonment rates.

#### Results

In 2010, two of the bears were in rock dens at the time of capture. On the other capture occasions, bears were denned in anthill (6), soil (4), or uprooted tree (1) dens. All of the sites used between original dens and new permanent dens were beds (7) or nest dens (3). The difference between a bed and a nest den is the amount of material used in its construction. Dens used as new permanent dens were rock (4), bed (3), nest (2), uprooted tree (1), anthill (1) and soil (1) dens.

#### Ground Darting and Adequate Anesthesia of Hibernating Bears was Possible with 25% of the doses of Medetomidine and Tiletamine-zolazepam Used for the same Bears in Summertime

We documented hypothermia, bradycardia and mild to marked alterations in pulmonary gas exchange and acid-base status. Intranasal oxygen supplementation markedly improved arterial oxygenation.

During winter captures, all bears moved as far as possible from the entrance into the den when capture personnel entered it. Two bears in dens under large rocks escaped using alternate exits. Due to difficulties in carrying out captures in rock dens, bears in rock dens were not captured in 2011. One was darted in the den and both were darted as they left the dens, running 40 and 200 meters respectively, before recumbency. On the remaining eleven occasions, bears were in soil or anthill dens. In these, the captures went smoothly, except for one instance where the drug in the dart froze and the bear required a second dart, and a second case where the bear was darted in the den and managed to escape around the grate.

Induction time was  $16\pm 8$  (6–26) minutes. Doses were  $0.03\pm 0.01$  (0.02-0.05) mg/kg medetomidine,  $1.7\pm 0.7$  (0.9-2.8) mg/kg zolazepam-tiletamine in all bears. In four bears, ketamine at 1.5 mg/kg was hand-injected and in six it was included in the dart at 1.1-3.0 mg/kg (Table 1). During summer captures, doses for bears darted once were  $0.10\pm 0.03$  (0.07-0.11) mg/kg medetomidine and  $4.7\pm 0.6$  (4.3-5.7) mg/kg tiletamine-zolazepam. Induction time in the eleven bears darted once was  $2\pm 1$  minutes. The two bears darted multiple times received a total dose of 0.13 mg/kg medetomidine and 6.5 mg/kg tiletamine-zolazepam, and 0.18 mg/kg medetomidine and 6.8 mg/kg tiletamine-zolazepam, respectively.

The bear darted with the highest dose in winter (0.05 mg/kg medetomidine, 2.5 mg/kg zolazepam-tiletamine and 3 mg/kg ketamine), a 2-year old, 27 kg male, was apneic on removal from the den at 12 minutes after darting. The apnea did not respond to 50 mg doxapram (Dopram<sup>®</sup>, Wyeth Lederle, Wyeth-Ayerst International Inc., Philadelphia, PA, USA) given intravenously and the bear was therefore intubated and ventilated manually with a bag valve mask (Ambu-bag<sup>®</sup>, Ambu Ltd. Cambridgeshire, United Kingdom). This bear was supplemented with oxygen-enriched air by connecting the oxygen tube to the bag valve mask. We did not take an arterial blood sample until after manual ventilation with oxygen enriched air began, so this bear was excluded from the blood-gas data presented in Table 2. The bear did not resume spontaneous breathing until after atipamezole was given at 2 hours and 24 minutes after darting.

**Physiological evaluation.** Heart rate, respiratory rate, and body temperature for winter and summer are presented in Table 2. Paired analysis of arterial blood samples was performed in the same ten bears in winter and in summer (Table 2). Due to cartridge errors, some variables were not available for the second sample of one bear during winter and for the first sample of one

Table 1. Body mass, age (years) and drug doses (mg) used for anesthesia of brown bears during winter and summer.

Bear	Weight (l	Kg)	Tiletamir	ne-zolazepam	Medetom	idine	Ketamine	Inductior from dar	n time (minutes ting)
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Winter	Summer
Male (3) <sup>§1</sup>	NR	63	62.5	250	1.25	5	N/A	16	3
Male <sup>1</sup> (2)	54	56	125	250	2.25	5	N/A	26	1
Female (3) <sup>§1</sup>	45	53	125	250	2.25	5	N/A	42	0
Female (3) <sup>1</sup>	55	55	125	250	2.5	5	75	13	3
Female (3)* <sup>1</sup>	51	53	62.5	250	1.25	5	75	13	1
Female (3)* <sup>1</sup>	53	58	62.5	250	1.25	5	75	13	1
Male (3) <sup>#1</sup>	66	77	125	500	2.5	10	100	22	14
Female (3) <sup>2</sup>	57	72	62.5	250	1.25	5	75	10	2
Male (3) <sup>2</sup>	58	51	62.5	250	1.25	5	75	12	5
Female (2) <sup>2</sup>	21	22	31	125	0.63	2.5	37	6	2
Male (4) <sup>2</sup>	59	47	62.5	250	1.25	5	75	7	2
Male (2) <sup>2</sup>	25	27	62.5	125	1.25	2.5	75	12	2
Female (2) <sup>#2</sup>	35	28	31	190	0.63	5	37	16	16
mean	48±14	51±17	77±35	245±51	$1.5 \pm 1.0$	5.0±1.0	70±19	16±10	2±1

\*Denotes the bears that had the best quality of anesthesia. For bears requiring several darts to be anesthetized in summer<sup>#</sup>, the dose presented is the total dose and the induction time is not included in the mean.

<sup>§</sup>Escaped from rock dens, darted while running.

'Induction not observed (ran 200 meters), not included in the mean.

<sup>1</sup>Captured in 2010. <sup>2</sup>Captured in 2011.

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bear during summer. Hypoxemia was recorded in arterial samples before oxygen supplementation in seven of ten bears in winter (PaO<sub>2</sub> 30–74 mmHg) and two of ten bears in summer (PaO<sub>2</sub> 66– 69 mmHg). A second arterial sample was collected from nine bears in winter receiving 0, 1 and 2 liters per minute of oxygen and ten bears in summer receiving 0.5 or 1 liter per minute. On the second winter sample, the seven bears receiving 1 liter per minute had PaO<sub>2</sub> levels of 100–387 mmHg and the bear receiving 2 liters per minute had a PaO<sub>2</sub> of 301 mmHg. On the second summer sample (while receiving either 0.5 or 1 liter per minute O<sub>2</sub>), bears had PaO<sub>2</sub> levels of 89–180 (Table 3). In winter, eight of the bears evaluated had initial pH values of less than 7.25 (marked acidemia) and the other two had mild acidemia (7.25–7.35). In summer, three of ten bears had marked acidemia (7.12–7.25), five had mild acidemia (7.25–7.34) and two were 7.35 (within the normal range).

During winter captures, hypercapnia was initially recorded in five of ten sampled bears and in the second measurement in seven of nine bears. In summer one of nine bears had hypercapnia on initial sampling. Hypocapnia was recorded in anesthetized bears both during winter and summer. All bears that were tested had higher glucose, hematocrit and hemoglobin during winter than during summer (table 2).

**Behavioral consequences.** Bears left their original dens following capture on twelve of thirteen occasions (summarized in Table 4). One of the twelve bears from which we obtained GPS and activity data remained at the original den. The 11 bears remained at their dens for  $3.2\pm3.6$  days before leaving, and spent  $6.2\pm7.8$  days before resuming inactivity at a new permanent den. On five occasions, bears moved directly from the original den to the new permanent den, spending  $2.2\pm1.1$  hours before locating and settling into the new den. On the remaining occasions, bears used  $1.8\pm0.5$  beds for  $12.4\pm7.0$  days before locating and settling into the new permanent den. One bear did however move from the original den to a new den within 1.5 hours. It remained at this den for 17.5 days, left and stayed at a bed for 2.0 days, before resuming inactivity at a new den for 22 days. From the activity pattern and duration, we consider the bear to have resumed inactivity at both new den sites. The data from this bear's denning was therefore only included in calculations of time spent at the original den (i.e. the den where it was captured).

Non-den captured bears had a den abandonment rate of 26% (n = 20), but the majority occurred in October/November and only 3 abandoned their dens during January-March (4%). Den captured bears were significantly more likely to abandon their dens compared to marked, non-captured bears during the same time period ( $\chi^2$  (1, N=76) = 59.1, p<.0005). However, the abandonment rates of den-captured bears were highly significant even when comparing with overall abandonment rates ( $\chi^2$  (1, N=76) = 20.5, p<.0005) or when excluding those occasions where bears moved dens early in the season ( $\chi^2$  (1, N=56) = 45.2, p<.0005).

Den emergence occurred from 5 April until 23 April in 2010, and for six of seven bears, 19 April until 22 April in 2011, similar to other bears in the study area in the respective years. One bear in 2011 emerged on 5 May, which was somewhat later than most other bears in the study area. The straight-line distance between the original and (final) new permanent dens was  $730\pm589$  m (225–2123 m, Table 4).

#### Discussion

The capture technique with ground-darting of hibernating brown bears in dens was successful. All bears were alert, and frightened, with three escaping from their dens and darted while running. This is in contrary to black bears, which can even be snuck up on when denning in open nests [13]. The best quality of **Table 2.** Physiological variables and blood gas results from seven brown bears anesthetized during winter and summer 2010 and 2011.

	Units	Winter						Summer					
Time from darting		15–35 mi	n		65–75 mi	n		20–30 min			60–65 min		
		Mean±S	ORange	Ν	Mean±S	ORange	Ν	Mean±SD	Range	Ν	Mean±SD	Range	Ν
Heart rate <sup>a,b,c,d</sup>	beats/ minute	32±8	20–50	12	20±6	12–30	10	79±15	42–96	10	67±8	58–80	10
Respiratory rate <sup>b</sup>	breaths/ minute	7±4	3–16	12	5±3	2–12	9	12±8	5–34	4	9±4	5–16	10
Rectal Temp <sup>a,b,d</sup>	(°C)	33.5±1.2	32.2-36.4	13	33.9±1.6	31.7–37.1	13	39.4±1.1	36.9-40.9	12	38.6±1.3	35.4-40.1	11
Lactate <sup>a,c,d</sup>	mmol/L	4.1±2.8	1.5–11.2	10	2.8±2.3	1.2-8.5	9	7.5±3.8	1.5-13.2	9	3.0±2.4	0.8–7.5	10
PaO <sub>2</sub> * <sup>a,c,d</sup>	mmHg	68±20	30–106	10	205±111	60–387	9	86±17	66–120	9	124±26	89–180	10
SaO2 <sup>d</sup>	%	89.1±14.8	48.0-98.0	10	97.3±5.8	82.0-100.0	9	91.4±3.7	85.0-95.0	8	97.6±1.4	95.0-99.0	10
pH* <sup>d</sup>		7.23±0.07	7.12–7.34	10	7.26±0.11	7.15-7.54	9	7.24±0.07	7.17–7.35	8	7.32±0.04	7.29–7.41	10
PaCO2* <sup>a,b</sup>	mmHg	52.9±9.1	36.9-64.2	10	59.2±14.7	22.1-71.8	9	36.1±7.7	22.2-49.8	8	40.1±4.4	33.2-45.4	10
BUN <sup>a</sup>	mg/dL	6±4	1–11	11	7±4	3–11	4	23±17	2–44	8	21±15	2–41	10
Glucose <sup>a,c,d</sup>	mmol/L	8.6±1.1	7.1–10.2	11	11.8±1.5	10.3–13.8	4	6.1±1.4	4.7–9.1	8	6.3±2.1	2.8–9.7	4
Hct <sup>a,b,c</sup>	%	59±3	54–65	11	55±3	51–57	4	41±5	33–47	8	39±5	28-44	10
HCO3 <sup>a,b,d</sup>	mmol/L	23.6±2.4	18.9–27.2	11	25.9±3.6	19.4–31.0	10	16.4±5.4	8.2-26.7	8	21.3±3.5	17.4-28.3	10

Variables corrected to rectal temperature are marked with an \*. Statistically signficant differences using a paired two-tailed t-test are denoted by; <sup>a</sup>Between winter and summer sample 1,

<sup>b</sup>winter and summer sample 2.

<sup>c</sup>winter sample 1 and 2 and d. summer sample 1 and 2.

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anesthesia during winter was achieved in the bears darted with the lowest doses of medetomidine, zolazepam-tiletamine combined with ketamine in the dart to deepen anesthesia without depressing respiration or prolonging recovery. The ketamine was added after experiencing depressed respiration at higher doses of medetomidine-zolazepam-tiletamine and a shallow plane of anesthesia at the low doses. Ground darting and anesthesia of hibernating bears was possible with 25% of the doses used in summer. The bear that became apneic during winter captures was darted with medetomidine-zolazepam-tiletamine at 50% of the mean dose given in summertime combined with 75 mg ketamine. The apnea may be attributed to the dose of medetomidine, which can depress respiration [29]. Although medetomidine tiletaminezolazepam combinations have a wide safety margin during anesthesia of brown bears in springtime [15], the therapeutic range may be narrower in hibernating bears.

**Table 3.** Partial pressure of oxygen (PaO<sub>2</sub>) before (Pre-O<sub>2</sub>) and during oxygen supplementation in individual bears anesthetized winter and summer captures.

	Winter	PaO <sub>2</sub> (mmHg	)		Summe	r PaO₂ (mmHg	g)	
	Kg	Pre-O <sub>2</sub>	O <sub>2</sub> suppl. (L/min)	During O <sub>2</sub>	Kg	Pre-O <sub>2</sub>	O <sub>2</sub> suppl. (L/min)	During O <sub>2</sub>
Male (3)§					62.5	69	1	89
Male (2)	54	62	2	301	56			
Female (3)	54.8	106	1	100	55	99	1	124
Female (3)*	50.8	67			53	96	1	180
Male (3)#	65.8	57	0	43*	77	66	1	138
Female (3)	57	59	1	185	72	76	1	104
Male (3)	58	70	1	208	51	77	0.5	92
Female (2)	21.3	82	1	387	22	93	0.5	134
Male (4)	59.4	76	1	141	47	120	1	126
Male (2)	25				27	82	0.5	116
Female (2) <sup>#</sup>	35	30	1	307	28		0.5	129

\*denotes the results of the only bear not given oxygen that was sampled during the second sampling interval.

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Sex (years of age)	Den type (original)	Days at original den	Times moved	Intermediate beds	Days before resumed inactivity at new permanent den	Distance between original and new dens (m)	Den emergence
Female (3)	Soil	2.1	2	1	16.8	320	4/22/10
Female (3)	Soil	0.5	S	2	1.5	775	4/22/10
Female (3)	Anthill	1.6	c	2	17.4	363	4/23/10
Male (3)	Rock	10.4	-	0	1 hour	225	4/15/10
Female (3)*	Rock	1.9	1	0	2 hour	342	4/14/10
Male (2)	Anthill	0.8	Э	2	15.3	264	4/5/10
Female (4)*	Soil	3.2	2**	1**	**	1013**	4/20/11
Female (3)	Soil	1.7	-	0	2 hour	1419	4/21/11
Male (3)	Anthill	1.7	c	2	10.3	534	4/19/11
Male (2)	Uprooted tree	Did not move	N/A	N/A	N/A	N/A	4/19/11
Male (2)	Anthill	10.5	1	0	2 hour	647	4/22/11
Female (2)	Soil	1.3	1	0	4 hour	2123	5/5/11

their permanent den and date of den emergence. Grey denotes bears in rock dens, \*denotes the individual captured twice. \*Moved directly to new permanent den, but relocated to yet another new permanent den, staying at an uncovered bed site for 49 hours in between. Distance was calculated to the final new permanent den. doi:10.1371/journal.pone.0040520.t004

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The hypoxemia recorded during nine of 19 anesthesia events in both winter and summer indicates that bears in both capture situations may benefit from oxygen supplementation. Since intranasal oxygen at a flow rate of 1 L/min increased the  $PaO_2$ to 100–387 mmHg in the seven bears that were supplemented with this flow rate during wintertime, evaluation of lower flow rates during hibernation is warranted. The failure of pulse oximetry to work during hibernation captures was likely due the low body temperatures and the vasoconstrictive effects of medetomidine [30].

Hypercapnia during anesthesia is commonly caused by druginduced hypoventilation (respiratory center depression) [31]. Despite the lower drug doses used in winter than in summer, seven of nine bears captured in winter developed mild to marked hypercapnea, whereas only two of ten bears developed mild hypercapnea during capture in June. Mild hypercapnia can be beneficial, because it causes a shift in the oxygen-hemoglobin dissociation curve, increasing the unloading of oxygen at tissues, enhancing oxygen delivery, and carrying capacity [31]. On the contrary, severe hypercapnia can cause tachyarrhythmia, hemodynamic instability, and coma [31]. The higher hematocrit and hemoglobin values recorded in winter than in summer were most likely due to dehydration from not eating or drinking during hibernation.

The decreased pH recorded during anesthesia of hibernating brown bears was mainly due to increased values of  $PaCO_2$ (respiratory acidemia), whereas in summer, bears more commonly developed lactic acidemia (Table 2). As previously documented, brown bears anesthetized by darting from a helicopter develop higher lactate levels than brown bears anesthetized in captivity [16]. In the present study, the lower lactate levels of most hibernating bears during anesthesia were in the same range as reported in captive bears [16], indicating less physical exertion than capture by darting from a helicopter. However, one bear that escaped from its den and ran approximately 300 meters in deep snow before being anesthetized developed lactate levels up to 11.2 mmol/L. Bradycardia and hypothermia were recorded during anesthesia of hibernating bears, consistent with previous studies on denning physiology [24].

The two captures in rock dens were more complicated than captures in other types of dens because both bears in rock dens escaped from their dens and were darted outside. When planning for den captures, den type and surrounding terrain must be considered.

Bears left their dens following the disturbance associated with entering the den and capture on twelve of thirteen occasions (Table S1), compared to only 4% den abandonment during the equivalent time of year or 26% overall in non-den captured bears in this study area. The 26% overall den abandonment rate is higher than documented in a previous study, which may be attributed to the higher resolution of GPS/Activity data compared to VHF telemetry data [21]. As in the present study, most of the non-capture related abandonments occured early in the denning period (November/December), and were mostly attributed to nonresearch related human disturbance [21,32]. The lower abandonment rates further into the denning period agrees with findings from an earlier study [21]. As all den captures occurred during late February/early March, the lower rate provides the most relevant comparison. Den abandonments in our den-captured bears are likely to have conferred an energetic cost to the bears, particularly for those bears that used a couple of attempts before successfully locating a den that they used for the rest of the denning period [17,21]. Although den emergence dates were similar to other bears in the study area and the bears appeared to be in good physical condition when recaptured in June, we recommend that researchers consider the effects of den abandonment when planning to immobilize hibernating brown bears. In an earlier study in our study area, 68% of the presumed pregnant females that abandoned their dens emerged from their new dens without cubs, compared to 6% who did not abandon their den [21]. Cub mortality following den abandonment due to human disturbance has also been documented in American black bears [33]. Thus, we conclude that immobilization of hibernating females that are suspected to be pregnant may be especially intrusive, even if they are immobilized prior to giving birth.

Once out of the dens, most of the bears made a couple of attempts before locating a den that they settled into for the rest of the denning period. Anthill and soil dens were the most common den types for the original dens, whereas rock dens, nest dens and beds were the most common types of the second permanent dens. The choice of second den type likely reflected availability and the terrain around the den sites, especially when considering the deep snow cover (approximately 70 cm).

# Conclusions

This paper describes the only documented method for capture of brown bears during hibernation. Bears were stable with consistent physiological variables under anesthesia and exhibited hypoxemia that was correctable by low doses of supplemental oxygen. They showed much greater sensitivity to the disturbance of the captures than that caused to black bears in North America with similar capture methods. The doses presented here should result in an appropriate level of anesthesia if the size of the bear can be correctly predicted. This study presents a capture method for sub-adult Scandinavian brown bears and cannot be extrapolated to other age-categories or species of bears that may not have the same behavioral responses to capture.

### **Supporting Information**

Figure S1 Radiotracking using VHF radiocollars/implants to find the location of the denning bear. (TIF)

Figure S2 Locating a bear denning underneath a rock den using VHF radio tracking. (TIF)

Figure S3 Snow is removed and a metal grate is held ready to cover the den entrance. (TIF)

Figure S4 Darting through the metal grate placed over the den entrance. On ten of thirteen occasions, bears were in anthill or earth dens such as this one. (TIF)

Figure S5 After removal from the dens, bears were placed on an insulated blanket and physiological monitoring was performed.

(TIF)

Table S1 Original, Intermediate and permanent den sites for each of the captured bears. (XLSX)

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## **Author Contributions**

Conceived and designed the experiments: JMA ALE SB VS OF JES. Performed the experiments: ALE VS SB OGS ÅF KM. Analyzed the data:

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