THE MATING SYSTEM OF THE BROWN BEAR IN
RELATION TO THE SEXUALLY SELECTED INFANTICIDE
THEORY

Brunbjørnenes parringssystem: i lys av teorien om seksuelt selektert
infanticid

SAM STEYAERT
The mating system of the brown bear in relation to the sexually selected infanticide theory

Brunbjørnens parringssystem i lys av teorien om seksuelt selektet infanticid

Philosophiae Doctor (PhD) Thesis

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Preface

‘Of the branches of biological science to which Charles Darwin’s life-work has given us the key, few, if any, are as attractive as the subject of sexual selection.’ – R.A. Fisher, 1915

Among large mammals, the brown bear is probably one of the most studied species. An ISI Web of Science search entry ‘(brown NEAR bear) OR (Ursus NEAR arctos)’ yields 1491 hits of publications in peer review journals (June 2012). The body of scientific publications with the brown bear as a study species largely outnumbers many other large mammals and conservation flagship species, such as African lions (Panthera leo, 606 hits), grey wolves (Canis lupus, 702 hits), Siberian tigers (Pathera tigris, 450 hits), bighorn sheep (Ovis canadensis, 573 hits), African elephants (Loxodonta africana, 1295 hits), and giant pandas (Ailuropoda melanoleuca, 621 hits). Various long-term brown bear research projects exist (e.g. The Interagency Grizzly Bear Study Team in the Greater Yellowstone Ecosystem, USA, and the Scandinavian Brown Bear Research Project, Scandinavia), and provide a sound scientific basis on the general ecology of the species. Additionally, these projects often open doors for other research fields, among others, physiology and biochemistry, genetics, veterinary science, and even human medicine and space research. Having the brown bear as a study species: one is standing on the shoulders of giants! The knowledge of the brown bear’s mating system, its reproductive strategies, and the role that infanticide plays in it is, however, far from complete. With this thesis, I want contribute to the existing knowledge, to help to unravel certain patterns in nature, figuring out how things work, and maybe even provide answers to general questions in ecology, conservation, and management. However, I am most aware, and most happy to realize how complex the natural world is, and that aiming for fully understanding the full picture is not ambitious, but an illusion.
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Summary

A species’ or population’s mating system is the product of sexual selection under a specific set of environmental conditions. Because reproduction is such as strong evolutionary force, understanding mating systems lies at the heart of behavioral ecology and can be important for conservation and management. This thesis deals with several aspects of the mating system of the brown bear (Ursus arctos).

We reviewed the literature to document the mating system of the brown bear in the context of social organization, reproductive physiology, life history, reproductive behavior, and the two main components of sexual selection, male-male competition and female mate choice. We evaluated the mating system of various bear populations according to three mating system classification frameworks (Emlen and Oring 1977; Clutton-Brock 1989; Shuster and Wade 2003) to document the plasticity of the mating system of the brown bear, as well as to find commonalities in the mating system of various populations. We concluded that plasticity is a main characteristic of the brown bear mating system and that polygamy would be an appropriate classification. We also identified many gaps in the knowledge on reproduction in bears, both biological aspects (e.g. estrus cycling, induced ovulation, delayed implantation, sexually selected infanticide (SSI)), and human influences on the mating system of the brown bear (e.g. habitat fragmentation, hunting).

For infanticide to be a male reproductive strategy, i.e. SSI, three requirements need to be fulfilled, i) the killer does not kill his own offspring, ii) the victimized mother enters estrus earlier than if her cubs would have survived, and iii) the killer has a high probability to father the victimized mothers’ next offspring. We provided evidence for prediction ii, i.e., females rapidly (1-2 days) enter behavioral estrus after litter loss, which is in accordance with preliminary results from an endocrine approach. The vast majority (92%) of females entered estrus after litter loss during the mating season, mated, and gave birth during the next birthing season. Litter loss during the mating season reduced interlitter intervals of females in our study system by at least 50 % and can thus have significant reproductive advantage for males.

We also documented infanticide (N = 8), infanticide attempts (N = 3), and litter loss due to unknown reasons (N = 1) between 2009 and 2011, and found that the patterns were in accordance to the SSI hypothesis. All cases occurred during the mating season, and all known perpetrators were adult males. Cub mortality during the mating season averaged 33 % between 2009 and 2011, and 92 % died because of infanticide. Our study yet lacked the data to document the genetic relationship between the killer, the victim and the victimized.
mothers’ subsequent offspring (prediction i and iii of the SSI hypothesis). However, genetic evidence for predictions i and iii has previously been documented in our study population (Bellemain et al. 2006a).

We investigated how resource selection of various classes of bears was related to each other. We found that females with cubs-of-the-year (hereafter females/cubs) selected their resources spatially and temporally very different than conspecifics (especially adult males) during the mating season. For example, females/cubs used areas relatively close to human settlements, far from forest roads, in the least rugged landscapes, and more often in less dense vegetation (e.g., older forest types). Males often used areas close to forest roads, avoided human settlements, used areas in the most rugged landscapes more than expected, and always selected for the most dense habitat types. After the mating season, female/cubs shifted their resource selection towards a similar mode as their conspecifics; i.e. selecting areas far from settlements, in the most rugged terrain, and in denser habitat types. Our results suggest that females/cubs adapt their resource selection in space and time, most probably in response to the risk of SSI. We also show that females/cubs probably pay a nutritive cost during the mating season by selecting their resources in a spatiotemporally different way than conspecifics. This cost probably adds to the females’ cost of reproduction.

We conducted a meta-analysis to evaluate variation in reproductive allocation (mean female body size in relation with mean litter size) among 28 brown bear populations throughout their geographical range. We found that mean litter size was related to mean female body size, but also that persecution history played an important role. In accordance with life-history theory, we found that reproductive allocation was higher in populations with a long (> 500 years) and inefficient persecution history than in populations with a short (< 150 year) and efficient persecution history. Our results suggest that humans can act as a selective pressure on life-history traits in a large mammals, and probably explain why certain populations of bears (e.g., in Europe) recover rapidly after protective measures, whereas others (e.g. North American) respond slowly.
List of papers

**Paper I**  

**Paper II**  
Steyaert, S.M.J.G., Swenson, J.E., Zedrosser, A. Litter loss triggers estrus in a nonsocial breeder. Submitted

**Paper III**  

**Paper IV**  

**Paper V**  
Steyaert S.M.J.G., Reusch C., Brunberg S., Swenson J.E., Hackländer K. and Zedrosser A. Coping with sexually selected infanticide: a food or safety trade-off? Manuscript

**Paper VI**  
Synopsis
Introduction

‘[Sexual selection] depends, not on a struggle for existence, but on the struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring.’ - Charles R. Darwin, 1859

The general behavioral strategies that an animal species applies to obtain mates is referred to a species’ mating system, and includes characteristics such as mate and copulation number, acquisition manner, and parental care (Emlen and Oring 1977); or in Darwin’s words: ‘...the special circumstances in which reproduction occurs within a species’ (Darwin 1871). Sexual selection eventually shapes a species’ reproductive strategies and its mating system.

In mammals, females typically invest much more in gametes than males, through, for example, gestation, lactation, and often extended parental care (Orians 1969; Trivers 1972; Clutton-Brock 1989; Andersson 1994). Male parental care is mostly absent in mammals, and male reproductive success is almost exclusively restricted by the ability to mate and to father offspring (Trivers 1972; Shuster and Wade 2003). Female reproductive success generally shows relatively little variance, whereas male reproductive success is proportional to mate and/or copulation number. Thus, males are expected to compete intensively for females, and females should be choosier and select their mates based on expressions of genetic quality, such as size, fighting skills, weaponry, etc. (Orians 1969; Andersson 1994). The difference between the sexes in the variance in reproductive success creates the opportunity for sexual selection. Sexual selection is considered to be an important evolutionary force (Trivers 1972; Klug et al. 2010), and can explain evolutionary patterns in, for example, behavior, morphology, and life histories (Andersson 1994; Klug et al. 2010).

Precopulatory competition is the most apparent type of competition among males for access to receptive females and is the driver behind the evolution of sexual dimorphism and polygynous mating systems (Radespiel et al. 2001). However, competition among males for siring offspring does not necessarily stop when sperm is delivered. Male-male competition can operate within the female reproductive tract through sperm competition, and after birth through infanticide as a male reproductive strategy (Trivers 1972).

Infanticide is the direct or indirect contribution to the death of a conspecific infant. Hrdy (1979) recognized five functional types of infanticide: 1) exploitation of the infant as a resource, 2) competition for resources (other than mates), 3) sexual selection (competition among males for mates), 4) parental manipulation of progeny, and 5) social pathology.
Today, the sexual selection hypothesis to explain infanticide is most supported in the scientific community, but it remains contested and heavily debated (Sommer 2000; van Schaik and Janson 2000; Miller et al. 2003).

Infanticide can be an adaptive male reproductive strategy (functional type 3), if males gain mating opportunities by killing unrelated dependent young (i.e., sexually selected infanticide, SSI) (Darwin 1871; Trivers 1972; Hrdy 1974). To be so, three requirements must be fulfilled. First, an infanticidal male should only kill offspring that he did not father. Second, litter loss should trigger estrus in the victims’ mother and shorten her interlitter interval. Third, the infanticidal male should have a high probability to sire the victimized mothers’ subsequent litter (Trivers 1972; Hrdy 1979). SSI is common in size-dimorphic mammals with a polygamous mating system that have lactational anestrus, and in which lactation lasts substantially longer than gestation (van Schaik 2000). In seasonal breeders, SSI can only be beneficial for males during the mating season (Bartos & Madlafousek 1994; Zedrosser et al. 2009). SSI is often linked to male takeovers of female groups or territories: new males cannot have fathered resident offspring, and can thus increase their reproductive success with no risk of killing their own offspring (Pusey & Packer 1994; Swenson et al. 1997). However, in nonsocial species, SSI can also be committed by resident males (Bellemain et al. 2006a). Because infanticide by males can be very costly for females and their dependent young, female strategies to minimize infanticide should be selected for (Ebensperger 1998). Counterstrategies against infanticide include pregnancy termination (i.e., minimizing the potential ‘damage’), multimale mating (i.e., concealing paternity), female territoriality, aggression, group defense, and avoidance of infanticidal conspecifics (Agrell et al. 1998; Ebensperger 1998).

Today, SSI has been documented among many species of primates, rodents, and carnivores (van Schaik and Janson 2000; Swenson 2003), and is even considered as one of the ‘pacemakers’ in the evolution of mammalian mating systems (Wolff and Macdonald 2004). However, infanticide as a male reproductive strategy remains hotly debated. Evidence for SSI is extremely difficult to document in the field (Hrdy 1984), especially for nonsocial species with an elusive lifestyle (Bellemain et al. 2006a). Therefore, evidence for SSI is often suggestive, because of the correlative nature of the research (i.e. offspring survival in relation to changing social structures (e.g., Bartos and Madlafousek 1994; Pusey and Packer 1994; Swenson et al. 1997)), because of small sample sizes of observed infanticides (Boggess 1984; Hrdy 1984), and because of the general lack of genetic proof (but see Borries et al. 1999; Bellemain et al. 2006a). In addition, patterns of infanticide and offspring survival sometimes
vary among populations (Palombit 2003). This contextual nature of infanticide also contributes to debate (Wielgus and Bunnell 1995; Miller et al. 2003; Swenson 2003; McLellan 2005).

Mathematical models suggested that a small time lag between litter loss and the next conception can make infanticide untenable as a male reproductive strategy (Hrdy and Hausfater 1984). Therefore, SSI has been suggested to be rare among seasonal breeders or under conditions that prevent the immediate return to breeding conditions after litter loss (Hausfater 1984; Hausfater and Hrdy 1984). However, suggestive evidence for SSI has also been documented in seasonal breeders, for example in red deer (Cervus elaphus) (Bartos and Madlafousek 1994), Japanese macaques (Macaca fuscata) (Soltis et al. 2000), white-throated round-eared bats (Lophostoma silviculum) (Knörnschild et al. 2011), and brown bears (Ursus arctos) (Swenson et al. 1997).

The general aim of the thesis was to improve our understanding about the role of SSI in the mating system of a nonsocial large carnivore. Below, I briefly introduce the model species, the brown bear, and present the main objectives of the thesis and their rationale.
The model species, the brown bear

The brown bear is a large nonsocial carnivore, and the most widespread species of Ursidae (Pasitschniak-Arts 1993). It occupies a large variety of habitats throughout the northern hemisphere, ranging from treeless arctic tundra, grasslands, boreal forest, to coastal, mountainous and desert habitats (Schwartz et al. 2003). Human presence is the most important factor that determines brown bear distribution in their historical range (Woodroffe 2000; Kaczensky et al. 2006). Currently, the brown bear is globally listed as a species of least concern (McLellan et al. 2008).

Brown bears are sexually dimorphic, with males being up to 2.2 times larger than females (Schwartz et al. 2003; Swenson et al. 2007). The largest individuals are found in coastal populations with access to seasonal salmon (*Oncorhynchus* spp.) runs in Alaska and Eastern Russia, where males can reach over 600 kg (Hilderbrand et al. 1999). Asymptotic autumn body masses reach 158 ± 4 kg for females and 273 ± 6 kg for males in Scandinavia (Swenson et al. 2007). Brown bears are solitary and nonterritorial, and have home ranges that overlap both intra- and intersexually (Craighead et al. 1995; McLoughlin et al. 2000; Dahle and Swenson 2003b). Matrilineal assemblages can develop as a result of male-biased natal dispersal (Støen et al. 2005), can influence female reproductive success (Støen et al. 2006; Ordiz et al. 2008).

Annual home ranges of males are typically larger (115 – 8171 km²) than those of females (24 – 2434 km²), and home range sizes vary across regions and seasons, and according to age and sex, population density, reproductive status, and food availability (McLoughlin et al. 2000; Dahle and Swenson 2003b; Rode et al. 2006).

Brown bears are seasonal breeders and have a mating season that lasts for approximately 2.5 months, from late spring to early summer. During the mating season, both males and females roam to acquire mates (Schwartz et al. 2003; Bellemain et al. 2006a; Spady et al. 2007), and mate a variable number of times with a variable number of mates (Craighead et al. 1995). The average ages of primiparity vary across populations and range between 5.2 to 10.3 years (Miller et al. 2003; Nawaz et al. 2008; Zedrosser et al. 2009), but primiparous individuals can be as young as three years (Frković et al. 2001; Zedrosser et al. 2004). Male bears usually reach sexual maturity around the age of 5 – 6 (White et al. 1998), and larger and older males are generally more successful in siring offspring (Zedrosser et al. 2007).

Female brown bears have delayed implantation (Mano et al. 2002, Schwartz et al. 2003b), are suggested to be induced ovulators, and can exhibit more than one estrus cycle during a
mating season (Craighead et al. 1995). As a consequence of polyestrus, different sets of ova can be fathered by different males (Craighead et al. 1995; Schwartz et al. 2003; Bellemain et al. 2006a; Spady et al. 2007). After implantation of fertilized ova during late autumn, 1-4 altricial cubs are born in the winter den, after a gestation period of approximately 6 to 8 weeks (Schwartz et al. 2003). The cubs stay with their mother for up to 4.5 years (usually 1.5-2.5) (Nawaz et al. 2008), and lactation can last for 2.5 years (Farley and Robbins 1995), during which females cannot enter estrus (i.e., lactational anestrus) (Dahle and Swenson 2003a; Spady et al. 2007). Paternal care is absent in the brown bear (Dahle and Swenson 2003a).

Cub mortality varies among populations and is typically higher than mortality in other age classes. Annual cub mortality can reach 66% (Miller et al. 2003). Cub mortality occurs mostly during the breeding season, and infanticide by males is considered to be a major cause of death (Craighead et al. 1995; Schwartz et al. 2003; Swenson 2003; McLellan 2005; Bellemain et al. 2006a; Zedrosser et al. 2009) and primiparous females lose cubs more often than multiparous females (Zedrosser et al. 2009). Various female counterstrategies to infanticide have been documented in brown bears, including direct defense (Craighead et al. 1995), promiscuity and multiple-paternity litters (Bellemain et al. 2006a), selecting escape habitat (Pearson 1975), elusiveness (Dahle and Swenson 2003b), and avoidance of sites with high infanticide risk (Wielgus and Bunnell 1995; Ben-David et al. 2004; Rode et al. 2006). Strong evidence for the SSI hypothesis in the brown bear has been documented (Swenson et al. 1997; Swenson et al. 2001b; Bellemain et al. 2006a), albeit also contested (Miller et al. 2003; McLellan 2005; Garshelis 2009). Refer to Paper I for an in-depth description and discussion on the mating system of the brown bear.
**Objectives and their rationale**

*What do we know about the mating system of the brown bear? (Paper I)*

A species’ or population’s mating system is the product of sexual selection in a certain environmental context, and is expressed through e.g., variability in mate number and reproductive success within and between the sexes, manners of mate acquisition, breeding seasonality, etc. (Orians 1969; Clutton-Brock 1989; Shuster and Wade 2003). Because reproduction is such as strong evolutionary force, understanding mating systems lies at the heart of behavioral ecology (Shuster and Wade 2003; Klug et al. 2010). In addition to the ethological value, knowledge of a species’ mating system can, in a broad context, be important for its conservation and management (Berger 1996; Festa-Bianchet and Apollonio 2003).

The first objective of the thesis was to update our knowledge on the mating system of the brown bear through a literature review and identify the main gaps in our knowledge on its mating system. The mating system of the brown bear has been classified as polygamy (Pasitschniak-Arts 1993; Zedrosser et al. 2009), promiscuity (Bellemain et al. 2005), scramble competition polygamy (McLellan 2005), and contest competition polygamy (Schwartz et al. 2003). Therefore, we also evaluated the mating system of various brown bear populations within the classification frameworks of Emlen and Oring (1977), Clutton-Brock (1989), and Shuster and Wade (2003) to document the plasticity of the mating system of the brown bear and to provide a general classification for the brown bears’ mating system based on commonalities in reproductive characteristics across populations.

*Sexually selected infanticide: can we prove it? (Paper II)*

The sexual selection hypothesis to explain infanticide predicts that i) a male kills only dependent unrelated conspecific offspring, ii) the offspring loss triggers estrus in the victim’s mother, and iii) the killer has a high probability to father the victims’ mothers’ subsequent litter (Hrdy 1979). Evidence for SSI is extremely difficult to document, and most studies rely on survival rates of dependent young in relation to changing social structures (Hrdy 1979; Bartos and Madlafousek 1994; Pusey and Packer 1994; Swenson et al. 1997). However, direct evidence for prediction i) and iii) can only be found by analyzing the genetic relationship between the victim, perpetrator, and the father of the victims’ mother’s subsequent litter (Borries et al. 1999). Borries et al. (1999) provided the first genetic support
for the SSI hypothesis, in the hanuman langur (*Presbytis entellus*). In our study population, Bellemain (2006a) found genetic support for the SSI hypothesis: presumed killers did not kill their own progeny (prediction i) and had a high probability to sire the victim’s mothers’ next litter (prediction iii). However, the results by Bellemain et al. (2006) remained suggestive, because the sample size was small and incomplete to evaluate both prediction i and iii per case.

The second prediction of the SSI hypothesis postulates that females should enter estrus after the loss of a complete litter, and therefore litter loss should shorten a female’s interbirth interval (Hrdy 1979). To optimize reproductive success, females are expected to resume breeding activity rapidly the loss (van Schaik 2000).

The second objective of the thesis was to evaluate the three requirements of the SSI hypothesis, and conclusively determine whether or not infanticide by males is a reproductive strategy in our study population. Therefore, we aimed to systematically document cases of infanticide in the field, and to analyze the genetic relationships between the killer, the victim, and the victimized mother’s next offspring. In addition, we evaluated if, and how fast, females enter estrus after losing their litter during the mating season.

**Avoiding infanticide in space and time, and what does it cost? (Papers III, IV, V)**

Predation is a strong selective force, and individuals are expected to select strategies that minimize predation and its risk (Lima and Dill 1990; Brown et al. 1999; Creel and Christianson 2008). Individuals that are more successful in avoiding predation have a higher potential for survival and reproduction (Lind and Cresswell 2005). Several adaptations against predation have evolved, and include traits that reduce detection (e.g., cryptic behavior, altered resource selection), facilitate escape (e.g., grouping, vigilance or selecting for escape habitat), and hinder handling success by predators (e.g., armor) (Vermeij 1982). Antipredator strategies have an obvious advantage, but they may come with a fitness cost (Stearns 1989; Brown and Kotler 2004).

Many species reduce predation risk by altering their resource selection in space and time, and therefore trade optimal resources for safety (Pianka 1976; Lima and Bednekoff 1998; Brown and Kotler 2004; Houston et al. 2011). Because energy intake is an important factor for an individual’s reproductive success, trading access to food to minimize predation risk can have a significant fitness cost (Stearns 1989; Creel and Christianson 2008). Predation vulnerability is typically highest during the first year of life (Lind and Cresswell 2005),
therefore, the food or safety trade-off is expected to be strongest among females with dependent offspring (Main et al. 1996; Main 2008). In many ungulates, for example, females with dependent young segregate from males as a female reproductive strategy and sometimes select for poor quality habitats with low predation risk (Bowyer 2004; Ruckstuhl 2007; Main 2008).

In carnivores, predation risk is often related to infanticide (Rode et al. 2006), which can be a reproductive strategy if the incentive for killing is obtaining mates rather than food (Trivers 1972; Hrdy 1979). Avoiding infanticidal males in space and time is an intuitive female counterstrategy against infanticide, but evidence for it is extremely rare (Ebensperger and Blumstein 2007). Suggestive evidence for avoiding infanticide in space and time as a female reproductive strategy has been provided for, among others, beluga whales (Delphinapterus leucas) (Loseto et al. 2006), orangutans (Pongo pygmaeus) (Setiawan et al. 1996), gorillas (Gorilla gorilla) (Stokes et al. 2003), alpine marmots (Marmota marmota) (Coulon et al. 1995), lions (Packer and Pusey 1983), and brown bears (Wielgus and Bunnell 1995).

Animals respond rapidly to changes in predation (Lima and Bednekoff 1998). The relation between behavior types and temporal variation in risk regime can therefore be used to determine risk factors and its effects (Lima and Bednekoff 1998; Brown and Kotler 2004). We evaluated the spatiotemporal infanticide avoidance strategy in relation to the SSI theory in the brown bear (Paper III). Because the risk of SSI only exists during the mating season, we predicted that females/cubs would segregate from adult males, but only during the mating season. After the mating season, we expected that various reproductive classes of bears would select their resources in a similar way.

The third objective of the thesis was to evaluate if females/cubs apply spatiotemporal strategies to minimize the risk of SSI, by e.g. altering their selection for resources (Paper III). Analogous with interspecific predation (Brown and Kotler 2004), we expected that avoiding infanticide through altered resource selection would come with a nutritive cost. We evaluated the potential trade-off between food and safety in relation to SSI theory (Paper V, Paper IV provides a description of the methodology).

**There is no ‘one size fits all’ (Paper I, VI)**

Plasticity is characteristic of animal mating systems, likely as a consequence of adaptive adjustments of males and females to a variable social and ecological context, and individual
variation, within and between populations (Emlen and Oring 1977; Vehrencamp and Bradbury 1978; Clutton-Brock 1989; Shuster and Wade 2003).

Also, in the brown bear, mating systems appear to be very different across populations. For example, male dominance hierarchies may develop in populations where bears aggregate around concentrated food sources (e.g., salt marches, spawning cutthroat trout \textit{(Oncorhynchus clarkii)}, or garbage dumps). In these populations, few males obtain access to mates, and subordinates can apply a satellite strategy (Craighead et al. 1995). In populations with no congregated food sources, males and females typically roam for mate acquisition and individuals of both sexes may obtain several mates, and males sometimes sequester females (Hamer and Herrero 1990). In populations with very low densities and with no apparent concentrated food sources, mating areas can develop, where several males and females may aggregate and mate (Fernández-Gil et al. 2006). Also, life-history parameters differ across populations. European female brown bears are generally smaller than their North American counterparts, are primiparous at earlier ages, have shorter interbirth intervals, and produce larger litters (Zedrosser et al. 2004; Zedrosser et al. 2009; paper I). Also, the occurrence and adaptive significance of infanticide may vary across populations of many species (Hausfater and Hrdy 1984; Palombit 2003), including bears (Swenson et al. 1997; Swenson et al. 2001b; Miller et al. 2003; McLellan 2005; Bellemain et al. 2006a). The variation in behavioral traits and life-history characteristics across populations of a species sometimes leads to hot debate and even polarization among scientists (Chalmers 1976; Sommer 2000).

The fourth objective of the thesis was to assess effects of various ecological and historical factors to explain variation in life-history parameters among brown bear populations. Therefore, we related female reproductive allocation (mean litter size in relation to mean average female body mass) to habitat quality, food availability, population density, and competition with other ursids. We also evaluated the persecution history of each study population, because humans can have strong impacts on wildlife species, their number and distribution (Woodroffe 2000; Woodroffe et al. 2005), behavior (Berger 2007; Muhly et al. 2011), and phenotypic and life-history traits (Coltman et al. 2003; Darimont et al. 2009).
Objectives of the thesis, summarized

The main goals of the thesis were to:

1) a. Review the literature, compile and condense the knowledge on the mating system of the brown bears and identify gaps in our knowledge (Paper I).
   b. Document the plasticity of the mating system of the brown bear and provide a general mating system classification (Paper I).

2) Evaluate the three predictions of the SSI hypothesis:
   i. Are infanticidal males unrelated to their victims?
   ii. Does litter loss during the mating season trigger estrus in female brown bears, and if so, how quickly? (Paper II)
   iii. Do infanticidal males also father the victims’ mothers’ subsequent offspring?

3) Evaluate spatiotemporal avoidance as a female strategy in relation to the SSI theory (Paper III), and related costs (Papers IV and V).

4) Evaluate patterns in life-history parameters among brown bear populations (Papers I and VI).

A key objective of the thesis was to answer research objective 2.i and 2.iii, based on the genetic relationship between the killer, the victim, and the victims’ mothers’ subsequent litter. We have collected field data from infanticide cases (see summary of results, and appendix 1 and 2). The genetic analyses had not completed at the time of writing, however.
Materials and methods

Study area

The study area was located in Dalarna and Gavleborg counties in south-central Sweden (~61°N, 15°E) and consists of approximately 13,000 km² of boreal forest. The dominating tree species are Norway spruce (Picea abies), Scots pine (Pinus sylvestris), lodgepole pine (Pinus contorta), and birch species (Betula pendula, B. pubescens), and the forest floor is mainly covered by lichens, heather (Calluna vulgaris), and berry-bearing species (Vaccinium myrtillus, V. vitis-idaea, Empetrum hermaphroditum) (Moe et al. 2007). The terrain is gently undulating, and elevations range between 200 and 700 m above sea level. The daily average temperature ranges from minimum -7°C in January to maximum 15°C in July, and snow cover lasts from late October to early May. The forest is intensively managed, and consists of a patchy landscape of relatively small forest stands (median patch size ~ 2.25 ha) of different age cohorts (Moe et al. 2007). The area is sparsely populated and contains a few scattered small settlements, which are mainly located in the north and the south of the study area (Martin et al. 2010). The area is intersected by a dense network of logging roads (0.7 km/km²) and a few high-traffic roads (0.14 km /km²) (Martin et al. 2010). Human presence in the study area is highest during summer and fall, and is mainly related to hunting as well as berry and mushroom picking (Nellemann et al. 2007).

Study population

After near extinction around 1930, the Swedish brown bear population recovered and consisted of an estimated ~3300 individuals in 2008 (Swenson et al. 1995; Kindberg et al. 2011). In our study area, the brown bear population density approximates 30 individuals/1000 km² (Bellemain et al. 2005). The population is intensively hunted during late summer and autumn (21 August until 15 October or when quotas are filled (Bischof et al. 2008)), and hunting quotas have increased almost six-fold during the last decade, up to 297 shot bears in 2011 (www.sva.se). Females with offspring are legally protected from hunting (Bischof et al. 2008).

Annual cub mortality in our study area averages 35 % (Swenson et al. 1997; Swenson et al. 2001b). The observed patterns of cub mortality provide strong support for the SSI hypothesis. Cub mortality occurs almost exclusively during the mating season, and is often caused by infanticide by adult males (Swenson 2003; Bellemain et al. 2006a; Zedrosser et al. 2009). Cub mortality is especially high during the 2 mating seasons after resident adult males
have been removed by hunting (Swenson et al. 1997; Swenson et al. 2001b), suggesting that immigrant males increase their reproductive success by killing existing cubs. Bellemain et al. (2006a) showed that resident males also commit infanticide during the mating season, and provided genetic evidence for 2 of the 3 SSI requirements, i.e. perpetrators do not kill their own progeny, and perpetrators have a high probability to sire the victimized mothers’ subsequent offspring. Zedrosser et al. (2009) documented that primiparous females more often lose their litter, and suggested that they are less experienced at avoiding infanticide than multiparous females. Additionally, female bears in our study system may adopt strategies to reduce the risk of infanticide, such as concealed paternity through multimale mating and multiple-paternity litters (Bellemain et al. 2006a), adopting an elusive lifestyle (Dahle and Swenson 2003b), and by selecting escape habitat (Swenson 2003).

Monitoring bears

All bears included in this study were captured within the framework of the Scandinavian Brown Bear Research Project (SBBRP), a long-term research project on the ecology of the brown bear in Scandinavia. The SBBRP aims to monitor individual bears during their entire life, and to create pedigrees of the study population. Therefore, bears were captured using aerial darting from a helicopter, and provided with a GPS (Global Positioning System, GPS Plus, Vectronic Aerospace GmbH, applied in the SBBRP since 2003) or a VHF collar (Telonics®, Model 500). In addition, each captured bear larger than 20 kg was provided with a sterilized implantable radiotransmitter (Telonics®, Model IMP/400/L HC) in the body cavity. The implantable radiotransmitters had a battery life of approximately 4-5 years, which assured that specific bears could be relocated and recaptured even after transmitter loss or failure. Captures were mostly conducted after den emergence in late April and early May. Most bears were captured as yearlings while accompanying their radiomarked mothers, or by detection of tracks in the snow from helicopter or snowmobile. Standardized biometrical measures (e.g., body mass, head circumference, etc.) were recorded for each immobilized bear, and hair and tissue samples were taken for genetic identification. For bears that were not captured as yearlings with their mother, a first premolar was extracted for age determination at their first capture. Refer to Arnemo et al. (2011) for further details on capturing and handling bears. All capture and handling conformed to the current law regulating the treatment of animals in Sweden and was approved by the appropriate Swedish ethical committee (Djurförsöksnämnden i Uppsala). The presence of cubs with their
mothers was monitored regularly throughout the year, with surveys from a helicopter, direct observations from the ground, and from tracks and sign of cubs observed at daybeds of their mothers.

**Spatiotemporal analyses**

GPS relocation data was the major data source for evaluating movement patterns of female bears in relation to their reproductive status (paper II), and to evaluate segregation in resource selection among various reproductive classes of bears (paper III). We used relocation data from bears that were partly or continuously monitored with GPS collars between 2005 and 2011. The GPS collars were scheduled to take at least one position every 30 minutes, thus theoretically fixing a minimum of 48 positions per day. For spatiotemporal analysis of relocation data, we removed GPS fixes with a Dilution Of Precision value $\geq 5$, and all two dimensional (2D) fixes in order to increase spatial accuracy (Lewis et al. 2007), and we focused on three reproductive classes of bears: adult males ($\geq 5$ years), lone adult females ($\geq 5$ years and not nulliparous), and females/cubs ($\geq 5$ years and accompanied with dependent young $< 1$ year old).

We related GPS relocation data to data layers that we derived from satellite imagery, a digital elevation model, and digital topographical maps. Spatial data layers were obtained via the National Land Survey of Sweden (www.lantmateriet.se) and the Swedish University of Agricultural Sciences (www.slu.se). We used ArcGIS 9.2 (ESRI) and Erdas Imagine 9.1 (Leica Geosystems) software for all geospatial and remote sensing processing. For a detailed description of the data derivation, refer to Steyaert et al. (2012).

**Individual-based field data**

During the mating seasons of 2009-2011, GPS collars of adult males, lone adult females, and females/cubs were scheduled to take one position every 10 minutes to facilitate detection of potential cases of infanticide or offspring loss. We visited all ‘encounter sites’ (i.e. sites where two or more bears occurred within a 30-m range and a 2-minute time window) between females/cubs and adult males or females/cubs and lone adult females. We also recorded sudden changes in movement patterns of females/cubs (from an elusive life style to roam-to-mate behavior, paper III). We searched encounter sites with a tracking dog to document potential cases of infanticide and back-tracked GPS locations of females after sudden movement changes to document potential cases of infanticide. In case we found cub
remains or signs of an aggressive interaction (e.g. tree climbing marks, tree damage, trampled soil, hair tufts, blood or tissue), we sampled feces, hair, and tissue for genetic analysis. All samples were stored dry in silica gel in a hermetically closed container and send to the Laboratoire d’Ecologie Alpine (LECA) in Grenoble, France, for genetic analyses after each field season. We defined an SSI attempt as an encounter between a GPS-marked male and a female/cubs, and if signs of aggressive interaction were confirmed at the encounter site.

We collected fecal samples of GPS-marked bears of known reproductive status between early May and late September 2010. We used near infrared spectroscopy to derive fecal indices of dietary quality (paper IV), which we used to evaluate differences in dietary quality among various reproductive classes of bears in relation to the SSI theory (paper V).
Summary of results

The mating system of the brown bear: a literature review (paper I)

We reviewed the literature to document the mating system of the brown bear in a context of social organization, reproductive physiology, life history, reproductive behavior, and the two main components of sexual selection, male-male competition and female mate choice. Despite the large body of scientific literature, we concluded that many aspects of the mating system of the brown bear are still unclear, including biological aspects, such as hormone and estrous cycling, sperm competition, mate choice, SSI, etc. but also human impacts on the mating system, e.g. through hunting or habitat degradation. We used the mating system classification frameworks of Emlen & Oring (1977), Clutton-Brock (1989) and Shuster & Wade (2003) to find commonalities among the mating system of various brown bear populations. We did this to provide a general mating system classification for the brown bear, but also to document the plasticity of its mating system. Mating systems and reproductive strategies appear to vary across populations, dependent on population density and the occurrence of concentrated food sources. Dominance hierarchies can develop in populations that aggregate at concentrated food sources during the mating season. In these systems, a few dominant males obtain most mates and subdominant males sometimes apply a satellite strategy. In most populations, however, no concentrated food sources occur during the mating season and males and females typically roam for mate acquisition and males compete for females in aggressive interactions. Also, males sometimes sequester and defend individual receptive females. In populations with very low densities, durable mating areas may develop. In general, the mating system of the brown bear can be classed as ‘polygamous’, because both sexes can mate a variable number of times with a variable number of mates during the course of their life. The knowledge of the mating system on a population level is important for bear management and conservation.
Infanticide cases 2009-2011: prediction I and III of the SSI hypothesis

During the study, we monitored 18 females/cubs ($N_{cubs} \geq 40$) at the onset of the mating season with GPS tracking (2009: 6 litters, 12 cubs; 2010: 7 litters, 17 cubs; 2011: 5 litters, 11 cubs). We recorded 9 cases of litter loss; in 8 of which we confirmed infanticide (cub remains and signs of intraspecific aggression (Figure 1)). In one case, 2 cubs from an unmarked female were presumably killed by a GPS-marked male (cub remains were retrieved from a cluster site of the male). In 3 cases, we collected cub remains after an encounter between a GPS-marked female/cubs and a GPS-marked male. In addition, we recorded 3 infanticide attempts by GPS-marked males on GPS-marked females/cubs. In total, 13 (33%) of the 40 cubs died during the mating season, of which 12 (92%) died because of infanticide, and in a minimum 4 of the 8 cases, the infanticide was committed by a male. In 6 of the 8 cases of infanticide, the entire litter was killed. We did not observe other cases of cub mortality, and all cub loss occurred between 5 May and 17 June, encompassing the peak of the mating season. All females that lost an entire litter were observed with at least 1 male during the ongoing mating system. Four of these gave birth during the subsequent birthing season. The reproductive fate of 2 females is not known, because they were killed by hunters after the mating season in which they lost their litter. From 4 infanticide cases, both the male and the female were also GPS-marked and monitored the previous year. In 3 of the 4 cases, the male and female never encountered each other during the previous years (within 30 m and a 2-minute time window) or their home ranges did not overlap during the previous mating season. For these 3 cases, we are confident that the males were not the father of the young they killed. In 1 case (female the male W0802 and the female W0503) consorted for several days during the previous mating season. Preliminary genetic data showed that W0802 was most likely not the father of the cub he killed. Appendices 1 and 2 provide more detailed information about the recorded litter loss, infanticide events and attempts.
Litter loss can trigger estrus in a nonsocial seasonal breeder (paper II)

The second prediction of the SSI hypothesis requires that offspring loss triggers estrus in the victimized mother. SSI has been documented almost exclusively in social species, and is often suggested to have little or no potential benefit for seasonal breeders, or under circumstances that restrict the victimized mother from rapidly entering estrus after the loss.

In paper II, we evaluated the second requirement of the SSI hypothesis in a nonsocial seasonal breeder with lactational anestrus. We predicted that females become receptive within < 7 days after litter loss during the mating season, and that they shift from an elusive lifestyle typical for females/cubs to the roam-to-mate behavior typical for receptive females. We used generalized additive mixed-effect models to evaluate movement rates of GPS-marked females. We compared receptive females, females/cubs, and females that lost their litter during the mating season (before the loss, and after the loss). We used a long-term demographic dataset to evaluate females’ reproductive fate after litter loss. We found that females/cubs moved less than receptive females. Also, females/cubs had a less strongly pronounced bimodal diurnal movement pattern than receptive females, and their daily average movement rates increased steadily during the mating season. The peak of average
daily movement rates of receptive females coincided with the peak of the mating season, when most male-female associations are observed. We found that females that lost their litter during the mating season moved significantly more than females that kept the litter throughout the mating season, especially 1-2 days before the loss. The movement patterns from receptive females and females after litter loss were undistinguishable already 1-2 days after the litter loss (Figure 2).

From 1988 to 2011, we recorded 61 disappearances of entire litters during the mating season. In 56 of these cases (92%), the females gave birth during the subsequent birthing period. Our results provided strong support for the second prediction of the SSI hypothesis, i.e., females can rapidly enter estrus after litter loss during the mating season. The long term dataset revealed that majority of females entered estrus after litter loss, mated successfully, and gave birth the subsequent birthing season. In the brown bears, litter loss during the mating season can shorten the interbirth interval by up to 85%. Thus, infanticide by males during the mating season can have an obvious reproductive advantage for males. Preliminary results from an endocrinological approach support our behavioral results.
**Spatiotemporal avoidance of infanticide (paper III)**

We evaluated spatiotemporal avoidance of infanticide as a female reproductive strategy in the brown bear. Because we expected SSI in our study population, we predicted that differences in resource selection are strongest between (i) females/cubs and adult males, and (ii) during the mating season. We used resource selection functions to quantify the differences in resource selection among adult males, lone adult females, and females/cubs, based on GPS relocation data (2006-2010). We evaluated responses to land cover, terrain ruggedness, and human-related variables for each reproductive class to understand their resource selection and potential infanticide avoidance behavior. We found that resource selection indeed differed most strongly between females/cubs and adult males (prediction i), and during the mating season (prediction ii). During the mating season, females/cubs selected their resources in the least rugged landscapes, in relative close proximity to settlements (Figure 3), and in more open habitat types. Adult males, in contrast, selected for the most rugged landscapes, avoided areas in relative close proximity to settlements (Figure 3), and used more dense habitat types. During the postmating season, resource selection of the 3 reproductive classes became more similar; all classes avoided settlements (Figure 3), selected for rugged terrain in rugged landscapes, and selected for denser vegetation types. We suggest that differential resource selection among reproductive classes of bears in our study system is probably partly explained as a female counterstrategy against SSI.

![Figure 3: Selection indices (values > 1 indicate selection, < 1 indicate avoidance) of brown bears in relation to distance to settlements for adult males (---), lone females (--), and females/cubs (—) fitted with spline smoothers, during the mating and postmating season in south-central Sweden.](image-url)
**Fecal near-infrared spectroscopy as a tool in wildlife research (paper IV)**

In this paper we evaluated the potential of near-infrared spectroscopy (NIRS) as an analytic tool to derive fecal measures of dietary quality in the brown bear, an omnivorous species with a wide dietary range. We also evaluated the effects of field exposure on fecal constituents (i.e., nitrogen, lignin, crude fiber (CF), ether extracts (EE), acid detergent fiber (ADF), neutral detergent fiber (NDF), ash, and dry matter (DM)), which are commonly used to derive fecal measures of dietary quality. We sampled feces (N = 172) from 45 GPS-marked brown bears in our study area between May and October 2010. For each sample, we recorded maximum field exposure time (h) and canopy cover (%). We used multivariate partial least square regression with a ‘leave-one-bear-out’ cross validation procedure to calibrate the NIRS method. We obtained very good ($r^2 \geq 0.9$) NIRS validation results for fecal nitrogen content and NDF, and good ($0.7 \leq r^2 < 0.9$) results for lignin, CF, EE, ADF, and ash. Validation results for DM were poor ($r^2 = 0.29$). The time a sample was exposed to field conditions negatively affected fecal nitrogen content. CF and NDF were strongly negatively correlated with fecal nitrogen content, and CF and NDF increased in fecal concentration the longer exposed to field conditions. We concluded that NIRS can be an accurate tool to evaluate diet quality measures from feces, and that time of field exposure should be controlled for when using fecal measures of dietary quality in wildlife studies.

**Avoiding infanticide in space and time is costly (paper V)**

In this paper, we provide further support for the hypothesis that avoiding infanticide in space and time can be a female reproductive strategy in brown bears (paper III), and that this strategy is costly in terms of nutritive quality. We hypothesized that females/cubs in a Scandinavian brown bear population with strong evidence for SSI pay a nutritive cost as a risk effect of SSI. We predicted that 1) during the mating season, females with cubs-of-the-year had diets of lower quality than a) lone females, but b) not than adult males. We predicted that 2) during the postmating season, females with cubs-of-the-year had diets of a) at least similar quality than lone females, and b) of similar or lower diet quality than adult males. We used fecal crude fiber (FCF) content as a proxy for diet quality, and used near-infrared spectroscopy to predict FCF content ($r^2 = 0.88$, Paper IV) in 491 fecal samples from free ranging GPS-marked adult males, lone females, and females/cubs that were collected during the 2010 mating and postmating season. We tested our hypotheses with linear mixed-effect regression models. We used FCF content (%) as the response variable and considered time in
the field (h), canopy cover (%), and oven drying time (h) for inclusion in the models, because field exposure and drying time (i.e., preprocessing the samples) can affect FCF content (Paper IV). We also considered reproductive status, age, and the interaction terms ‘age * reproductive status’ and ‘canopy cover * time in the field’ for inclusion in the models. We ran all possible combinations of model terms and used second-order bias-corrected AIC ($AIC_C$), $AIC_C$ differences ($\Delta AIC_C$), weights ($AIC_CW$) and evidence ratios ($E_I$) for model selection and evaluation. We created separate models for the 2 predictions, because of technical reasons and the nature of the hypothesis. Reproductive status was an important model term during both seasons. The 3 as well as 13 highest ranked models included ‘reproductive status’ during the mating season ($E_I = 14.7$) and postmating season ($E_I = 16.6$), respectively. We found that females/cubs had a significantly lower diet quality than lone females during the mating season. Diet quality of adult males did not differ from that of lone females and females/cubs during both seasons. Our results suggest that bears of different classes apply different strategies to cope with various risk factors. Females/cubs are freed from the risk of SSI during the postmating season, and thus have the opportunity to select their resources in a more optimal way. In contrast, lone females and adult males have no strong risk factor, such as SSI, during the mating season. However, during the postmating season, adult males and lone females are hunted intensively, whereas females/cubs are legally protected from hunting. We suggest that shifting risk regimes act differently upon various reproductive classes, explaining our observed patterns in diet quality. We suggest that risk effects of infanticide may be widespread among species with SSI and add to the female cost of reproduction.
Variation in life-history parameters among bear populations (paper VI)

We conducted a meta-analysis on reproductive allocation data (mean litter size in relation to average female body mass) of 28 brown bear populations across its geographical range. We used a linear model to evaluate factors related to food availability and habitat quality (i.e., normalized difference vegetation index, access to salmon), competition (i.e., population density and competition with American black bears (*Ursus americanus*)), female body mass, and persecution history (short term, < ~15 generations (150 years) and long term, > ~50 generations (500 years)). As expected, we found that mean female body mass and mean litter size were positively related. We also found that persecution history had a strong effect on female reproductive allocation, with populations having a long persecution history producing larger litters at a given body mass. Other variables had no apparent effect on female reproductive allocation. Our results suggest that nonselective human persecution can induce life-history changes in brown bears; populations with long persecution history show a larger investment in reproductive investment relative to their body mass than populations with a short persecution history.
Figure 5. The predicted relationship between mean litter size and mean female mass (kg) in brown bears in relation to persecution history (long term, > 500 years of persecution history, full line, black dots; short term < 150 years of persecution history, dashed line, open dots). Dots represent specific populations (N = 28). Dashed lines represent 95% confidence regions.
Discussion

An animal’s mating system is context dependent and reproductive tactics by individuals of different ages, sexes, and body condition can vary (Emlen and Oring 1977; Vehrencamp and Bradbury 1978; Clutton-Brock 1989; Gross 1996; Shuster and Wade 2003). Not surprisingly, we showed that plasticity is also a characteristic of the mating system of the brown bear (Papers I, II, III, V, and VI). For example, manners of mate acquisition vary across populations according to specific environmental conditions (e.g. clustering of food resources, population density) (Paper I), or SSI may be common in some populations and absent in others (Miller et al. 2003; Swenson 2003). Also, life-history parameters vary across populations (Paper I, VI), and human persecution probably acts as a selective force upon some of these parameters (Paper VI) (i.e., reproductive allocation). Within populations, strategies of movement and resource selection depend strongly on reproductive status (Paper II, III, V), and are likely related to SSI.

The SSI hypothesis

The SSI hypothesis is today generally accepted as an adaptive male reproductive strategy among behavioral ecologists (Swenson 2003; Wolff and Macdonald 2004; Knörnschild et al. 2011). Support for the SSI hypothesis was found in field studies, for example, in lions (Pusey and Packer 1994), savanna baboons (Papio cynocephalus) (Palombit 2003), langurs (Hrdy 1974; Borries and Koenig 2000), or under controlled conditions, e.g., in root voles (Microtus oeconomus) (Andreassen and Gundersen 2006), bank voles (Myodes glareolus) (Opperbeck et al. 2012), and red deer (Bartos and Madlafousek 1994), as well as with theoretical work and mathematical modeling (Hrdy 1979; Hausfater 1984; Hausfater and Hrdy 1984; Janson and van Schaik 2000; van Schaik and Janson 2000).

Previous research in our study population provided strong support for the SSI hypothesis (e.g., Swenson et al. 1997; Swenson et al. 2001b; Swenson 2003; Bellemain et al. 2006a; Bellemain et al. 2006b), and we provided additional support for it with this thesis. We used movement data as a proxy for behavioral estrus, and showed that females rapidly (1-2 days) changed to roam-to-mate behavior after litter loss. We used empirical data to show that females also entered estrus and engaged in mating activity after litter loss; the vast majority (92 %) of females that lost a litter during the mating season gave birth during the subsequent birthing season. This implies that litter loss can shorten the interbirth interval of females by at least 50%, in case cubs are weaned at the age of ~ 1.5 years. Consequently, SSI can be
advantageous for males in our study population. The correlative approach (relating movement patterns to reproductive status) did not answer how rapid females physiologically enter estrus after litter loss, however. Therefore, an endocrine approach is needed. Fecal concentrations of estradiol indicate estrus in bears (Ishikawa et al. 2003; Dehnhard et al. 2006). In 2011, we started to systematically collect fecal samples from females during the mating season. Preliminary results show that females can enter estrus already 2 days after a litter loss (M. Dehnhard, personal communication), which corresponds with our behavioral results.

Research on the adaptive significance of infanticide is often criticized, because of the low data volume and quality. Sample sizes of infanticide cases are typically small (Boggess 1984; Hrdy 1984), because infanticide is extremely difficult to observe and document in the wild (Hrdy 1974; Pusey and Packer 1994; Bellemain et al. 2005). For example, the team of Borries et al. (1999) witnessed one case of infanticide in hanuman langurs during more than 37,000 hours (~ 4.2 years) of direct observation. They collected data on another 34 cases of presumed infanticide or attempts. Despite the rarity of observation or documentation, Borries et al. (1999) could provide the first genetic evidence for the SSI hypothesis. In our study population, only one infanticide has been witnessed since the start of the project in 1984 (J. Katajisto, S. Brunberg, personal communication). Until 2009, 8 cases of infanticide had been detected in our study area. All of the cases provided genetic support for predictions i or iii of the SSI hypothesis (Bellemain et al. 2006a). In this thesis, we used high resolution GPS-tracking to systematically document infanticide, and recorded 11 infanticide cases or attempts during 3 mating seasons. The observed infanticides or attempts followed a pattern that is generally consistent with the SSI hypothesis. All observations occurred during the just before the mating season, and no GPS-marked female lost offspring after the mating season (Figure 6).
Figure 6. Infanticide cases and attempts in relation to the number of male-female associations of GPS-marked bears over time (in days from 1 May). We defined an association as an encounter in space (within 30 meters) and time (within a time window of 2 minutes) between a GPS-marked male and female. We assigned a 1 for each day during which an encounter was observed between a GPS-marked male and a female, and summed these ‘encounter days’ over the years 2008-2011, and scaled the observed number of male-female associations per day between 0 and 1 (black dots, association intensity). We added a small amount of noise to the data and a LOESS smoother (thick black line) to aid in viewing patterns. The vertical lines represent documented cases of infanticide or attempts, recorded in this study and in Bellemain et al. (2006a). The vertical dashed lines mark the start (9 May) and end (19 July) date of the mating season, based on a 0.1 association intensity cutoff value.

In 7 of the 11 infanticide cases or attempts, the perpetrators were GPS-marked males. In 3 cases, the perpetrators were assumed to be males, because the victimized female was observed shortly afterwards with a male. In 1 case (W0303, Appendix 1), the sex of the perpetrator remains unknown. In the 4 cases in which both perpetrator and victimized mother were known, we are confident that the perpetrator did not kill its own offspring, because the home ranges of the bears did not overlap or the male and the female did not associate the previous mating season, or because of the preliminary genetic results. The absolute sample of cases collected between 2009 and 2011 may appear low (N = 11). In a relative context, however, 44% (8/18) of the GPS marked females/cubs that were intensively monitored between 2009 and 2011 experienced infanticide or infanticide attempts (2009, 2/6 females/cubs; 2010, 5/7; 2011, 1/5).
Female reproductive strategies in relation to the SSI theory

Contrasting behavior, space use, or movements in relation to factors like sex, reproductive status, time, and risk can be very valuable to test optimality theory-oriented hypotheses (Parker and Smith 1990; Lima and Bednekoff 1998; Nathan et al. 2008). These indirect approaches have been applied to relate female strategies to cope with infanticide by males (e.g., Wielgus and Bunnell 1995; Loseto et al. 2006; Libal et al. 2011). If infanticide by males indeed can reduce female reproductive success, strategies that minimize infanticide and its risk should be selected for (Packer and Pusey 1983; Agrell et al. 1998; Ebensperger 1998; Wolff and Macdonald 2004). These strategies can operate before conception, during gestation, and after giving birth (Ebensperger 1998). Multimale mating by females is common among mammals (Agrell et al. 1998), and can conceal paternity, and deter potentially infanticidal males from killing offspring they might have sired (Wolff and Macdonald 2004). Also, multimale mating promotes multiple paternity litters (Laliberte and Ripple 2009), which is beneficial for paternity concealment (Bellemain et al. 2006b). Pregnancy termination may be beneficial in terms of invested resources in offspring that would otherwise be susceptible to infanticide (Agrell et al. 1998; Roberts et al. 2012). In several rodents (e.g., house mouse (Mus musculus) (Bruce 1959)) and some primates (wild geladas (Theropithecus gelada) (Roberts et al. 2012)), for example, females commonly terminate pregnancy after exposure to unfamiliar males. Maternal aggression during lactation is aimed to protect their offspring (Maestripieri 1992; Agrell et al. 1998), and territoriality and grouping (e.g., communal nesting in house mice (Manning et al. 1992) and in prairie voles (Microtus ochrogaster) (Getz et al. 1993)) can be beneficial for deterring and confusing potentially infanticidal males. Avoidance of infanticidal males in space or time, by altering resource selection, avoiding high risk areas, or selecting for escape habitat seems an obvious counterstrategy; definitive evidence for it is, however, rare (Ebensperger & Blumstein 2007).

In this study, we provided support for a spatiotemporal avoidance strategy by females/cubs in relation to SSI (Papers III, V). During the mating season, resource selection was not or negatively correlated between females/cubs and adult males during most parts of the day (except during midday). Females/cubs selected their resources very differently from adult males, for example, by using less dense habitat types, in less rugged landscapes, and in relatively close proximity to settlements. After the mating season, when the risk for SSI is over, females/cubs selected their resources in a similar way as their conspecifics. We showed...
that resource selection was a complex and multiscaled spatiotemporal mechanism that varied in time (diurnal and seasonal) and across reproductive classes of bears. The observed patterns in resource selection of females/cubs in relation to conspecifics were in accordance with the expected behavior under the risk of SSI. Also, our results provided support for the hypothesis that females/cubs perceived human disturbance as a lower risk factor than infanticide by conspecifics, and that females/cubs might use humans as a virtual shield against infanticidal males. Associating with humans to reduce infanticide risk has also been suggested in North American populations that aggregate at concentrated food sources, such as salmon streams (Nevin and Gilbert 2005; Rode et al. 2006).

Predation is a strong selective force, and strategies to reduce predation have an obvious fitness benefit, i.e., increased survival chances (Lima and Dill 1990). However, avoiding predation can be costly, because it often comes with a trade-off between food or safety (Brown and Kotler 2004; Main 2008), and trade-offs are typically paid in the currency of fitness (Stearns 1989). The trade-off between selecting good quality habitat and safety is a blooming subject in ecology, but almost exclusively in relation to interspecific predation (Lima and Bednekoff 1998; Creel and Christianson 2008). Ben-David et al. (2004), however, studied the consumption of salmon (\textit{Oncorhynchus} spp.) during late summer and fall by females/cubs in an Alaskan brown bear population based on stable isotopes in hair samples and spatial analysis, and concluded that females may indeed trade the use of salmon as a food source against the risk of infanticide. The adaptive significance of infanticide was assigned to competition over resources. Their research showed that infanticide other than SSI can also be an important source of cub mortality, and suggests that the adaptive significance of infanticide can vary across populations. To our knowledge, we are the first to document a trade-off between food and offspring safety as a consequence of SSI, a result that supports the hypothesis that females/cubs alter their resource selection to reduce infanticide risk (Paper III). Analogous with interspecific predation, our results suggest that avoiding SSI can add to the female cost of reproduction (Magnhagen 1991; Lima 1998; Creel et al. 2007; Main 2008).

\textit{Alternative explanations for infanticide}

In addition to the sexual selection hypothesis, Hrdy (1979) proposed 4 alternative hypothesis for explaining infanticide in mammals, i.e., the predation hypothesis, the resource competition hypothesis, the parental manipulation hypothesis, and nonadaptive explanations.
In our study system, we cannot rule out that infanticide occurs also in other forms than SSI. The observed patterns, however, do generally not support these alternatives.

The predation hypothesis postulates that infanticide is a mechanism to exploit infants as a food resource, and predicts that i) infanticide should be followed by the consumption of the infant, and ii) mostly committed by energy-stressed individuals. Of the 13 cubs found between 2009 and 2011, 7 (54%) were not or only partly consumed. Of the other 6 cubs, we only retrieved indigestible parts, such as bones and teeth. If bears actively preyed upon cubs, a higher proportion of consumed cubs would be expected. We have no data on the body condition of the perpetrators and can thus not evaluate prediction ii of the predation risk hypothesis. The predation risk hypothesis does not make predictions about the sex of the perpetrator nor the time in which infanticide risk would be expected to be highest. However, if infanticide would be a foraging strategy, it would be expected that both sexes commit infanticide, and when the cubs are most vulnerable, i.e. during the pre-mating season, or during fall, when bears should accumulate fat for hibernation. In some populations, however, cannibalism is not uncommon in bad bear-food years (e.g., south Siberia (Gillin et al. 1997)).

The resource competition hypothesis states that infanticide increases access to physical resources (food, nest sites, etc.) for the perpetrator and its offspring (Hrdy 1979; Ebensperger 1998). This hypothesis predicts that infanticide rates increase with population density and decreased resource availability, and should be selective for the sex with the highest probability of becoming a competitor (Ebensperger 1998). Strong suggestive evidence for the resource competition hypothesis has been documented in e.g. wild rabbits (*Oryctolagus cuniculus*), where females sometimes kill infants from unrelated females for access to burrows (Künkele 1992), and in the common marmoset (*Callithrix jacchus*), in which dominant mothers kill offspring of subordinate females for increased access to foods and helpers (Digby 1995). In our study population, receptive females are an important limiting resource for males. Nevertheless, males often kill entire litters, irrespective of the sex of the killed cubs (supported by preliminary genetic results, E. Bellemain, personal communication). Also, mortality in yearlings is female biased and mainly caused by adult males (Swenson et al. 2001a). It is thus not likely that infanticide by males is aimed to increase long-term future breeding opportunities for itself and its offspring in bears in our study system. Under the resource competition hypothesis for infanticide in bears, also females would be expected to be perpetrators, as a form of reproductive suppression. In our study population, reproductive suppression exists between closely neighboring females, as does reproductive synchrony between females the live further apart (> 20 km) (Ordiz et al.
We have, however, never documented infanticide by females in our study area, and reproductive suppression and resource competition among females probably operate in ways other than infanticide (Ordiz et al. 2008). Most females in our study system live in kin-related spatial structures (Støen et al. 2005). The resource competition hypothesis to explain infanticide requires that the involved individuals are unrelated (Hrdy and Hausfater 1984). Thus, because of the generally close genetic relationship females in our study, infanticide by females is not expected to be common. The density dependent and resource availability aspects of the resource competition remain unexplored in our study system and require more attention.

The parental manipulation hypothesis for infanticide states that parents may increase their lifetime reproductive success by eliminating particular offspring (Hrdy 1979). Infanticide as a parental strategy is typically committed shortly after birth, and can be committed by both sexes (Hrdy and Hausfater 1984). Parental manipulation is relatively common among humans (*Homo sapiens*), e.g., gendercide in rural societies in China and south India (George et al. 1992), or the killing of newborn twins or deformed newborns by their mothers in certain Amazonian tribes (Bugos and McCarthy 1984). In our study population, genetic evidence suggested that males do not kill their own offspring, and thus that paternal manipulation is unlikely to occur. We have no record of females committing infanticide in our study area, and modeling results suggest that abandoning singleton cubs would have very little selective advantage (<1%) (Zedrosser 2006). For being most efficient, maternal litter manipulation should occur shortly after birth. For the brown bear, this implies mid-winter during hibernation, not the mating season. Maternal manipulation is thus unlikely to explain the infanticide cases presented in this thesis and in Bellemain et al. (2006a), but might occur during denning.

Nonadaptive explanations for infanticide include all forms of infanticide that do not directly contribute to the fitness of the killer, such as accident and pathology. Nonadaptive explanations for infanticide receive very little support in the literature and fail to explain the commonly observed patterns in sex bias of victims and their killers, and the timing of the killing (Hrdy 1979; Hausfater and Hrdy 1984; Sommer 2000). Also mathematical modeling fails to support infanticide as a nonadaptive strategy (Ebensperger 1998; Ebensperger and Blumstein 2007). In our study population, it is unlikely that the observed patterns can be assigned to accidents or pathological behavior. Cubs appear to be killed by directed aggression and not by accident, as in e.g. certain pinnipeds (e.g. northern elephant seals...
(Mirounga angustirostris)) in which pups sometimes are killed when males fight for a harem (Ebensperger 1998).

The five hypotheses for explaining infanticide, as proposed by Hrdy (1979), are not mutually exclusive, and several forms of infanticide may operate within a population. Also, the benefits of infanticide can be additive for the perpetrator. For example, a male would benefit energetically from consuming the cubs he killed to obtain mating opportunities. In addition, killing unrelated offspring may also reduce a males’ future competition for himself and his offspring. Because of the nonexclusiveness of the hypothesis, proximate and ultimate causes of infanticide are difficult to unravel and require more attention.

Variation in life-history parameters

The earliest records of brown bears were found in China, and date from approximately 500,000 years before present (BP) (Pasitschniak-Arts 1993). Brown bears entered Europe some 250,000 BP, and reached eastern Beringia 50-70,000 BP (Leonard et al. 2000). Bears started to spread throughout the northern American continent some 13,000 BP, after several invasions of genetically distinct populations (Leonard et al. 2000). In Europe, 2 major mitochondrial lineages exist, the western and the eastern lineage, and 2 clades are distinguished in the western lineage (Taberlet et al. 1997; Waits et al. 2000). Bear populations thus show considerable genetic variation, and have further evolved under specific and dynamic environmental contexts. Not surprisingly, populations show considerable variation in e.g. size, morphology and behavior (Schwartz et al. 2003), and also in life-history parameters, such as age at primiparity, mean litter size, and interlitter interval (Zedrosser et al. 2009, Papers I and VI).

Humans harvest pressure is an important selective force (Hendry et al. 2008), and outpaces many other agents for trait changes that occur under natural conditions (Darimont et al. 2009). Most examples of human-induced evolutionary change are from fisheries. Conover and Munch (2002), for example, show that selective harvesting can affect somatic growth and population productivity already after 4 generations of selective harvest. Trait changes as a consequence of selective harvesting have also been reported in mammals. In bighorn sheep (Ovis canadensis), for example, selective hunting can favor genotypes for smaller body size and horn size. As an evolutionary response, body weight and horn size have declined in less than 40 years, as a consequence of selective hunting (Coltman et al. 2003).
In Paper VI, we present strong evidence that human persecution history may be a selective force on reproductive allocation in brown bears. Human persecution is the single-most important factor for the current distribution of brown bears (Servheen et al. 1999; Zedrosser et al. 2001; Schwartz et al. 2003; McLellan et al. 2008). Persecution history, however, differed considerably among North American and Eurasian populations. In Europe, the first records of officially organized carnivore extirpation efforts date from around ~ 800 AD, and primitive weapons and traps were used until modern firearms became available in the 19th century. In Europe, persecution of large carnivores to (near) extinction was a slow centuries-long process (Swenson et al. 2000; Woodroffe et al. 2005). In the North American continent, settlers with modern weapons eradicated brown bears over most of their geographical range in less than 2 centuries (Mattson and Merrill 2002).

Life-history theory predicts that, under reduced adult survival (e.g., by predation), selection will favor genotypes that are capable of reproducing earlier, at smaller size, and with higher reproductive allocation (Stibor 1992). In Paper VI, we show that persecution history is an important determinant for current reproductive allocation in 28 bear populations. In European populations, with a long and rather inefficient persecution history, genotypes that reproduced at younger ages and with higher reproductive allocation probably were favored, and adapted under a constant, but rather inefficient pressure of the human predator. Persecution in North America and Asia probably occurred too fast in evolutionary time for adapting a strategy that favors large litters relative to female body size. Today, under enlightened management with regard to carnivore management and conservation, many European bear populations have recovered from critically low population sizes (Zedrosser et al. 2001), and annual population growth rates up to 16 % have been recorded (Sæther et al. 1998; Swenson et al. 1998). North American populations appear to respond less rapid to conservation measures, and the maximum recorded annual population growth rate is 8.5 % (Hovey and McLellan 1996). Our results suggest that human persecution history plays an important role in the different modes of recovery between European and other North American populations.

**Perspectives**

A PhD project is a small, but important step stone in the continuous process of education and in gaining and generating knowledge. Part of generating knowledge is asking questions and
formulating hypotheses. Many additional questions emerged during this research, of which I present some here.

Sexually selected infanticide theory – During this thesis, we found strong support for the SSI hypothesis in our study population. We were able to systematically document infanticide cases and attempts, but we could not conclusively determine whether or not it is a male reproductive strategy. Providing genetic proof for a larger number of infanticide cases is needed to answer prediction i and iii of the SSI hypothesis. Further endocrinological research is needed to answer prediction ii.

The SSI hypothesis and the role of hunting in promoting SSI is a hotly debated topic among bear biologists and managers. In some populations, strong evidence for the SSI hypothesis exists (Wielgus and Bunnell 1995; Swenson et al. 1997), whereas infanticide seems to have no strong effect on cub survival in several North American populations (Miller 1990; Miller et al. 2003; McLellan 2005). Study results are often generalized, and different results can lead to scientific conflict (and progress!) (Chalmers 1976). Miller et al. (2003) and McLellan (2005), for example, strongly criticized studies that support SSI in bears. They made predictions about how SSI should operate in other populations, without taking into account that populations and individuals can be very different in e.g., life history, persecution history, food availability, reproductive behavior, etc. SSI can operate in some populations while being absent in others (Palombit 2003), and even within populations, some individuals can be infanticidal, whereas other are not (Hrdy 1984). Thus, explaining variation in the occurrence and importance of SSI across populations (and species) in relation to ecological and historical factors is a future challenge.

Female reproductive strategies – During this thesis, we found strong support for several behavioral strategies, e.g., avoidance of infanticidal individuals (Paper III) and the costs associated with this behavior (Paper V). However, do these strategies really pay off in terms of fitness? The next step is to evaluate fitness effects of certain behavioral strategies (e.g. avoiding certain food sources, human shields, living elusively, SSI, etc.).

Brown bears have delayed implantation and conception occurs during the mating season. The fertilized ova remain dormant in the uterus until implantation, which occurs around November-December (Spady et al. 2007). No unifying explanation for delayed implantation exists, and the effect of the environment on delayed implantation is poorly understood. A common hypothesis to explain delayed implantation in carnivores is that it synchronizes events according to optimal environmental conditions, i.e., the mating season, when individuals are in prime condition, and the time of parturition, when resources are at a
maximum (Lindenfors et al. 2003). However, this hypothesis does not apply to the brown bear; mating occurs shortly after den emergence, after a 6-7 month period of fasting, and parturition occurs during denning, when virtually no food resources are available. Do females have control over the number of implanted ova? Does this relate to environmental and social factors? The mechanism of delayed implantation in the brown bear remains an open question.

Social network analysis has become a powerful tool to unravel social relations among individuals and groups. The types of these relations (i.e., antagonistic, mating, kin relations) are important to determine population structure. Social network studies are almost exclusively carried out by direct observations in socially living species, such as yellow-bellied marmots (*Marmota flaviventris*) (Croft et al. 2011) and certain primates (e.g., humans (Bearman et al. 2004)). However, also in elusive species living in a less-apparent social setting (nonsocial or solitary living species), social interactions are important, i.e. for acquisition of mates (Shuster and Wade 2003), to maintain kin-related social structures (Støen et al. 2005), and to develop dominance hierarchies (Zedrosser et al. 2007). The frequency, timing, duration, and direction of male-female encounters in relation to individual-based data, such as body size, relatedness, hormonal status, and major histocompatibility complex (MHC) can provide new insights and knowledge in mate choice, and social network analysis is a suitable tool for that.

**Ecology in a world of rapid change** – There is ample evidence that climate change affects ecosystems worldwide (Post et al. 2009). These patterns are spatially heterogeneous, and ecological communities are thus expected to show regional responses, rather than one global unidirectional response (Walther et al. 2002). For example, annual average temperature increased by 0.7-1°C per decade during the last 3 decades at northern latitudes. In northern Sweden, precipitation decreased by ~ 20% per decade during the last 3 decades, while precipitation increased by ~ 10% per decade in south central Sweden (Walther et al. 2002). These changes affect ecological communities. For example, red foxes (*Vulpes vulpes*), have expanded their ranges northwards and become a serious threat for arctic foxes (*Alopex lagopus*) (Post et al. 2009). Climate change may also affect brown bears. Billberries, the staple food of brown bear populations at northern latitudes (Dahle et al. 1998), produce up to 80% less berries after mid-winter thaw events due to the removal of the insulating snow cover (Bokhorst et al. 2008). According to climate models, these mid-winter warm spells are expected to occur more frequently in the future, due to a changing climate (Bonsal et al. 2001). Long-term studies, such as the SBBRP, can play an important role in evaluating and predicting potential ecological and demographical effects of climate change (Clutton-Brock
and Sheldon 2010). A plausible expectation would be, for example, that bear populations that rely on berries as a bulk food could decrease in density after repeated failures in berry production.

Habitat fragmentation and degradation is an important factor determining the distribution and number of many –if not all– wildlife species (Woodroffe 2000; Woodroffe et al. 2005). Direct effects are obvious: if (key) habitat for a species disappears, so do the species that live therein. However, habitat alteration can also work in a less direct way, and perhaps act differently upon reproductive classes. In Paper III, we show that reproductive classes indeed selected their resources differently. Females/cubs selected for less dense habitat types, and relatively far from forest roads. Also, females/cubs use older forest types more often, probably to facilitate escape possibilities for the cubs (by climbing large pines). Males used areas close to forest roads more than expected, and always preferred dense habitat. In our study area, intensified logging activities resulted in a patchy landscape of small forest stands of different age cohorts and a strong reduction in old growth forest and standing volume (Linder and Östlund 1998). Today, less than 60 % of the forest is older than 35 years (Swenson et al. 1999), a dense network of logging roads exist (Martin et al. 2010), and road upgrading, planning and building is a continuous process (Henningsson et al. 2007). Thus, good quality habitat for females/cubs probably decreased over time, as logging activities increased, and perhaps favored infanticide by males.
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Acknowledgements

I first heard about the Scandinavian Brown Bear Research Project in spring 2004 when I was tracking bears and wolves (snow and mud tracking, the old-school way) in Slovakia. After reading a few ‘bear project’ papers, I found it hard to believe that social organization and reproduction in wildlife could be that complex (indeed, my perception of animal behavior was rather naïve). My interest in wildlife grew as never before during that stay in Slovakia, and a boys’ dream of becoming a forest and wildlife ranger steadily evolved to one of becoming a wildlife researcher. Today, (only) eight years later, I am proud to deliver this thesis in the framework of the SBBRP, one of my initial role models in science. So, how can I in only a few words properly express my gratitude to all the people in and around the thesis, and on my path hereto?

I drove up north to the field station in Tackåsen in my white little Opel (the egg, many thanks to Dirk and Mieke!), in June 2008 for my first field season in the bearproject. I experienced a fantastic summer and autumn doing fieldwork for my master’s degree, having fun and making friends, and I also got one step closer to this PhD. This would not have been possible without Ole-Gunnar Støen for taking me as a MSc student, and Ron van Lammeren, and Willy ten Haaf (Wageningen University, the Netherlands) for creating and providing such a supportive educational environment.

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I unfortunately spend less time with Klaus at Institute of Wildlife Biology and Game Management at the BOKU in Vienna. Nevertheless, I found it very valuable and pleasant to meet, to talk, to discuss and arrange work, and also just to be at the BOKU. I don’t know of any other university setting than the ‘BOKU standl’, where students and professors so regularly meet, the beer so lavishly flows and where and a thick curtain of smoke sometimes
blocks the view. Good times. I thank Martin, Jelte, Linda and Paul for the friendship, the hospitality, housing, and the great times during my winter in Vienna.

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Since 2008, I spend part of each spring and summer in the study area in central Sweden for fieldwork. For me, the field season is one of the highlights of the year, and no field season is the same; the soap story of a population bears in the urge to mate continues in its own rather unpredictable way, adventures of all kind will happen, and the woods, lakes and rivers provide a great change from the office and the computer screen. During the field season, Tackåsen transforms from a tiny settlement (6 permanent inhabitants) to a real busy place, with capture teams, volunteers, students, researchers of various disciplines (with specific and sometimes conflicting wishes), dog trackers, and the sporadic journalist. All of this (but also building, once more repairing another broken car, saving students, story-telling and what not) is coordinated or managed in a very impressive way by Sven Brunberg. Also, I gained most of my field and bear experience from Sven, for which I am of course very grateful. I thank Boss, because collecting infanticide cases would be a hopeless job without his superb nose and excellent tracking skills. I thank the field crews from 2008 until now for the unforgettable times and the great work, and for the many friendships that have developed. I especially want to thank Shane, Martin, and Linda, who became real close friends of mine, and my good friend Bram, for coming over to help out and spending a spring of poop picking. You guys rock.

I did not always have the greatest times in Ås and Norway; missing friends and family, adapting to the Norwegian way of life, focusing mostly on work and sometimes ignoring social life. However, I also had of course really good times, for whom I thank Andrés, Marcus, Richard, Beate, Mauritz and Jenny, Rafael, Bela, Clara, Arezoo, Karen, Silje, Veronica, and many others. I thank Beatriz for a great autumn and winter, the trips to Drøbak and the sometimes late night parties. I also thank friends from home, for their visits and for the warmth and hospitality when back in the lowlands: Wouter, Eva, Bram, Fab, Geertje, Katrien, Raoul, Anne, Caps, Jurgen, … Special thanks to Marte, for the very nice times we spend together, the bouldering, climbing, concerts, fishing, wines and trips; for the translations and for getting me to speak a little Norwegian. Thank you so much!
Finally, there are no words to express my gratitude to my parents, Eric and Chris, for their love, for creating that warm nest where their kids always can rely on, and for supporting and encouraging me with the decisions I make in life. I also thank my two brothers, Korneel and Thomas, for support, visits and adventures, and for just being my two great brothers.
Appendices

**Appendix 1. Summary table of litter loss, infanticide cases and attempts 2009-2011**

Summary of the documented infanticide cases, cub disappearances and infanticide attempts during the mating seasons 2009-2011. ‘Perpetrator’ indicates the presumed killer, ‘First male’ and ‘Date first male’ indicates the date and the ID (if known) of the first male the female was observed together with. Consorted (Cons.) indicates whether or not the presumed perpetrator was observed together with the victimized mother during the mating season the previous year.

<table>
<thead>
<tr>
<th>Female ID</th>
<th>Perpetrator Type</th>
<th># killed</th>
<th># survived</th>
<th>Date</th>
<th>First male</th>
<th>Date first male</th>
<th>Cons.</th>
</tr>
</thead>
<tbody>
<tr>
<td>W0209</td>
<td>- infanticide</td>
<td>≥2</td>
<td>0</td>
<td>5/5/2009</td>
<td>W0917</td>
<td>24/05/2009</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>cub disappearance</td>
<td>1</td>
<td>0</td>
<td>15/5/2009</td>
<td>W0827</td>
<td>23/06/2009</td>
<td>-</td>
</tr>
<tr>
<td>W0720</td>
<td>W0915 attempt</td>
<td>0</td>
<td>2</td>
<td>7/6/2009</td>
<td>W0827/W022</td>
<td>15/6/2009</td>
<td>-</td>
</tr>
<tr>
<td>W0010</td>
<td>- infanticide</td>
<td>&gt;1</td>
<td>0</td>
<td>16/5/201</td>
<td>unmarked</td>
<td>20/06/2009</td>
<td>-</td>
</tr>
<tr>
<td>W0620</td>
<td>- infanticide</td>
<td>3</td>
<td>0</td>
<td>31/5/201</td>
<td></td>
<td>18/05/2010</td>
<td>-</td>
</tr>
<tr>
<td>W0303</td>
<td>- infanticide</td>
<td>1</td>
<td>2</td>
<td>11/5/201</td>
<td></td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>W0503</td>
<td>W0802 infanticide</td>
<td>≥1</td>
<td>0</td>
<td>3/6/2010</td>
<td>W0802</td>
<td>09/06/2010</td>
<td>yes</td>
</tr>
<tr>
<td>W0217</td>
<td>W0805 infanticide</td>
<td>1</td>
<td>1</td>
<td>12/6/201</td>
<td></td>
<td></td>
<td>no</td>
</tr>
<tr>
<td>W0217</td>
<td>W0805 attempt</td>
<td>0</td>
<td>1</td>
<td>12/6/201</td>
<td></td>
<td></td>
<td>no</td>
</tr>
<tr>
<td>W9615</td>
<td>W0827 attempt</td>
<td>0</td>
<td>2</td>
<td>17/6/201</td>
<td></td>
<td></td>
<td>no</td>
</tr>
<tr>
<td>W9403</td>
<td>W0718 infanticide</td>
<td>2</td>
<td>0</td>
<td>6/6/2011</td>
<td>W0718</td>
<td>20/06/2011</td>
<td>no</td>
</tr>
</tbody>
</table>
Appendix 2. Description of infanticide cases.

**Case 1.** Female W0209 lost her 2 cubs at her 2008 – 2009 winter den around 5-8 May 2009. On 5 May, she moved 60 m north of the den, where she remained until 8 May, after which she suddenly left the area and started to show movement patterns typical for receptive females (Paper III). We collected one dead but intact cub and tissue from a partly consumed cub at the densite. We also collected bear feces containing cub remains near the den. W0209 was observed with males W0917 and W0719 later on in the mating season. W0209 gave birth to 3 cubs in 2010.

**Case 2.** Female W0010 lost her entire litter on 15 June 2009. We detected the case due to a sudden change in her spatial behavior. We collected cub remains at the site of infanticide, which showed clear signs of an aggressive interaction between bears, i.e., trampled soil, claw marks on trees, broken branches, hair tufts, etc. W0010 was observed with a male (either W0805 or W0228; the GPS collars of these bears had failed, but pictures were taken with a camera trap of the female and a male with a non-functional collar) on 20 June 2010. W0010 was killed by hunters during the 2009 bear hunt. Her reproductive fate is thus unknown.

**Case 3.** Female W0620 lost her 3 cubs on 16 May 2010. We found the remains by backtracking her GPS locations, after she had showed a sudden increase in movements. The site showed signs of an aggressive interaction between bears, i.e. trampled soil, tree damage, claw and climbing marks on trees, and many hair tufts. Site investigation at daybeds of her daybeds suggested that she was accompanied by another bear on 18 May 2010 (i.e. presence of multiple daybeds and several scats). W0620 was observed together with three GPS-marked male bears later on in the mating season (W0811, W0917, W1019) and gave birth to one cub in 2011.

**Case 4.** Female W0303 showed increased movements during the last week of June 2010. We found cub remains at her daybed of 31 May. Two cubs had survived the event. At cluster sites preceding and after the infanticide event, we found signs of aggressive interactions between bears (tree climbing marks of cubs and adult bears, hair tufts, trampled soil, etc.). The 2 remaining cubs were weaned (W1101 and W1102) in 2011.

**Case 5.** We recorded an encounter between female W0503 and male W0802 on 3 June 2010. W0503 had at least 1 cub at the onset of the mating season of 2010. We found ribs of a bear cub, blood, and hair tufts at the encounter site. We tracked W0802 and found scats containing a bear cub around a daybed of 4 June 2010. Female W0503 increased her movement rates immediately after the infanticide event. W0802 repeatedly tracked W0503,
but it was not until 14 June when W0503 and W0802 met and stayed together for 9 consecutive days. W0503 and W0802 were observed together in 2009 during 4 consecutive days. Preliminary genetic data suggest that W0802 was not the father of the cub he killed. W0503 was shot during the 2010 bear hunt. Her reproductive fate is thus unknown.

**Case 6.** We detected encounters between female W0217 and male W0805 on 12 and 13 June 2010. Female W0217 had 2 cubs at the onset of the mating season of 2010. We found cub remains, signs of an aggressive interaction, and a bear scat containing a bear cub at the encounter site of 12 June. We found signs of an aggressive interaction at the encounter site of 13 June. One cub survived the events and was weaned in 2011.

**Case 7.** We found 2 dead bear cubs from an unmarked female at a cluster site of GPS locations of six-year-old male W0827 while conducting fieldwork for other purposes. The site showed clear signs of an aggressive interaction between bears (broken trees, trampled soil, climbing marks on trees, hair tufts, etc.).

**Case 8.** The 2 cubs of female W9403 were killed on 6 June 2010 after an encounter with male W0718 and female W9615. The site showed clear signs of an aggressive interaction, such as tracks on the gravel road, cub intestines up to 400 meter from the encounter site, hair tufts, broken branches, etc. The GPS positions indicated that the interactions occurred between W0718 and W9403, and not with female W9615 who was nearby. One cub was partly consumed, and 1 cub had bite marks on the abdomen. The home ranges of W0718 and W9403 did not overlap in 2010. W0718 and W9403 were observed together from 20 to 25 June 2010. Afterwards, W9403 was also observed with 4 other males (W0802, W0805, W0812, W1019). W9403 gave birth to 2 cubs in 2012.
Paper I
REVIEW

The mating system of the brown bear *Ursus arctos*

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ABSTRACT

1. Research on mating systems and reproductive strategies is valuable for providing ethological knowledge, important for the management and conservation of a species, and in a broader sense, important for biodiversity conservation.

2. We reviewed the literature to document the mating system of the brown bear *Ursus arctos*. We determined that many aspects of the reproduction of the brown bear remain unclear, including (i) biological aspects, such as hormone and oestrous cycling, sperm competition, mate choice, sexually selected infanticide, etc. and (ii) human impacts on the mating system, occurring when humans alter population size and structure, through, for example, hunting or habitat degradation.

3. We considered three mating system classification frameworks from the literature (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003) and applied various brown bear populations to them. We did this (i) to document the plasticity of the mating system of the brown bear, and (ii) to find commonalities among the reported mating system classifications in order to provide a general and common classification of the brown bear’s mating system.

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4. The mating system of the brown bear can, in general, be classed as 'polygamous'. Subclassifications can nevertheless be valuable on smaller spatial scales.
5. Within the polygamous mating system of the brown bear, biological aspects and human impacts can influence reproductive strategies at the individual and population level. Mating system classification frameworks often lack a common terminology, which contributes to the variety of published classifications of the mating system of the brown bear.

Keywords: female mate choice, male-male competition, polygamy, reproductive strategies, sexual selection

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INTRODUCTION
An animal species’ mating system refers to the general behavioural strategies employed in obtaining mates, and includes features such as number of mates, manner of mate acquisition, characteristics of association and parental care (Emlen & Oring 1977). Mating systems and strategies are driven by the strength of sexual selection, which in turn is determined by male-male competition and female mate choice (Shuster & Wade 2003, Shuster 2009). Over 90% of mammalian species are polygynous, and the energetic investments in gametes and rearing offspring are typically larger for females than for males, especially in the absence of paternal care (Orians 1969, Trivers 1972, Clutton-Brock 1989, Andersson 1994, Shuster & Wade 2003). Mate selection is thus a much more important decision for females than for the rather indiscriminate males (Orians 1969, Trivers 1972). For females, mate choice should be based on expressions of male genetic quality, such as size, fighting skills or weaponry, in order to optimize individual fitness (Orians 1969, Andersson 1994, Arnold & Duvall 1994). Because receptive females are generally considered to be the limiting resource in reproduction, males face intra-sexual competition for mates (Trivers 1972, Emlen & Oring 1977, Arnold & Duvall 1994, Shuster & Wade 2003). Male reproductive success is often found to be proportional to the number of mates or copulations, and shows considerable variance as a consequence of intra-sexual competition for females, whereas female reproductive success generally varies less (Bateman 1948, Trivers 1972, Andersson 1994, Shuster & Wade 2003, Shuster 2009). Although there is a large body of literature on sexual selection and mating system theory, no universal agreement exists on terminology and mating system classification (Andersson 1994). Knowledge of mating systems not only has ethological value, but is important for species-specific conservation and management, and for biodiversity conservation in general (Berger 1996, Palermo et al. 2007).

Brown bears Ursus arctos have been the subject of intensive research (see, e.g. Pasitschniak-Arts 1993, Craighead et al. 1995a, Servheen et al. 1999, Swenson et al. 2000, Schwartz et al. 2003b, Kaczensky et al. 2004, Garshelis 2009) and substantial knowledge on their biology and life history has been gained over the last decades. However, many aspects of the reproductive biology of the brown bear remain poorly documented. The literature suggests that there is variation in the brown bear’s mating system, reproductive strategies, and reproductive parameters; their mating system has been described as polygamous (Pasitschniak-Arts 1993, Zedrosser et al. 2009), promiscuous (Swenson et al. 2001a, b, Schwartz et al. 2003b, Bellemain et al. 2009).
scramble competition polygamous (Dahle & Swenson 2003c, McLellan 2005) and contest competition polygamous (Zedrosser et al. 2007a). Both the lack of a common mating-system terminology and the apparent variation in the mating system of the brown bear probably contribute to the large variety of mating system classifications assigned to this species.

In this paper we summarize and review the literature on brown bear reproductive behaviour and biology, and classify the mating system of the brown bear, based on three existing mating system classification frameworks. Emlen and Oring (1977) and Clutton-Brock (1989) provide two widely accepted theoretical classification frameworks based on the spatiotemporal clustering of resources, which include reproductive partners. Shuster and Wade (2003) provide a more recent classification framework based on the statistical quantification of the strength of sexual selection and the evolution of mating systems.

ECOLOGY AND SOCIAL ORGANIZATION

The brown bear is one of the eight species of bears and one of the six members of the genus *Ursus* (Schwartz et al. 2003b). It is a holarctic omnivorous member of the Carnivora and the most widespread species of Ursidae (Pasitschniak-Arts 1993, Schwartz et al. 2003b). Brown bears occupy a large variety of habitats, ranging from treeless arctic tundra, grasslands, boreal forest, to coastal, mountainous and desert habitats, reflecting their adaptive nature (Swenson et al. 2000, Schwartz et al. 2003b). Human presence is the most important factor determining the distribution of brown bears in their historical range (Kaczensky et al. 2006); it alters their ecology and behaviour, such as habitat selection and circadian rhythms (Pasitschniak-Arts 1993, Swenson 1999, Klinka & Reimchen 2002, Ciarniello et al. 2007, Nellemann et al. 2007). The brown bear is currently listed globally as a species of least concern, which has stable or increasing population sizes in North America, northern Asia, and northern and central Europe (Anonymous 2008). However, southern Europe and Asia harbour several small, isolated and critically endangered populations (Swenson et al. 2000, Anonymous 2008).

Brown bears are sexually dimorphic: males are 1.2–2.2 times larger than females (Lefranc et al. 1987, Jakubiec 1993, Schwartz et al. 2003b, Swenson et al. 2007). Body size varies geographically and seasonally, and is related to local food supply (Hilderbrandt et al. 1999, Meiri et al. 2007, Garshelis 2009). Brown bears generally reach 95% of their asymptotical size at nine and 14 years of age for females and males, respectively (Kingsley et al. 1983, Swenson et al. 2007). Growth rates, however, depend on food conditions and population densities, and thus show variation among populations (Kingsley et al. 1988, Zedrosser et al. 2006, Zedrosser et al. 2007a). Adult body mass ranges from 80kg to over 600kg; the largest individuals are found in coastal Alaskan populations with access to seasonal salmon runs (Hilderbrandt et al. 1999, Schwartz et al. 2003b).

Brown bears are considered to be solitary and non-territorial (Craighead et al. 1995a, Dahle & Swenson 2003a, b, c, Bellemain et al. 2006a). This implies that social interactions and consorting is limited to the breeding season only, and that they have home ranges instead of strict territories (Schenk & Kovacs 1995, Hawkins & Racey 2009). However, Støen et al. (2005) showed evidence of territoriality in female brown bears in a Scandinavian population: related females apparently excluded unrelated females from common areas. Home range sizes and bear densities vary according to
geographical range and food supply, and overlap both inter-sexually and intra-
sexually: male home ranges are large and overlap with the home ranges of several
females (Hilderbrandt et al. 1999, McLoughlin et al. 2000, McLellan & Hovey 2001,
Dahle & Swenson 2003c, Støen et al. 2005). Annual home range sizes range between
24–2434km² and 115–8171km² for females and males, respectively (McLoughlin et al.
2000). Population densities range between an estimated 1.2 individuals/1000km² in a
Russian population (Chestin et al. 1992), and 551 individuals/1000km² in an Alaskan
population (Miller et al. 1997, McLoughlin et al. 2000). Within populations, seasonal
home range sizes vary according to age and sex, population density, reproductive
status during the mating season, and the occurrence of temporally available con-
gregated foods (e.g. salmon, garbage, army cutworm moths Euxoa auxiliaris; Craig-
head et al. 1995a, Dahle & Swenson 2003c, Preatoni et al. 2005, Rode et al. 2006,
Bellemain et al. 2006a).

Natal dispersal is typically male biased (Støen et al. 2005), and is considered to be
a mechanism to avoid inbreeding (Bellemain et al. 2006b, Zedrosser et al. 2007b). Up
to 92% and 46% of subadult males and females, respectively, were found to disperse
in Scandinavia. Maximum dispersal distances were 467km and 90km for males and
females, respectively (Støen et al. 2006a). In southwestern Canada, natal dispersal
occurs less often and over shorter distances, averaging 49.1km for males and 14.3km
some ungulate species (Clutton-Brock et al. 1982, Poteaux et al. 2009), philopatry of
time brown bears can lead to the formation of matrilineal assemblages, in which
sexual relatedness is spatially autocorrelated (Støen et al. 2005, Poteaux et al.
2009). The formation of matrilineal assemblages can alter fitness parameters
(Ishikawa et al. 2003, Dalerum et al. 2006), such as reproductive success and survival
(Støen et al. 2005). Støen et al. (2006b) and Ordiz et al. (2008) suggested that soci-
ality in female brown bears may be more pronounced than generally acknowledged.

REPRODUCTIVE PHYSIOLOGY
Reproductive seasonality probably evolved through natural selection to optimize
juvenile survival rates as an adaptation to adverse environmental conditions (Baker
1938, Bronson 1985). Seasons and their climate are signalled by photoperiod (Spady
et al. 2007). Photoperiod, regulates the status of reproductive hormones, which also
can be modified by social factors, metabolic state and nutrition (McMillin et al. 1976,
Palmer et al. 1988, Tsubota et al. 1998, Spady et al. 2007). The variance in photope-
riod over geographical ranges therefore may explain the corresponding variance in
breeding seasonality within a species, such as the brown bear (Fernández-Gil et al.
2006, Spady et al. 2007). The mating season of the brown bear lasts for approxi-
mately 2.5 months, from late spring to early summer (Craighead et al. 1995a, White
brown bears in the Southern Hemisphere show a 6-month shift in mating behaviour
compared with their northern counterparts (Spady et al. 2007). Autumn reproductive
behaviour and copulation have been reported anecdotally in wild brown bears in
coastal British Columbia, Canada (Nevin & Gilbert 2005), Kamchatka, Russia (Vaisfeld
& Chestin 1993) and Hokkaido, Japan (Kohira & Mori 2010).

The oestrous cycle of female brown bears remains poorly understood, and most
studies have been carried out on bears in captivity (Schwarzenberger 2007). Research
on reproductive behaviour in captive female brown bears has shown that concen-
trations of faecal estradiol are elevated during oestrus, and progesterone levels appear to increase after the oestrus period (Mano et al. 2002, Ishikawa et al. 2003, Dehnhard et al. 2006). Observational studies from the wild suggest that oestrus lasts for between 1 and 50 days (Craighead et al. 1995a, Ishikawa et al. 2003).

Female brown bears have delayed implantation (Mano et al. 2002, Schwartz et al. 2003b). The fertilized ova remain dormant in the uterus for about five months, prior to implantation in November–December. The hormone prolactin, which is controlled by photoperiod, is important in reactivating corpora lutea (Spady et al. 2007). Dehnhard et al. (2006) observed a sharp increase in faecal progesterone levels in captive fertilized female brown bears in December, coinciding with the approximate moment of implantation.

Induced ovulation occurs in female American black bears Ursus americanus (Boone et al. 2004) and may occur in polar bears Ursus maritimus (Rosing-Asvid et al. 2002) and brown bears (Hamer & Herrero 1990, Craighead et al. 1995a, McLellan 2005, Bellemain et al. 2006b). The oestrus period of captive unmated female brown bears separated from males lasts longer than that of their mated counterparts, suggesting that copulation may terminate oestrus (Ishikawa et al. 2003). Ishikawa et al. (2003) also described sexual behaviour, such as intra-sexual mounting, presenting and masturbation in captive unmated female brown bears during the breeding season. The variation in duration and timing of oestrous is large, both between females and within females, over years (Pasitschniak-Arts 1993, Craighead et al. 1995a, Spady et al. 2007). This variation, which might be related to the mechanism of induced ovulation, results in some level of reproductive asynchrony (Ims 1990), a prerequisite for the potential of sexual selection (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003).

Because brown bears have delayed implantation, each corpus luteum becomes dormant following ovulation and luteal progesterone secretion stops. This may allow females to re-enter oestrus (Spady et al. 2007). Craighead et al. (1995b) reported seasonal polyoestrous in female brown bears, in which two cycles were separated by four to 18 days of sexual inactivity. Stenhouse et al. (2005) suggested that polyoestry is common in free-living female brown bears, because 51% of the reproducing females that they monitored engaged in more than one male-female association per breeding season. Polyoestrous cycling facilitates the development of different sets of ova, and thereby increases the potential of these to be fertilized by different males (Pasitschniak-Arts 1993, Craighead et al. 1995b, Schwartz et al. 2003b, Spady et al. 2007). Multiple paternity occurs relatively frequently in brown bears (Bellemain et al. 2006b). In Scandinavian populations, in 14.5 and 28% of the litters with ≥2 and ≥3 young, respectively, young were sired by different fathers (Bellemain et al. 2006a, b).

Brown bear females show lactational anoestrus (Dahle & Swenson 2003b, Spady et al. 2007). Females that lose offspring by either death or family break-up can enter oestrus already after 2–7 days (Swenson 2003, McLellan 2005, Bellemain et al. 2006a, Swenson & Haroldson 2008). Pseudo-oestrous also occurs in brown bears (Ishikawa et al. 2003). Pseudopregnancy and spontaneous ovulation have been shown to occur in other bear species, and may occur in the brown bear as well (Mano et al. 2002).

Male brown bears show a circannual rhythm in reproductive behaviour and testis development (White et al. 1998, Spady et al. 2007). The males’ annual reproductive period encompasses the receptive period of female brown bears, lasts for 4–5 months, and varies among individuals (Erickson et al. 1968). Male testis size corre-
lates with seasonal variation in serum testosterone levels and sperm production (Gomendio et al. 2006). Testis mass during the mating season is up to twice that during hibernation in adult male bears (McMillin et al. 1976). Testis size, that is, mass, length and diameter, is also positively correlated with age, body mass and body length (White et al. 1998). Spady et al. (2007) distinguished four phases in the annual testis cycle: (i) quiescence, characterized by no mating or spermatogenesis; (ii) recrudescence, characterized by increasing testis size and the preparation for mating and spermatogenesis; (iii) peak testicular function during the mating season and (iv) regression, when testis function diminishes after the mating season. Testicle mass increases linearly with age, at least until the age of 14.4 years (White et al. 1998).

**LIFE HISTORY**

Brown bears reproduce slowly. They are long lived, reach sexual maturity relatively late, and have prolonged reproductive cycles (Pasitschniak-Arts 1993). Cubs are born during winter denning, between January and March, after a gestation period of approximately 6–8 weeks (Schwartz et al. 2003b). The short in utero developmental phase after delayed implantation is probably a mechanism to preserve female muscle mass and proteins during hibernation, by switching to milk production (Ramsay & Dunbrack 1986, Hissa 1997). Sex ratio at birth usually is assumed to be 50:50. In some populations, however, male-biased sex ratios in newborns have been reported (55–59% males; Craighead et al. 1974, Knight & Eberhardt 1985). This sex bias is assumed to compensate for greater male than female cub mortality, because of the more bold and curious nature of male cubs, which may result in more accidents and predation (Schwartz et al. 2003b). The sex ratio of 1326 newborn brown bears in captivity in North America was unbiased (51% males; Anonymous 1993).

Neonates are highly altricial and weigh between 350g and 500g, depending on litter size and maternal condition (Couturier 1954); paternal care is absent (Dahle & Swenson 2003a). Lactation lasts for 1.5 to 2.5 years, and peaks around midsummer in the first year of life of the cubs (Farley & Robbins 1995, Craighead et al. 1995a).

Reproductive parameters, such as average age of primiparity, mean litter size, mean litter interval, mean age of first weaning (Kovach et al. 2006), and reproductive rate, vary among populations (Ferguson & McLoughlin 2000, Nawaz et al. 2008; Table 1). The earliest ages of primiparity recorded were three years, in Austria (Zedrosser et al. 2004) and Croatia (Frkovic et al. 2001). Average ages of primiparity range from 5.2 to 10.3 years in a highly productive Swedish population and in a high latitude population in Denali National Park, Alaska, respectively (Swenson et al. 2001b, Miller et al. 2003, Zedrosser et al. 2009). Kovach et al. (2006) argue that the mean age of first weaning, though not often reported in the literature, is a more appropriate demographic parameter than mean age of primiparity. Litter sizes typically range from one to three cubs and may be positively correlated with the number of female copulations (Jakubiec 1993, Pasitschniak-Arts 1993, Craighead et al. 1995a, Schwartz et al. 2003b). Litters comprising four cubs are uncommon (Schwartz et al. 2003b); Vaisfeld and Chestin (1993) reported one case of five brown bear cubs in a litter under natural conditions in Karelia, Russia. Litters of up to six cubs have been observed in captivity (Laikre et al. 1996) and under natural conditions (Pazetnov & Pazetnov 2005). Mean inter-birth intervals show considerable variation among populations, depending on offspring survival and environmental and geographical conditions, and range from 2.4 to 5.7 years (Nawaz et al. 2008). Maternal care continues...
Table 1. Reproductive parameters of 34 brown bear populations in North America, Europe and Asia

<table>
<thead>
<tr>
<th>Population</th>
<th>Lat. (°N)</th>
<th>AP</th>
<th>MLS</th>
<th>MLI</th>
<th>RR</th>
<th>AFW</th>
<th>CS</th>
<th>Ref.</th>
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<tr>
<td>Central Sweden</td>
<td>61</td>
<td>5.2</td>
<td>2.3</td>
<td>2.4</td>
<td>0.96</td>
<td>117</td>
<td>0.65–0.83</td>
<td>Sæther et al. (1998)</td>
</tr>
<tr>
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<td>67</td>
<td>5.4</td>
<td>2.4</td>
<td>2.6</td>
<td>0.92</td>
<td>120</td>
<td>0.96</td>
<td>Sæther et al. (1998)</td>
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<td>Croatia</td>
<td>45</td>
<td>2.39</td>
<td></td>
<td></td>
<td></td>
<td>128</td>
<td></td>
<td>Frikovic et al. (2001)</td>
</tr>
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<td>Cantabrian Mountains, Spain</td>
<td>43</td>
<td>5.3</td>
<td>2.3</td>
<td>3.3</td>
<td>0.7</td>
<td></td>
<td></td>
<td>Wiegand et al. (1998)</td>
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<tr>
<td>Deosai National Park, Pakistan</td>
<td>34</td>
<td>8.25</td>
<td>1.33</td>
<td>5.7</td>
<td>0.23</td>
<td>73</td>
<td>0.94</td>
<td>Nawaz et al. (2008)</td>
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<td>Hokkaido, Japan</td>
<td>44</td>
<td>1.8</td>
<td>2.3</td>
<td>3</td>
<td>0.6</td>
<td>103</td>
<td>0.45</td>
<td>Mano et al. (2002), Kohira et al. (2009)</td>
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<td><strong>North America</strong></td>
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<tr>
<td>Anderson Horton Rivers, Canada</td>
<td>69</td>
<td>6</td>
<td>2.27</td>
<td>4.9</td>
<td>0.78*</td>
<td></td>
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<td>Case and Buckland (1998)</td>
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<td>Kugluktuk, Canada</td>
<td>66</td>
<td>8.7</td>
<td>2.26</td>
<td>3.3</td>
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<td>164</td>
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<td>Clarkson and Liepins (1994)</td>
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<td>2</td>
<td>4</td>
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<td>7.8</td>
<td>1.59</td>
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<td>2.22</td>
<td>3</td>
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<td>Wielgus and Bunnell (1995)</td>
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<td>51</td>
<td>6.7</td>
<td>1.8</td>
<td>4.4</td>
<td>0.41</td>
<td></td>
<td>0.91</td>
<td>Garshelis et al. (2005)</td>
</tr>
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<td>2.2</td>
<td>3.1</td>
<td>0.42*</td>
<td>114</td>
<td>0.87</td>
<td>McLoughlin et al. (2000), McLellan (1994)</td>
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<tr>
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<td>53</td>
<td>6</td>
<td>2</td>
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<td></td>
<td>129</td>
<td></td>
<td>McLoughlin et al. (2000), Lefranc et al. (1987)</td>
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<td>1.98</td>
<td>4.1</td>
<td>0.48</td>
<td>117</td>
<td>0.56</td>
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<td>2.17</td>
<td>3.9</td>
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<td>McLoughlin et al. (2000), Case and Buckland (1998)</td>
</tr>
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<td>2.06</td>
<td>5.6</td>
<td>0.37</td>
<td>207</td>
<td>0.34</td>
<td>McLoughlin et al. (2000), Lefranc et al. (1987)</td>
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<td>Kodiak Island, USA</td>
<td>57</td>
<td>6.7</td>
<td>2.23</td>
<td>4.6</td>
<td>0.48</td>
<td>202</td>
<td></td>
<td>McLoughlin et al. (2000), Lefranc et al. (1987)</td>
</tr>
<tr>
<td>Kuskokwim Mountains, USA</td>
<td>63</td>
<td>6.3</td>
<td>1.9</td>
<td>4.5</td>
<td>0.42</td>
<td>170</td>
<td></td>
<td>Van Daele et al. (2001)</td>
</tr>
<tr>
<td>Nelchina Basin, USA</td>
<td>62</td>
<td>5.6</td>
<td>2.1</td>
<td>3.2</td>
<td>0.88*</td>
<td>144</td>
<td></td>
<td>McLoughlin et al. (2000), Lefranc et al. (1987)</td>
</tr>
<tr>
<td>Black Lake, USA</td>
<td>56</td>
<td>6.3</td>
<td>2.57</td>
<td>3</td>
<td>0.86</td>
<td>256</td>
<td>0.57</td>
<td>Lefranc et al. (1987)</td>
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<tr>
<td>McNeil River, USA</td>
<td>58</td>
<td>6.8</td>
<td>2.24</td>
<td>3.9</td>
<td>0.57</td>
<td>160</td>
<td></td>
<td>Sellers and Miller (1999)</td>
</tr>
<tr>
<td>Admiralty Island, USA</td>
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<td>8</td>
<td>1.84</td>
<td>3.9</td>
<td>0.47</td>
<td>168</td>
<td></td>
<td>McLoughlin et al. (2000), McLellan (1994), Lefranc et al. (1987)</td>
</tr>
<tr>
<td>Alaska Range, USA</td>
<td>65</td>
<td>6.2</td>
<td>2.2</td>
<td>4</td>
<td>0.51*</td>
<td>154</td>
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<tr>
<td>Southeastern USA</td>
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<td>7.2</td>
<td>2</td>
<td>2.6</td>
<td>0.77</td>
<td></td>
<td>0.58</td>
<td>Kovach et al. (2006)</td>
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<td>Cabinet-Yaak, USA</td>
<td>48</td>
<td>6.6</td>
<td>2.1</td>
<td>3</td>
<td>0.7</td>
<td>125</td>
<td>0.86</td>
<td>McLellan (1994), Aune et al. (1994)</td>
</tr>
<tr>
<td>Swan Mountains, USA</td>
<td>48</td>
<td>6.6</td>
<td>1.6</td>
<td>3</td>
<td>0.53</td>
<td>79</td>
<td>0.79</td>
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<td>East Front, Montana, USA</td>
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<td>6</td>
<td>2.14</td>
<td>2.6</td>
<td>0.82</td>
<td>125</td>
<td>0.86</td>
<td>McNeil River, USA</td>
</tr>
<tr>
<td>Greater Yellowstone Ecosystem 1983–2002, USA</td>
<td>44</td>
<td>5.81</td>
<td>2</td>
<td>2.78</td>
<td>0.64*</td>
<td>152</td>
<td>0.74</td>
<td>Schwartz et al. (2006)</td>
</tr>
<tr>
<td>Yellowstone National Park 1959–1970, USA</td>
<td>44</td>
<td>5.7</td>
<td>2.2</td>
<td>3.2</td>
<td>0.69</td>
<td>152</td>
<td>0.74</td>
<td>Craighead et al. (1974)</td>
</tr>
<tr>
<td>Yellowstone National Park 1975–1989, USA</td>
<td>44</td>
<td>5.7</td>
<td>1.9</td>
<td>2.6</td>
<td>0.73</td>
<td>134</td>
<td>0.85</td>
<td>Stringham (1990)</td>
</tr>
</tbody>
</table>

Lat. (°N), latitude of the study area in degrees North; AP, age of average female primiparity (years); MLS, mean litter size; MLI, mean litter interval (years); RR, reproductive rate (MLS/MLI); AFW, average female body mass (kg; corrected according to McLellan 1994); CS, annual cub survival probability.

*RR was not calculated as MLS/MLI, but taken from the literature. Empty cells indicate no information was available in the literature.
for, on average, between 1.4 and 3.5 years in most brown bear populations (McLellan 1994), but was reported to continue for up to 4.5 years in a high-alpine low-production population in South Asia (Nawaz et al. 2008). Reproductive rate, that is, the average number of offspring raised per adult female per year, varies from 0.23 to 0.96 in a high-altitude population in Deosai National Park in Pakistan and a Scandinavian population, respectively (Sæther et al. 1998, Swenson et al. 2001b, Swenson et al. 2007, Nawaz et al. 2008).

Female reproductive maturation and senescence was modelled by Schwartz et al. (2003a), based on the litter production of 4756 radio-collared female brown bears from 20 study areas. Inflection points in fertility occurred at the ages of four to five, and 28–29 years. Females in their prime, between nine and 20 years old, were estimated to produce most offspring (Schwartz et al. 2003a). No female older than 29 years gave birth (Van Daele et al. 2001), and the oldest observed free-ranging female was 34 years old. The oldest captive female brown bear was 42 years old (Schwartz et al. 2003a). Thus, post-reproductive survival is limited. Post-weaning maternal care is advantageous for the offspring in brown bears (Dahle & Swenson 2003a), but is not necessary for their survival (Swenson et al. 1998); therefore, according to the senescence theory (Williams 1957), there is no selective advantage of long-term survival after losing reproductive ability (Schwartz et al. 2003a).

The average age of reaching sexual maturity in male brown bears was estimated to be 5.5 years in continental North America (White et al. 1998). The youngest males observed to be reproductively successful were 3.5 years old in a Swedish population (Zedrosser et al. 2007a). Age at sexual maturity in male brown bears is related to nutritional factors and varies between ecoregions (White et al. 1998, Schwartz et al. 2003b). Older and larger males generally have higher annual reproductive success (Zedrosser et al. 2007a) than younger, smaller males. Size and age are correlated with dominance and experience, and probably reflect genetic superiority (Trivers 1972, Shuster & Wade 2003, Isaac 2005, Bellemain et al. 2006b, Zedrosser et al. 2007a). The oldest males observed in captivity and in the wild were 50 and 30 years old, respectively, but no male older than 27 years has been documented to be reproductively successful (Schwartz et al. 2003a, Zedrosser et al. 2007a).

Cub mortality in brown bears varies among populations and is typically higher than mortality in other age classes. Kovach et al. (2006) reported annual cub mortality in southwestern Alaska to average 2.8%, whereas, in Denali National Park in Alaska, annual cub mortality can reach 66% (Miller et al. 2003). Mano et al. (2002) report neonate mortality and mortality before the breeding season to be low. In two Swedish populations, primiparous females were more likely to lose cubs than multiparous females (Zedrosser et al. 2009). Infanticide is considered to be a major cause of death among brown bear cubs, at least in some populations. Resource competition, exploitation, social pathology and male reproductive strategy (Hrdy 1979) may explain infanticide in brown bears (Swenson et al. 1997, McLellan 2005, Bellemain et al. 2006a, b, Fernández-Gil et al. 2010). Most cub mortality occurs during the breeding season, and about 80% of conspecific killing is carried out by adult males (Schwartz et al. 2003b). Females in poor body condition may abandon their dependent offspring as an adaptive maternal strategy. This allows them to re-enter oestrus during the ongoing breeding season, and produce offspring with potentially higher survival rates (Tait 1980).
REPRODUCTIVE BEHAVIOUR

In brown bears, reproductive individuals of both sexes mate a variable number of times with a variable number of partners during a given mating season (Pasitschniak-Arts 1993). Females typically mate with three to four males during a breeding season, although females have been observed to mate with up to 20 partners (Craighead et al. 1995a). Males show more variation, and mate with between one and eight females per breeding season, although many males do not obtain any matings (Craighead et al. 1995a). Aggression and sexual harassment occur rarely within a reproducing pair (Craighead et al. 1995a, Fernández-Gil et al. 2006). Pairs typically travel together while the male monitors the female’s oestrous status, which is believed to be signalled by pheromones, by smelling her genitalia (Clevenger et al. 1992, Craighead et al. 1995a). Pairs tend to copulate several times, and successful copulations last from less than one minute to one hour (Clevenger et al. 1992, Craighead et al. 1995a, Fernández-Gil et al. 2006). Male vigour, female receptivity and competing males may influence copulation duration (Craighead et al. 1995a, Schwartz et al. 2003b). Consorting lasts from less than a day to several weeks (Herrero & Hamer 1977, Craighead et al. 1995a, Swenson 2003). Reproductive associations are generally comprised of one male and one female bear, but associations with two or more females per male, or more than two males per female, are not uncommon (Sparrowe 1968, Stenhouse et al. 2005, Fernández-Gil et al. 2006). Fernández-Gil (pers. com.) reported an association comprised of two adult males and three adult females in the Cantabrian Mountains, Spain. Home range sizes of reproductive individuals tend to increase during the breeding season; both sexes roam to mate (Glenn et al. 1976, Swenson et al. 2000, Dahle & Swenson 2003c, Stenhouse et al. 2005), and track each other, probably by using scent cues (Green & Mattson 2003, Dahle & Swenson 2003c).

The use of specific mating areas of four to 125 ha has been described in a small brown bear population in Spain (Fernández-Gil et al. 2006). Some of these areas have been used for up to five consecutive years, and up to seven different adult brown bears have been observed there in a 24-hour period (Fernández-Gil et al. 2006). Solitary species in low-density populations can show reduced reproductive success as a consequence of difficulties in finding mates (Stephens et al. 1999), by the Allee effect (Allee et al. 1949). Fernández-Gil et al. (2006) suggest that specific mating areas facilitate meeting and reproducing, and thereby counteract aspects of the Allee effect. Repeated use of mating areas by brown bears, albeit over shorter time periods, has also been observed in the Rocky Mountains, Canada (Hamer & Herrero 1990).

Social hierarchies can develop in highly clustered bear populations at food congregations (e.g. the former Yellowstone Trout and Rabbit Creek garbage dumps in Yellowstone National Park, USA), and here, male bears may monopolize reproductive females to some extent by displacing subordinate males from breeding attempts (Stonorov & Stokes 1972, Craighead et al. 1995a). Craighead et al. (1995a) suggested that male dominance hierarchies at these congregations depend on size and mass, but also on aggressiveness and willingness to fight. Craighead et al. (1995a) distinguished four hierarchy classes in the Yellowstone Ecosystem food congregations, where up to 80 bears congregated at a time: (i) alpha male, (ii) beta males, (iii) contenders and (iv) non-contenders; and showed that the dominance hierarchy was highly variable and unpredictable from year to year. No relationship was found between frequency of copulation and dominance status, however. Subordinate
males obtained copulations, but predominantly with females late in the oestrus cycle, or when dominant individuals were preoccupied in aggressive interactions (Craighead et al. 1995a).

Long-term sequestering of single females by single males has been observed on mountain ridges in the Rocky Mountains (Hamer & Herrero 1990, Brady & Hamer 1992). Similar behaviour has been documented in low-density populations of polar bears, where males sequestered females on cliffs, in small bays or on small island plateaus (Ramsay & Stirling 1986, Zeyl et al. 2009). Hamer and Herrero (1990) and Herrero and Hamer (1977) suggested that this behaviour assures paternity for the sequestering male, as long as he sequesters the female during her entire oestrus and mates successfully with her.

Females with dependent offspring have been reported to avoid prime bear habitat both spatially and temporally, and even select for areas with relatively high human presence (McLellan 1994, Wielgus & Bunnell 1995, Craighead et al. 1995a, Swenson 2003, Kaczensky et al. 2006, Rode et al. 2006). However, Fernández-Gil et al. (2010) suggested that habitat fragmentation and human disturbance could influence the ability of females with cubs to avoid adult males and sexually selected infanticide. Habitat segregation as a female anti-infanticide strategy also has been reported for a range of other species, mainly primates, rodents and carnivores (Hrdy 1979, Ebensperger 1998).

MALE–MALE COMPETITION

Trivers (1972) distinguished three main types of male–male competition. Besides direct precopulatory contest, competition can continue within the female’s reproductive tract (sperm competition), and after females have given birth (by sexually selected infanticide).

Male-male competition for access to receptive females based on the outcomes of aggressive physical encounters is referred to as contest competition, and is considered a driving force in the evolution of sexual dimorphism and polygynous mating systems (Strier 2000, Radespiel et al. 2001). Aggressive behaviour and fights form the basis of loose and dynamic dominance hierarchies in male brown bears (Sparrowe 1968, Craighead et al. 1995a), and antagonistic encounters vary greatly in duration, intensity, and final outcome (Craighead et al. 1995a). Individuals can be severely injured during fights (Craighead et al. 1995a, Fernández-Gil pers. com.), and the inflicted wounds can be lethal, especially for smaller individuals (Craighead et al. 1995a). Body size, age, experience, condition and aggression (and signs of this, such as scars and wounds) are considered to be determinants of male dominance status (Craighead et al. 1995a, Fagen & Fagen 1996, Zedrosser et al. 2007a). Craighead et al. (1995a) found that all dominant males in Yellowstone National Park ranged between the ages of 12 and 17 years. Zedrosser et al. (2007a) found that the annual reproductive success of male Scandinavian brown bears was positively correlated with both age and body size. However, the importance of both variables varied between populations and was related to population density and composition: body size was apparently most important in populations with a highly male-biased operational sex ratio. Also, outbred males appeared to have a relatively high annual reproductive success (Zedrosser et al. 2007a), which is consistent with the mate choice theory based on heterozygosity (Brown 1997). Scramble competition, the competitive searching for mates, may be a complementary or alternative male mating strategy to
contest competition when receptive females are spaced widely and unpredictably (Strier 2000, Radespiel et al. 2001).

Sperm competition has been documented in a range of species with mating systems characterized by female promiscuity, and is considered a strong force in shaping sexual selection (Trivers 1972, Dixson & Anderson 2004, Gomendio et al. 2006). Conclusive evidence of the occurrence of sperm competition does not exist in ursids, but it may occur in brown bears (Dahle and Swenson 2003c, Bellemain et al. 2006b, Zedrosser et al. 2007a), American black bears (Schenk & Kovacs 1995) and polar bears (Dyck et al. 2004).

Sexually selected infanticide is an adaptive male mating strategy (Darwin 1871) in which males kill the unrelated, dependent offspring of conspecifics, thereby shortening the victimized female’s time interval to the next oestrus (Hrdy 1979). This offers the perpetrator a higher probability of siring offspring, either directly by mating with the victimized female after she re-enters oestrus (Trivers 1972, Hrdy 1979, Janson & Van Schaik 2000, Swenson 2003), or indirectly by reducing intra-male competition through lowering the typically male-biased operational sex ratio (McLellan 2005). Slowly reproducing species with long maternal care are especially prone to this type of behaviour (Van Schaik 2000). Sexually selected infanticide may be a population-regulating mechanism in some brown bear populations (Ordiz et al. 2008, Fernández-Gil et al. 2010), and can be facilitated by the removal of dominant males and by the subsequent influx of immigrant males (Swenson et al. 1997). The importance of sexually selected infanticide as a population regulatory factor is dynamic, and can vary within a species (Hrdy 1979, Janson & Van Schaik 2000, Swenson 2003).

Sexually selected infanticide in the brown bear has been documented in two Scandinavian (Swenson et al. 1997, Bellemain et al. 2006a) and one Spanish population (Fernández-Gil et al. 2010), and has been suggested to occur in populations in British Columbia, Canada and in the Central Pyrenees of France and Spain (Wielgus et al. 2001, Chapron et al. 2009). Support for the sexually selected infanticide hypothesis has been reported for other ursids as well, that is, the American black bear (Wielgus & Bunnell 1995) and the polar bear (Taylor et al. 1985). Many researchers do not accept that infanticide in bears is sexually selected (McLellan 2005, Garshelis 2009), but ascribe infanticide to reducing prospective and immediate resource competition, or to intra-specific predation (Craighead et al. 1995a, Derocher & Wiig 1999, Miller et al. 2003, Garshelis 2009). McLellan (2005) argued that sexually selected infanticide did not occur in brown bears, but that, if it were to occur, it should follow his proposed ‘mate recognition hypothesis’ of sexually selected infanticide. This states that all males, irrespective of age, should kill conspecific offspring that they have not sired, given the opportunity (McLellan 2005).

Because female lifetime reproductive success can be reduced through infanticide, females have evolved counterstrategies against this behaviour (Hrdy 1979, Swenson 2003). Ebensperger (1998) summarized six female counterstrategies to infanticide: (i) pregnancy termination, (ii) maternal aggression, (iii) group defence, (iv) avoidance of infanticidal individuals, both in space and in time, (v) promiscuity and (vi) territoriality. Of these strategies, ii–v have been reported in brown bears [e.g. (ii) McLellan 2005, Fernández-Gil et al. 2010; (iii) Craighead et al. 1995a; (iv) Dahle and Swenson 2003c, Ben-David et al. 2004, Rode et al. 2006 and (v) Craighead et al. 1995b, Swenson et al. 2001b, Bellemain et al. 2006a, b].
FEMALE MATE CHOICE

Female brown bears are promiscuous, and control mating acts and partners to some extent (Craighead et al. 1995a, Fernández-Gil et al. 2006). Females have been observed initiating mating on some occasions (Fernández-Gil et al. 2006), and both sexes show roam-to-mate behaviour (Dahle & Swenson 2003c). McLellan (2005) suggested that females signal their receptivity to attract the best or most dominant males. In most species, females tend to be the more selective sex in relation to mate choice, because of their higher investment in gametes (Darwin 1871, Clutton-Brock 1989). To optimize reproductive success, females should therefore select for high-quality males. Age and morphological traits, such as body size, weaponry and signs of aggression or willingness to fight, are considered to reflect male quality (Andersson 1994). The apparent success of larger, older or more aggressive male brown bears might be explained, in part, by female choice for these traits as signs of genetic quality.

Infanticide, in whatever form, is common in brown bears (Craighead et al. 1995a, Swenson et al. 1997, Garshelis 2009), and promiscuity by females is generally acknowledged to be an aid in countering infanticide by males through paternity confusion, either directly by mate recognition or indirectly by multiple paternity (Ebensperger 1998). Bellemain et al. (2006b) suggested a mating strategy dilemma for female brown bears in a population exhibiting sexually selected infanticide, where females have to choose between mating with the phenotypically best male, or with nearby males that they are likely to encounter in the future (suggesting promiscuity as a strategy to counter infanticide by males). Bellemain et al. (2006b) found that the oldest, largest and most heterozygous of all nearby males had the highest chance of becoming the father of the female’s next offspring. Promiscuous mating by females has potential benefits such as the assurance of fertilization (Wilson et al. 1997), sperm competition (Stockley & Purvis 1993), and selection of the most compatible partner and his sperm (Gray 1997).

Støen et al. (2006b) and Ordiz et al. (2008) found that age at primiparity was affected by social factors in a matrilinearly organized Scandinavian brown bear population: females that were not living in a matrilineal assemblage were younger at primiparity. In addition, females were reproductively suppressed when in the vicinity (home range centroids <10km apart) of another female with cubs of the year (Ordiz et al. 2008). This results in a spatially and temporally oscillating female reproductive asynchrony, thereby offering higher mate availability to females (Ims 1990, Ordiz et al. 2008).

MATING SYSTEM CLASSIFICATION

The classical works of Emlen and Oring (1977) and Clutton-Brock (1989) considered mating system research in an ecological context of spatiotemporally distributed resources, including receptive females, and the potential of mate detection, monopolization and reproduction (Apollonio et al. 2000). Even with the lack of agreement on terminology and classification, the frameworks are generally accepted and are often used as a starting point in mating system studies (Andersson 1994, Shuster & Wade 2003). Shuster and Wade (2003) provided a key to identify the detailed mating system of a species, based on the spatiotemporal distribution of sexually receptive females, the variance in reproductive success within and between both sexes as a measure of the strength of sexual selection, and a number of
evolutionary traits, such as sperm competition, female copying, sexual dimorphism, paternal care, sexual conflicts and potential alternative mating strategies. The key requires preclassification in one of 12 major classes of mating system. These are: sedentary pairs, iterant pairs, mass mating, polygamy, male dominance, social pairs, mating swarms, leks, feeding sites, nesting sites with female care, nesting sites with male care and polyandrogyny (Shuster & Wade 2003).

Various authors have classified the mating system of the brown bear differently, that is, as polygamy (Pasitschniak-Arts 1993, Zedrosser et al. 2009), promiscuity (Swenson et al. 2001b, Schwartz et al. 2003b, Bellemain et al. 2006a, b), scramble competition polygamy (Dahle & Swenson 2003c, McLellan 2005) and contest competition polygamy (Schwartz et al. 2003b). The variation in descriptions of the mating system may have been caused by differences in the spatiotemporal availability of receptive mates within and among populations (Emlen & Oring 1977, Herrero & Hamer 1977, Clutton-Brock 1989), by plasticity in the sense of Shuster and Wade (2003), that is, alternative mating strategies, or by the lack of consistent terminology, as pointed out by Andersson (1994) and Shuster and Wade (2003).

Based on the framework of Emlen and Oring (1977), the mating system of the brown bear can be classified as polygynous or polyandrous, because individuals of both sexes frequently gain access to multiple mates (Table 2). Using the classification system of Clutton-Brock (1989), both sexes can be considered promiscuous in brown bears, where promiscuity is defined as males attempting to mate with any receptive female, and females mating with several males in successive breeding attempts (Table 2). Clutton-Brock (1989) associated mating systems with four main forms of mate guarding: (i) the defence of individual females during part or all of their period of receptivity; (ii) the defence of feeding territories that overlap the ranges of individual females or groups of females partly or completely; (iii) the defence of particular groups of females, either during the mating season or throughout the year without defence of any fixed area and (iv) the defence of dispersed or clustered mating territories within a portion of females’ ranges (Clutton-Brock 1989). Only mate guarding form (i) occurs in the brown bear. It encompasses the ‘sequestering’ strategy and the ‘roving male’ strategy, in which females range widely and are solitarily and unpredictably distributed at low population densities, and males range widely in search of oestrous females, consorting with them and defending them against other males (e.g. Dahle & Swenson 2003a, b, c, McLellan 2005). Mate guarding form (i) also is applicable to the reproductive behaviour that bears exhibit around clumped food resources, such as spawning salmon (e.g. Sellers & Aumiller 1994) or garbage dumps (e.g. Craighead et al. 1995a). Around clumped food resources, males develop a dominance hierarchy (Craighead et al. 1995a), which may be used to obtain access to receptive females also visiting these food resources. Subdominant males may gain access to receptive females through a satellite strategy (Table 2).

Shuster and Wade (2003) defined a given mating system as polygamous if both sexes had variable numbers of mates, and if male and female mating success was approximately equal; they defined a mating system as polygynandrous if male mating success was more variable than female mating success. Both definitions seem to apply to the mating system of the brown bear (Table 2). Evidence from North America (Craighead et al. 1995a) and Scandinavia (Zedrosser et al. 2007a), however, suggests that variation in reproductive success in males is more pronounced than in females. This implies that, according to Shuster and Wade (2003), polygynandry best...
Table 2. Mating system classification of the brown bear according to the frameworks of Emlen and Oring (1977), Clutton-Brock (1989) and Shuster and Wade (2003)

<table>
<thead>
<tr>
<th>EO</th>
<th>CB</th>
<th>SW</th>
<th>Interpretation</th>
<th>Example populations</th>
</tr>
</thead>
</table>
| Polygyny/  | Polygamy/           | Polygamy/           | Highly mobile males during the breeding season, males search for and attempt to mate with several females. Both sexes may mate a variable number of times with a variable number of mates during a breeding season (Dahle and Swenson 2003c, Bellemain et al. 2006a, Swenson et al. 2000, Craighead et al. 1995b, Green and Mattson 2003, Stonorov and Stokes 1972). Males may also sequester, defend and attempt to mate with individual receptive females. This may occur sequentially during a breeding season. This sequestering may be at the expense of females’ reproductive interests and feeding opportunities (Brady and Hamer 1992, Hamer and Herrero 1990, Herrero and Hamer 1977). | Waterton Lakes National Park, Canada (Brady and Hamer 1992)  
Banff National Park, Canada (Hamer and Herrero 1990, Herrero and Hamer 1977)  
North and South Sweden (Dahle and Swenson 2003c, Bellemain et al. 2006a, Swenson et al. 2000)  
Greater Yellowstone Ecosystem, USA, after garbage dump closures, USA (Craighead et al. 1995b, Green and Mattson 2003)  
Alaska, USA (Stonorov and Stokes 1972) |
| polyandry*  | Polygamy/           | Polygamy/           | Both sexes may mate a variable number of times with a variable number of mates during a breeding season. Mating areas may develop, i.e. groups, with >1 male, when population densities are very low (Herrero and Hamer 1977). | Cantabrian Mountains, Spain (Fernández-Gil et al. 2006)  
Banff National Park, Canada (Herrero and Hamer 1977) |
| [promiscuity,  | Polygamy/           | Polygamy/           | In populations where individuals of both sexes aggregate at food congregations (Craighead et al. 1995b, Craighead et al. 1974), dominance hierarchies may develop. Subdominant males may gain access to receptive females through a satellite strategy. | Greater Yellowstone Ecosystem, USA, before garbage dump closures (1968–71; Craighead et al. 1995b, Craighead et al. 1974). |
| polygamy]   | polygamy           | polygamy (possible |                                                                        |                                                    |
|             |           | convergence to leks)|                                                                        |                                                    |
|             |           | [contest competition] |                                                                        |                                                    |
| Polygamy/   | Dominance   | Male dominance      |                                                                 |                                                    |
| Polygamy/   | polygamy/   | male dominance      |                                                                 |                                                    |
| Polygamy/   | polygamy/   | Male dominance      |                                                                 |                                                    |
| Polygamy/   | polygamy/   | Male dominance      |                                                                 |                                                    |
| Polygamy/   | polygamy/   | Male dominance      |                                                                 |                                                    |

EO, Emlen and Oring; CB, Clutton-Brock; SW, Shuster and Wade. ‘Main’ and ‘Detailed’ represent the main and detailed mating system classes according to SW. For the classification according to Shuster and Wade (2003), we assumed that reproductive success in both sexes differed between individuals, and both yes/no options of sperm competition and female copying were considered.

*Includes female defence polygyny. **Mate guarding form (i) implies guarding individual females during their receptive period. ***Polygamy is, according to Shuster and Wade (2003), characterized by plasticity, and thereby includes both guarding and roving male mating strategies. ‘Possible convergence to leks’ here implies that durable mating areas may develop, and not classical leks in the strict sense of the term. Alternative terminology in the literature is indicated within square brackets [ ].
describes the mating system of the brown bear. Based on the identification key by Shuster and Wade (2003), the mating system of the brown bear can be described as male dominance (dominance polygynandry), polygamy, cursorial polygyny or polygamy, or as polygamy with possible convergence to leks (not classical leks, but mating areas; Shuster & Wade 2003; Table 2). There is no evidence of bears using leks in the same way as black grouse *Tetrao tetrix* (Alatalo et al. 1991) or fallow deer *Dama dama* (Apollonio et al. 1992), that is, (i) males display in locations without resources required by females, (ii) the locations of leks may shift between years and (iii) females frequent leks for mating purposes only and leave afterwards to raise offspring on their own (Shuster & Wade 2003). However, there is evidence from Europe and North America that bears sometimes use mating areas (Herrero & Hamer 1977, Hamer & Herrero 1990, Fernández-Gil et al. 2006).

In summary, variation in reproductive behaviour of the brown bear is related to the spatiotemporal clustering of individuals, as in other species (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003). Brown bears may aggregate during the breeding season at abundant and predictable food resources (e.g. Craighead et al. 1995a), or from a reproductive perspective, perhaps to counter difficulties in finding mates (e.g. Fernández-Gil et al. 2006). In populations that do not aggregate during the breeding season, the strategies of sequestering and defending a few females (e.g. Herrero & Hamer 1977), or searching out and attempting to mate with several receptive females (e.g. Dahle & Swenson 2003c), might be chosen by individual males depending on their dominance level and personality (Craighead et al. 1995a, Fagen & Fagen 1996), and on the population density, which may affect male black bear mating strategies (Costello et al. 2009).

The spatiotemporal distribution of receptive females is one of the most important factors shaping the mating system of a species (Emlen & Oring 1977, Clutton-Brock 1989, Shuster & Wade 2003). In species without paternal care, such as the brown bear, the spatiotemporal distribution of the availability of food is probably the most important factor determining the size and spacing of female home ranges (Clutton-Brock & Harvey 1978). Resources are probably too dispersed, and home ranges too large, to be actively defended by either female or male brown bears. Therefore, the benefits of territoriality, such as resource reliability (Waser & Homewood 1979), are probably diminished in brown bears. Because paternal care is absent, males may increase their reproductive success, that is, the number of offspring they produce, by attempting to mate and reproduce with several females. The operational sex ratio in the brown bear is, at least in unhunted populations, heavily male biased, due to long inter-litter intervals (Pasitschniak-Arts 1993), asynchrony in female oestrous cycling (Craighead et al. 1995a, Spady et al. 2007) and female-induced reproductive suppression (Ordiz et al. 2008). A high potential for sexual selection is expected in species with a polygamous mating system and a male-biased operational sex ratio (Emlen & Oring 1977, Shuster & Wade 2003), and thus in the brown bear. This is reflected in the large size dimorphism between male and female brown bears, probably as a result of intense male-male competition for receptive females.

CONCLUSIONS
The commonality among the mating system classifications applied to the brown bear is that individuals may mate a variable number of times with a variable
number of mates, and are thus polygamous in the broadest sense of the term. We therefore suggest that the brown bear’s mating system should generally be classed as ‘polygamous’, but stress the need for research on the brown bear’s reproductive biology at smaller spatial scales (e.g. at the population level). Within a polygamous mating system, at the species level, individual brown bears seem to show plasticity regarding mating strategies, based on geographical and ecosystem characteristics, as well as individual and sex-specific behaviour. Most classification frameworks focus mainly on male reproductive behaviour and strategies, because males generally show more variation in reproductive success than females. This approach might underestimate the role of females in shaping the mating system of a species (Reynolds 1996).

Many aspects of brown bear reproductive biology remain poorly understood. From a physiological perspective, these aspects include sperm competition, female reproductive cycles and hormone status, and the roles of olfaction in reproduction and kin recognition. These aspects affect aspects of reproductive behaviour, including sexually selected infanticide, mate selection and male mating strategies, which need further attention.

Brown bear populations worldwide are influenced by humans, through hunting, recreational activities, habitat degradation, etc. (Swenson 1999, Weisberg & Bugmann 2003, Bischof & Zedrosser 2009). These human influences can have direct demographical effects, which are generally known or acknowledged (e.g. hunting). In addition, indirect demographic effects may occur (Anthony & Blumstein 2000), that is, those that affect population growth rates, because of an altered population structure (Bischof et al. 2009), as well as evolutionary and habitat effects (Allendorf & Hard 2009). Human impacts on the reproductive behaviour and mating system of the brown bear remain unclear, and may differ among populations. This is illustrated by the following example: removing brown bear males from some populations in British Columbia and Alberta, Canada and Montana and Alaska, United States, appeared to have no effect, or even a positive effect, on cub survival and infanticide was not considered to be a major cause of cub mortality (Miller et al. 2003, McLellan 2005). The opposite appears to be true in a population around Kananaskis, Alberta and in two Scandinavian populations, where the removal of adult males disrupted an established social structure by provoking an influx of potentially infanticidal, immigrant, males, thereby lowering cub survival through sexually selected infanticide (Swenson et al. 1997, Swenson 1999, Wielgus et al. 2001, Bellemain et al. 2006a, b).

Human impacts may have contributed to some of the reported variation in the mating behaviour of the brown bear. Alteration of the social structure of a population, and potential effects on the population’s reproductive parameters, should be considered when planning reintroduction programmes, defining hunting quotas and their selectivity, and instigating other management measures, such as the translocation of nuisance individuals. To understand more fully the plasticity of the mating system of the brown bear, research is needed at local and regional levels.

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Litter loss triggers estrus in a nonsocial seasonal breeder

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Abstract
Sexually selected infanticide (SSI) is a male reproductive strategy in which (i) males kill unrelated conspecific offspring, (ii) offspring loss triggers estrus in the victimized mother, and (iii) the perpetrator has a high probability to sire the victimized mothers’ subsequent litter. SSI is almost exclusively documented in social species and is suggested to be rare among seasonal breeders. We evaluated prediction (ii) in a nonsocial seasonal breeder with lactational anestrus and strong evidence for SSI (prediction i and iii), the brown bear. We hypothesized that females become receptive within <7 days after litter loss and shift from the elusive lifestyle of females with cubs to the roam-to-mate behavior of receptive females. We used movement rates of GPS-marked females and a long-term demographic dataset to evaluate females’ reproductive fate after litter loss. Females with cubs moved less than receptive females and the probability of litter loss increased with movement rate. Movement patterns from receptive females and females after litter loss were undistinguishable 1-2 days after the litter loss and 92% of the females experiencing litter loss gave birth the subsequent birthing season. This suggests that SSI is advantageous also in seasonal breeders.

Key words: lactational anestrus, sexual selection, sexually selected infanticide, reproductive strategy, reproductive fate, Ursus arctos
Introduction

Reproductive strategies have evolved through natural and sexual selection as adaptations to optimize lifetime reproductive success in a certain environmental setting (Pianka, 1976; Bronson, 1985). These adaptations can be physiological (e.g., estrus cycling, the mechanism of implantation or ovulation), morphological (e.g., sexual ornaments, body size) and behavioral (e.g., contest competition for mates, multimale mating), and can vary within and between the sexes (Gross, 1996). Ultimately, a species’ suite of reproductive strategies determines its mating system (Clutton-Brock, 1989; Shuster and Wade, 2003).

Lactation is a universal mammalian attribute (Millar, 1977) and restricts parental care in mammals predominantly to females (Shuster and Wade, 2003). Because lactation is energetically very costly and is of crucial importance for offspring fitness, strong selective pressures act upon characteristics of lactation and associated reproductive traits (Millar, 1977; Schulz and Bowen, 2005). In many species, mammary stimulation inhibits estrus through the production of hormones, such as prolactine and oxytocins (i.e., lactational anestrus) (Kann and Martinet, 1975; Asa, 2012), and females are expected to resume breeding activity rapidly after mammary stimulation terminates to maximize their reproductive success (Sommer, 2000). This is especially true in seasonal breeders after litter loss during the mating season (Weir and Rowlands, 1973; Swenson and Haroldson, 2008). Wolff and Macdonald (2004) show litter loss-induced estrus cycling in 106 (80%) of 133 species of mammals belonging to 33 families and 9 orders.

Infanticide can be a male reproductive strategy (Darwin, 1871), i.e. sexually selected infanticide (SSI), provided that three conditions are fulfilled (Hrdy, 1979). First, an infanticidal male should only kill unrelated offspring. Second, the infanticide should trigger estrus in the victimized mother and shorten her interlitter interval. Third, the infanticidal male should have a high probability of siring the victimized females’ subsequent litter (Trivers, 1972; Hrdy, 1979). Species vulnerable to SSI are expected to have a longer lactation than gestation period, and exhibit lactational anestrus (van Schaik, 2000). Evidence for SSI is extremely difficult to document in the field, especially for nonsocial species with an elusive lifestyle, and SSI is almost exclusively documented in social species (Bellemain et al., 2006). Mathematical modeling suggests
that a small time lag between litter loss and the next conception can make infanticide untenable as a male reproductive strategy (Hrdy and Hausfater, 1984). Therefore, SSI has been suggested to be rare among seasonal breeders or under conditions that prevent immediate return to breeding conditions after litter loss (Hausfater, 1984; Hausfater and Hrdy, 1984; Hrdy and Hausfater, 1984). However, suggestive evidence for SSI has also been provided for seasonal breeders, such as red deer (Cervus elaphus) (Bartos and Madlafousek, 1994), Japanese macaques (Macaca fuscata) (Soltis et al., 2000), white-throated round-eared bats (Lophostoma silviculum) (Knörnschild et al., 2011), and brown bears (Ursus arctos) (Swenson et al., 1997).

The brown bear is a large nonsocial carnivore with a polygamous mating system, lactational anestrus, and a breeding season that lasts from late spring to early summer (Steyaert et al., 2012). Infanticide in the brown bear is common (Craighead et al., 1995). There is evidence for the SSI hypothesis (Swenson et al., 1997; Swenson, 2003; Bellemain et al., 2006), albeit contested (Miller, 1990; Miller et al., 2003; McLellan, 2005). Bellemain et al. (Bellemain et al., 2006) found genetic evidence for two requirements of the SSI hypothesis, i.e., that males did not kill their own progeny and that presumed perpetrators had a high probability of siring the victimized mother’s next litter. The mechanism explaining the second prediction (i.e., that females should enter estrus after litter loss) remains unclear for the brown bear specifically, and for seasonal breeders generally.

Here, we evaluate patterns of reproductive behavior in relation to the SSI hypothesis for a nonsocial seasonal breeder, using the brown bear as a model species. We hypothesize that after litter loss during the mating season, females shift to mating behavior within a few days (< 7). Because receptive females typically roam for mates, and females with cubs-of-the-year (hereafter females/cubs) are expected to live secretively to minimize the risk for infanticide (Dahle and Swenson, 2003), we predict that (i) females/cubs move less than receptive females during the mating season. Because a secretive lifestyle should be favored by females/cubs to avoid infanticide (Ebensperger, 1998; Dahle and Swenson, 2003), we predict (ii) a positive relationship between movement of females/cubs and litter loss. Because we expect that females enter estrus rapidly after litter loss during the mating season and roam to acquire mates,
we predict (iii) that movement patterns of receptive females and females that experience litter loss rapidly (a few days) become undistinguishable after the litter loss event.

**Methods**

*Study area and species*

The study was conducted in the Dalarna and Gavleborg counties in south-central Sweden (61°N, 15°E). The area is covered with intensively managed boreal forest (>80%, mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)), bogs, and lakes. Refer to Martin et al. (Martin et al., 2010) for a detailed study area description.

The brown bear is a nonsocial, size-dimorphic large carnivore with a polygamous mating system (Steyaert et al., 2012) in late spring and early summer (Spady et al., 2007). Males and receptive females expand their home ranges and typically roam to acquire mates (Dahle and Swenson, 2003). At northern latitudes (55-60 °N), most male-female associations are observed around early-mid June (Stenhouse et al., 2005, the authors, unpublished data). Cubs (typically 2-3) are born during winter denning (Schwartz et al., 2003) and lactation can last up to 2.5 years, with a peak during the cubs’ first midsummer (Farley and Robbins, 1995). Cubs stay with their mother for 1.5 to 4 years and short-term separations during this period are rare (Swenson and Haroldson, 2008). Cub mortality varies among populations and can be as high as 66 % (Miller et al., 2003). Most mortality occurs during the mating season, and is often caused by infanticide by adult males (McLellan, 1994; Swenson et al., 1997; Bellemain et al., 2006; Zedrosser et al., 2009). Primiparous females are more likely to lose their offspring than multiparous females (Zedrosser et al., 2009). Zedrosser et al. (Zedrosser et al., 2009) suggested that primiparous (generally younger) females more often lose their litter, because they are less experienced in avoiding infanticidal males and offspring defense than multiparous (generally older) females. Females/cubs use spatiotemporal avoidance of conspecifics during the mating season (Wielgus and Bunnell, 1995; Ben-David et al., 2004; Nevin and Gilbert, 2005) and multimale mating (Bellemain et al., 2006) as counterstrategies to SSI. For a detailed review of the mating system of the brown bear, see Steyaert et al. (Steyaert et al., 2012).
Relocation data, movement rate, and reproductive status

We used relocation data from female bears that were monitored partly or continuously with GPS collars (GPS Plus collars, Vectronic Aerospace GmbH) between 2005 and 2011. For details on capture and handling, refer to Arnemo et al. (2011). The GPS collars were scheduled to take one position every 30 minutes, thus theoretically fixing 48 positions per day. We removed GPS fixes with a Dilution Of Precision value ≥ 5, and all two dimensional (2D) fixes in order to increase spatial accuracy (Lewis et al., 2007). This reduced the average fix success rate from 94% to 73%. To ensure full data coverage during the mating season, we selected data from 1 May to 31 July. We calculated movement rate (km/h) based on the Euclidean distance between 30-minute consecutive GPS locations per bear. We defined three reproductive classes of bears: receptive females (≥ 5 years and not nulliparous), females/cubs (≥ 5 years and accompanied with dependent young < 1 year old), and females that lost their litter during the mating season (hereafter females/litter loss). We monitored the presence of cubs with their mothers continuously during the mating season, with surveys from a helicopter, direct observations from the ground, and from tracks and signs of cubs collected at clusters of the mothers’ GPS positions (hereafter ‘cluster sites’, minimum 3 consecutive GPS positions within a 15-m radius circle).

For each prediction we created a separate data set, comprising of movement data from receptive females and females/cubs (prediction 1), females/cubs and females/litter loss (before the date of cub loss) (prediction 2), and receptive females and females/litter loss (after the date of cub loss) (prediction 3).

Statistical analysis

We used Generalized Additive Mixed Models (GAMMs) to test our predictions. We used movement rate as the response variable and included ‘year’ and ‘bear ID’ as random factors. Because brown bears show temporal variation in their behavior (Moe et al., 2007; Martin et al., 2010), we included ‘time of day’ (1-48) and ‘Julian day’ (1-92, starting from 1 May) for each reproductive status as nonlinear model terms. We used cyclic cubic regression splines to fit ‘time of day’, because this method connects the beginning and end points of a cycle (here ‘day’) and thin plate regression splines to fit ‘Julian day’, in which the beginning and end points of a cycle are not constrained by
each other. Life history theory predicts that successful offspring raising increases with age and experience (Weladji et al., 2006). Younger and smaller females, for example, are perhaps less aware of their physical environment, less experienced in perceiving risks factors, and may have lower potential to defend their offspring against predators (Paitz et al., 2007; Zedrosser et al., 2009). Therefore, we considered ‘age’ and ‘primiparity/multiparity’ as fixed variables in our models.

For predictions 1 and 3, we considered the fixed variables ‘age’, ‘reproductive status’, and the interaction term ‘age * reproductive status’ for inclusion in our models. For prediction 2, we considered the fixed variables ‘primiparity/multiparity’, ‘reproductive status’ and the interaction term between these two variables to for inclusion in our models. For predictions 1 and 3, we could not include ‘primiparity/multiparity’ as a variable, because of singularity problems (receptive females were per definition not nulliparous). For prediction 2, we did not include ‘age’, a proxy for females experience, because age and primiparity were closely related ($r = -0.47, p < 0.001$). For each model, we included a variance component, which allowed heterogeneity among the different reproductive classes. For each prediction, we selected the most parsimonious model from all possible combinations of the three fixed variables (including a null model) based on Akaike’s Information Criteria differences (second-order bias corrected, $\Delta \text{AIC}_C$) and weights ($\text{AIC}_C^W$) (Akaike, 1973; Anderson, 2008). Candidate models with $\Delta \text{AIC}_C$ values < 2 are presented in Appendix 1. We used the ‘mgcv’ package (Wood, 2011) in R 2.14.0 (RDevelopmentCoreTeam, 2009) for statistical analysis. We validated the statistical models to test each prediction by plotting model residuals versus the fitted values (Zuur et al., 2009).

Results
We obtained relocation data from 29 females that were monitored during at least one mating season between 2005 and 2011 (N = 58). Of these, 23 had the reproductive status ‘receptive female’ during at least one mating season in the study period. We recorded cub survival throughout the mating season in 27 cases, from 23 different females. We recorded litter loss during the mating season in 11 cases, but could only accurately estimate the date of litter loss in 8 cases, from 7 different females. In 5 cases, we confirmed litter mortality and obtained precise estimates of date and time of cub
death, based on GPS data from the mother and the remains of cubs we collected in the
field. For the remaining three cases, we are confident to have estimated the correct day
of litter loss or separation, because of presence/absence of cub tracks and signs at
cluster sites. We recorded movement rates between 2 valid relocations in 100,161 cases,
averaging 1,642 (167 - 3,120) measures per individual. We found no signs of
heteroskedasticity in the model residuals, suggesting good model validity (Zuur et al.,
2009).

Prediction 1: females/cubs move less than receptive females during the mating season
The most parsimonious model (AIC_{cw} = 0.46) to test differences in movement rates
between receptive females and females/cubs included ‘reproductive status’ and ‘age’ as
fixed variables (Table 1). Females/cubs moved less than receptive females (β = -0.276,
se = 0.016, t = -17.0, p < 0.001) during the mating season. Age had no significant effect
on female movement rates (β = -0.0002, se = 0.002, t = -0.085, p = 0.932). The
regression splines ‘time of day’ (females/cubs, edf = 7.855, F = 175.61, p < 0.001;
receptive females, edf = 7.913, F = 542.8, p < 0.001) and ‘Julian day’ (females/cubs,
edf = 7.467, F = 571.25, p < 0.001; receptive females, edf = 8.471, F = 96.98, p <
0.001) affected the movement rates of both reproductive classes (Table 1). Receptive
females showed a distinct bimodal diurnal movement pattern, with peaks around 4:00 –
6:00 and 21:00 – 22:00 (~ 0.7 km/h) and a distinct low (~ 0.2 km/h) around midday
(Figure 1). This bimodal pattern was much less distinct for females/cubs, with
maximum movement rates around 21:00 at ~ 0.25 km/h (Figure 1). The average
movement rate of receptive females during the mating season was 0.46 km/h, and
peaked around early June (Julian day 30-35) at ~ 0.6 km/h. Movement rates of
females/cubs averaged 0.16 km/h during the mating season, and gradually increased
from ~ 0.04 km/h in early May to ~ 0.23 km/h in late July (Figure 2). Two candidate
models had nearly identical ΔAIC_{C} values < 2 (candidate 1, ΔAIC_{C} = 1.0604; candidate
3, ΔAIC_{C} = 1.06, Appendix 1). The results of these two models agreed with those of the
most parsimonious model (Appendix 1).
Prediction 2: a positive relationship between movement rate and litter loss

The most parsimonious model ($\text{AICC}_{w} = 0.49$) to test for differences in movement rates between females/cubs and females/litter loss only included ‘reproductive status’ as a fixed variable. Females that had lost their litter moved more before the date of loss than females with litters that survived during the entire mating season ($\beta = 0.043, \text{se} = 0.008, t = 5.125, p < 0.001$) (Table 1). Also, the splines ‘time of day’ and ‘Julian day’ were significant determinants for females/cubs before the loss (time of day, $\text{edf} = 6.095, F = 38.94, p < 0.001$; Julian day, $\text{edf} = 7.76, F = 66.54, p < 0.001$) and females/cubs (time of day, $\text{edf} = 7.417, F = 57.81, p < 0.001$; Julian day, $\text{edf} = 4.757, F = 299.66, p < 0.001$) (Table 1). The average daily movement rates of females/litter loss increased approximately 2 days before the loss (Figure 3). The candidate model that included ‘reproductive status’ and ‘primiparity/multiparity’ had $\Delta\text{AIC}_C$ and $\text{AICC}_{w}$ values of 1.76 and 0.204, respectively (Appendix 1). Similar to the most parsimonious model, females that had lost their litter moved more before the date of loss than females with litters that survived during the entire mating season ($\beta = 0.042, \text{se} = 0.009, t = 4.912, p = 0.002$), and ‘primiparity/multiparity’ did not affect movement patterns of females before the date of litter loss ($\beta = 0.004, \text{se} = 0.009, t = 5.125, p = 0.6378$) (Appendix 1).

Prediction 3: from being elusive towards roam-to-mate behavior after litter loss

The most parsimonious model ($\text{AICC}_{w} = 0.28$) to evaluate movement rates of females/litter loss and receptive females only included the fixed variable ‘age’ ($\beta = 0.008, \text{se} = 0.004, t = 1.967, p = 0.0492$) (Table 1). Movement patterns of receptive females and females that experienced litter loss were not distinguishable because ‘reproductive status’ was not included in the most parsimonious model. Time of day and ‘Julian day’ significantly affected movements of receptive females (time of day, $\text{edf} = 7.913, F = 529.3, p < 0.001$; Julian day, $\text{edf} = 8.472, F = 97.67, p < 0.001$) and females/litter loss after the event of loss (time of day, $\text{edf} = 7.814, F = 311.1, p < 0.001$; Julian day, $\text{edf} = 6.564, F = 58.19, p < 0.001$). The average daily movement rates of females that experienced litter loss increased until approximately 4 days after the loss. From one day after litter loss, the 95% confidence region of average daily movement rates of females/litter loss included the seasonal average movement rate of
receptive females (Figure 3). Six other candidate models had ΔAICc values <2, including the null model (Appendix 1). ‘Reproductive status’ was never included as a significant model term in any of the models (-0.129 < β < -0.009, 0.03 < se = 0.074, -1.739 < t < -0.309, 0.082 < p < 0.757) (Appendix 1).

We evaluated the ‘age’ effect of the most parsimonious model separately for females after cub loss and receptive females as a post-hoc analysis with GAMMs. After controlling for ‘time of day’ and ‘Julian day’, ‘year’, and ‘bear ID’, we found that age had a strong positive significant effect on movement rates of females that had lost their litter (β = 0.018, p <0.001), but not for receptive females (β = 0.003, p = 0.570).

**Female reproductive fate after litter loss**

Four of the eight GPS marked females that we documented losing their litters gave birth during the next birthing period. Three females were shot during the hunting season prior to the next birthing period, so it is unknown if they would have reproduced successfully. Two of these shot females, however, displayed mating behavior and were observed consorting with males shortly (5 and 6 days) after litter loss. One female consorted with various males after litter loss, but her reproductive fate is unknown. From 1988 to 2011, we recorded 61 disappearances of complete litters during the mating season. In 56 of these cases (92%), the females gave birth during the consecutive denning period.

**Discussion**

Our results show that movement patterns differed among females/cubs, receptive females, and females that experienced litter loss during the mating season. Receptive females generally moved more than females/cubs and showed a stronger bimodal diurnal movement pattern. Also, the average daily movement rates of receptive females peaked around early June, whereas daily movement rates of females/cubs increased gradually during the mating season. We found that females that had lost their litter moved more before the loss event than females that did not experience litter loss, especially relatively shortly before the event of loss (~ 2 days) (Figure 3). Already one day after litter loss, average daily movement rates of receptive females and females/litter loss were indistinguishable, but older females moved more than younger ones after litter loss (Figure 3). We used movement data as a proxy for behavioral
strategies (Nathan et al., 2008) and hormonal data. However, 92% of the females that experienced the loss of an entire litter during the mating season gave birth during the next birthing season, which supports our use of movement data as proxy for mating behavior and hormonal data.

The movement patterns of females/cubs and receptive females supported prediction 1 and showed that movement rate can be a good correlate for reproductive status. The peak of average daily movement rates of receptive females coincided with the peak of the mating season (Stenhouse et al., 2005), supporting the hypothesis that females roam-to-mate as a reproductive strategy (Dahle and Swenson, 2003). Increased and adjusted movement patterns of females in estrus or during the mating season also have been reported in other polygamous species, such as red deer (Stopher et al., 2011), roe deer (Capreolus capreolus) (San José and Lovari, 1998), and pronghorn antelope (Antilocapra americana) (Byers et al., 2005). Among mammals, females are the choosier sex regarding mates, because they invest more in gametes than to males (Trivers, 1972). To obtain high-quality mates, females can use active search strategies. Female searching behavior, however, is poorly understood and rarely documented in the literature and requires more research (Lovari et al., 2008; Stopher et al., 2011).

Two mechanisms may explain the movement patterns of females/cubs during the mating season. First, reducing activity and movement can be a strategy to reduce predation risk in general (Sih and McCarthy, 2002), including the risk for infanticide by conspecifics (Ebensperger, 1998; Swenson, 2003). Second, the mobility of dependent offspring can be a restricting factor for their mothers’ movements. We found that movement rates of females that experienced litter loss were higher before the event of litter loss than those of females that kept their litter throughout the mating season, irrespective of their reproductive history (prediction 2). This suggests that females/cubs have the physical capacity for increased movement rates, but with a large reproductive cost, i.e. a higher risk for litter loss. Other research also provides suggestive evidence that females/cubs reduce their movements during the mating season to lower the risk for infanticide (e.g., Dahle and Swenson, 2003; Swenson, 2003; Martin, 2009), and spatiotemporal infanticide avoidance strategies have been suggested in various other brown bear populations (Wielgus and Bunnell, 1995; Ben-David et al., 2004; Rode et al., 2006), as well as in primates (Hrdy, 1979), rodents (Coulon et al., 1995), cetaceans
(Loseto et al., 2006), and felids (Packer and Pusey, 1983). Our results are not unambiguous, however, because external factors, such as disturbance by humans or conspecifics also may provoke increased movement rates (i.e. flight). In an experimental field study, Moen et al. (2012) found that in 80% of the occasions, brown bears fled when approached (within 50 m) by humans on foot (up to 101 minutes flight time and 6,291 m flight distance). These increased movements may expose individuals to greater risks, such as predation and accidents (Lima and Dill, 1990), and perhaps abandonment or loss of offspring.

We found that movement rates of receptive females and of females after litter loss were not distinguishable, already from one day after the litter loss (prediction 3). This rapid shift was expected for a seasonal breeder with lactational anestrus and sexually selected infanticide (Weir and Rowlands, 1973; Swenson and Haroldson, 2008). The second requirement of the sexual selection hypothesis to explain infanticide states that after infanticide, the victimized mothers can be fertilized earlier than if her offspring had survived (Hrdy, 1979). Females should immediately return to breeding conditions after litter loss, if it is to be advantageous as a male reproductive strategy in a seasonal breeder, (Hausfater, 1984; Hrdy and Hausfater, 1984; van Schaik, 2000). Based on mathematical modeling, Hausfater (1984) and Hrdy & Hausfater (1984) concluded that SSI should be unlikely in seasonal breeders and other environmental conditions that preclude immediate return to estrus. Our results showed that female brown bears that lost their litter during the mating season shifted rapidly (~ 1 day) to a roam-to-mate behavior similar to receptive females, and that the majority of these females also entered estrus and mated during the ongoing breeding season and gave birth during the next birthing season. The literature suggests that female brown bears can enter estrus 2-7 days after litter loss or family break up (Swenson and Haroldson, 2008; Steyaert et al., 2012). Mean interlitter intervals of female brown bears vary among populations, from 2.4 (Sæther et al., 1998) years in central Sweden to 5.7 years in a high-altitude population in Pakistan (Nawaz et al., 2008). If a female loses an entire litter of cubs-of-the-year during the mating season, entering estrus, mating, and giving birth during the next birthing season results in a females interlitter interval of approximately 12 months. Thus, infanticide can shorten interlitter intervals in female brown bears by 50% (in the case of a two-year interlitter interval) to 80-85% (in the case of a five- or six-year
interlitter interval). Thus, infanticide can drastically reduce interlitter intervals in female brown bears and provide a considerable reproductive advantage for infanticidal males.

There is a growing body of evidence for SSI in seasonal breeders other than brown bears, for example hanuman langurs (Borries, 1997), red deer (Bartos and Madlafousek, 1994), Japanese Macaques (Soltis et al., 2000), white-throated round-eared bats (Knörnschild et al., 2011), ringtail lemurs (Lemur catta) (Jolly et al., 2000), and wild patas monkeys (Eriprocebus patas) (Enstam et al., 2002). Van Noordwijk and van Schaik (2000) estimated the vulnerability for SSI of 211 mammals based on their life history parameters (i.e. breeding and birthing seasonality, lactation and gestation duration, delayed implantation, promiscuity, etc.). They suggested that 142 of these species were vulnerable for SSI and that 41 of these species (mainly carnivores, pinnipeds, and primates) show seasonality in birthing and mating. Thus, SSI is probably more common among seasonal breeders than observed or reported.

We found that age significantly affected movement rates of females after cub loss, with older females moving more than younger ones. We suggest that older females are probably more experienced than younger ones (Paitz et al., 2007; Zedrosser et al., 2009) and perhaps more actively roam for mate acquisition to maximize reproductive success after litter loss than younger females. Also, reproductive allocation might be related to age (older females are typically larger than younger ones (Zedrosser et al., 2004)), potentially making it energetically more challenging for younger and smaller females to engage in reproduction (Cichoń, 2001).

**Conclusions**

We found support for the three predictions for female movement rates in relation to SSI theory. The movement rates of females/cubs were relatively slow during the mating season and reflected their elusive lifestyle, which they probably adopted to minimize infanticide risk (Dahle and Swenson, 2003). The movement rates of receptive females were much higher than those of females/cubs, especially during the peak of the mating season, and reflected their roam-to-mate behavior. We found that females that had lost their litters during the mating season moved more before litter loss than females that kept their litters throughout the mating season. The circumstances (disturbances and/or internal factors) under which litter loss occurred were largely unknown and require better documentation, as do the effects of litter loss on female hormone status. Our
results demonstrated that litter loss induced a rapid behavioral change in a seasonal breeder with lactational anestrus. Females that experienced litter loss shifted rapidly from an elusive lifestyle to the movement patterns typical for receptive females, which roam to acquire mates during the mating season (Dahle and Swenson, 2003). This rapid should be expected for seasonal breeders with lactational anestrus in which infanticide has evolved as a male reproductive strategy. One requirement of the sexual selection hypothesis is that killing dependent offspring shortens the interlitter interval of the victims’ mother. In the case of brown bears, offspring loss during the mating season can shorten the interlitter interval at least by half and up to 85%. Additional long-term demographic data showed that almost all (92%) females that lost their litter during a mating season entered estrus, mated, gave birth and emerged with cubs from their winter den during the next spring. Our results complete the three requirements for the sexual selection hypothesis to explain infanticide in the brown bear (Bellemain et al., 2006), and we suggest that infanticide as a male reproductive strategy is more prevalent among seasonal breeders than observed or reported, especially in species with strong sexual selection and life histories similar to those of the brown bear.

Acknowledgements
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References


Figure 1: Mean diurnal movement rates (km/h) fitted with a moving average spline of lone female brown bears (—) and females with cubs-of-the-year (····) during the mating season in central Sweden during 2006 - 2011. The shaded areas represent the 95% point-wise bootstrapped confidence regions around the means. The vertical dashed lines delineate one day, from midnight to midnight.
Figure 2: Mean daily movement rates (km/h) fitted with a moving average spline for lone female brown bears (—) and females with cubs-of-the-year (-----) during the mating season in central Sweden during 2005 - 2011. The shaded areas represent the 95% point-wise bootstrapped confidence regions around the means.
Figure 3: The change in movement rates (km/h) of female brown bears after litter loss (---) in central Sweden, during the mating seasons of 2006-2011. We centered the average daily movements of individual females that had lost their litter at the day of loss (day 0, vertical dashed line). The shaded area represent the 95% point-wise bootstrapped confidence region around the mean daily movement rates of all females that lost litters. The horizontal dashed lines represent seasonal average movement rates of lone females (---) and of females that keep their litters throughout the mating season (-----).
Table 1: Summary of the most parsimonious GAMMs for the three predictions to test for differences in movement rates among reproductive classes of female brown bears in central Sweden in the mating season during 2006-2011. These reproductive classes are: receptive females (>5 years and not nulliparous), females with cubs-of-the-year (>5 year, with cubs-of-the-year, females/cubs), females/cubs before litter loss, and females/cubs after litter loss. We used movement rate (km/h) as the response variable. ‘Time of day’ and ‘Julian day’ were included as regression splines (S), ‘reproductive status’, ‘age’ or ‘primiparity/multiparity’ as fixed variables (F), ‘year’ and ‘bear ID’ as random components (R), and a variance component (V) that allowed heterogeneity between different levels of reproductive status. Parameter estimates (β), standard errors (se), test statistics (t) and p–values (p) are shown for the intercept and the fixed variables. Spline statistics are summarized per ‘Julian day’ and ‘time of day’, and per reproductive status.

### Prediction 1: comparing movement rates between females/cubs and receptive females

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + F(age) + R(year) + R(ID) + V(reproductive state) (AICcw = 0.46)

<table>
<thead>
<tr>
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</tr>
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</tr>
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</tr>
<tr>
<td>Age</td>
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<td>-0.085</td>
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</thead>
<tbody>
<tr>
<td>time of day : females/cubs</td>
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<td>175.6</td>
</tr>
<tr>
<td>time of day : receptive females</td>
<td>7.913</td>
<td>542.8</td>
</tr>
<tr>
<td>Julian day : females/cubs</td>
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<td>571.3</td>
</tr>
<tr>
<td>Julian day : receptive females</td>
<td>8.471</td>
<td>96.98</td>
</tr>
</tbody>
</table>

### Prediction 2: comparing movement rates between females/cubs before litter loss and females/cubs

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + R(year) + R(ID) + V(reproductive state) (AICcw = 0.49)

<table>
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</tr>
<tr>
<td>reproductive state (females/cubs before litter loss vs. females/cubs)</td>
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<td>0.008</td>
<td>5.125</td>
<td>&lt;0.001</td>
</tr>
</tbody>
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<tr>
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<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>time of day : females/cubs</td>
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<td>57.81</td>
</tr>
<tr>
<td>time of day : females/cubs before litter loss</td>
<td>6.095</td>
<td>38.94</td>
</tr>
<tr>
<td>Julian day : females/cubs</td>
<td>4.757</td>
<td>299.66</td>
</tr>
<tr>
<td>Julian day : females/cubs before litter loss</td>
<td>7.760</td>
<td>66.54</td>
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</tbody>
</table>

### Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females

Movement rate ~ S(time of day) + S(Julian day) + F(age) + R(year) + R(ID) + V(reproductive state) (AICcw = 0.28)

<table>
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<td>age</td>
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<td>0.049</td>
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<tr>
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<td>529.2</td>
</tr>
<tr>
<td>time of day : females/cubs after litter loss</td>
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<td>311.1</td>
</tr>
<tr>
<td>Julian day : receptive females</td>
<td>8.472</td>
<td>97.67</td>
</tr>
<tr>
<td>Julian day : females/cubs after litter loss</td>
<td>6.564</td>
<td>58.19</td>
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Appendix 1. Summary of the results of the candidate models with second order bias corrected ΔAIC values <2 for the three predictions to test for differences in movement rates among reproductive classes of female brown bears in central Sweden in the mating season during 2006-2011. These reproductive classes are: receptive females (>5 years and not nulliparous), females with cubs-of-the-year (>5 year, with cubs-of-the-year, females/cubs), females/cubs before litter loss, and females/cubs after litter loss. We used movement rate (km/h) as the response variable. ‘Time of day’ and ‘Julian day’ were included as regression splines (S), ‘reproductive status’, ‘age’ or ‘primiparity/multiparity’ as fixed variables (F), ‘year’ and ‘bear ID’ as random components (R), and a variance component (V) that allowed heterogeneity between different levels of reproductive status. Parameter estimates (β), standard errors (se), test statistics (t) and p–values (p) are shown for the intercept and the fixed variables. Spline statistics are summarized per ‘Julian day’ and ‘time of day’, and per reproductive status.

**Prediction 1: comparing movement rates between females/cubs and receptive females**

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + F(age) + F(reproductive state * age) + R(year) + R(ID) + V(reproductive state) (ΔAICC = 1.06, AICcW = 0.27)

<table>
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<td>11.006</td>
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<td>reproductive state (females/cubs loss vs. receptive females)</td>
<td>-0.226</td>
<td>0.051</td>
<td>-4.465</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>age</td>
<td>0.002</td>
<td>0.003</td>
<td>0.592</td>
<td>0.554</td>
</tr>
<tr>
<td>reproductive state * age</td>
<td>-0.005</td>
<td>0.004</td>
<td>-1.017</td>
<td>0.309</td>
</tr>
<tr>
<td>time of day: receptive females</td>
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<td>time of day: females/cubs</td>
<td>7.855</td>
<td>175.61</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>Julian day: receptive females</td>
<td>8.471</td>
<td>96.96</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day: females/cubs</td>
<td>7.468</td>
<td>571.02</td>
<td>&lt;0.001</td>
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</table>

**Prediction 1: comparing movement rates between females/cubs and receptive females**

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive stage) + F(reproductive stage * age) + R(year) + R(ID) + V(reproductive state) (ΔAICc = 1.06, AICcW = 0.27)

<table>
<thead>
<tr>
<th>Variable</th>
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<th>p</th>
</tr>
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<td>11.006</td>
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</tr>
<tr>
<td>reproductive state (females/cubs vs. receptive females)</td>
<td>-0.226</td>
<td>0.051</td>
<td>-4.465</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>receptive females * age</td>
<td>0.002</td>
<td>0.003</td>
<td>0.592</td>
<td>0.554</td>
</tr>
<tr>
<td>females/cubs * age</td>
<td>-0.003</td>
<td>0.003</td>
<td>-0.763</td>
<td>0.445</td>
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<tr>
<td>time of day: receptive females</td>
<td>7.913</td>
<td>545.1</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>time of day: females/cubs</td>
<td>7.855</td>
<td>175.6</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day: receptive females</td>
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<td>95.5</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>Julian day: females/cubs</td>
<td>7.468</td>
<td>571</td>
<td>&lt;0.001</td>
<td></td>
</tr>
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</table>
### Prediction 2: comparing movement rates between females/cubs before litter loss and females/cubs

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + R(year) + R(ID) + V(reproductive state) ($\Delta$AIC$_C$ = 1.76, $\Delta$IC$_W$ = 0.204)

<table>
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<td>0.001</td>
<td>-1.241</td>
<td>0.215</td>
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</table>

| time of day : females/cubs                         | 7.418   | 57.84 | <0.001 |
| time of day : females/cubs before litter loss      | 6.096   | 38.94 | <0.001 |
| Julian day : females/cubs                          | 4.766   | 298.35| <0.001 |
| Julian day : females/cubs before litter loss       | 7.758   | 66.63 | <0.001 |

### Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + F(age) + F(reproductive state * age) + R(year) + R(ID) + V(reproductive state) ($\Delta$AIC$_C$ = 1.93, $\Delta$IC$_W$ = 0.107)

<table>
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<th>p</th>
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<td>8.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>reproductive state (females/cubs after litter loss vs. receptive females)</td>
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<td>0.074</td>
<td>-1.739</td>
<td>0.0821</td>
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<td>0.004</td>
<td>0.738</td>
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</tr>
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<td>reproductive state * age</td>
<td>0.012</td>
<td>0.007</td>
<td>1.65</td>
<td>0.099</td>
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</tbody>
</table>

| time of day : receptive females                     | 7.913   | 529.2 | <0.001 |
| time of day : females/cubs after litter loss        | 7.814   | 311.15| <0.001 |
| Julian day : receptive females                      | 8.472   | 97.64 | <0.001 |
| Julian day : females/cubs after litter loss         | 6.575   | 57.75 | <0.001 |

### Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + F(age) + R(year) + R(ID) + V(reproductive state) ($\Delta$AIC$_C$ = 1.92, $\Delta$IC$_W$ = 0.107)

<table>
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<td>0.007</td>
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| time of day : receptive females                     | 7.913   | 554.62| <0.001 |
| time of day : females/cubs after litter loss        | 7.814   | 326.6 | <0.001 |
| Julian day : receptive females                      | 8.472   | 97.67 | <0.001 |
| Julian day : females/cubs after litter loss         | 6.575   | 57.8  | <0.001 |
**Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females**

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state) + F(reproductive stage * age) + R(year) + R(ID) + V(reproductive state) (ΔAIC_C = 1.93, ΔAIC_CW = 0.107)

<table>
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<th>t</th>
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<tbody>
<tr>
<td>intercept</td>
<td>0.414</td>
<td>0.049</td>
<td>8.51</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>0.074</td>
<td>-1.739</td>
<td>0.082</td>
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<tr>
<td>receptive females * age</td>
<td>0.003</td>
<td>0.004</td>
<td>0.738</td>
<td>0.461</td>
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<td>females/cubs after litter loss * age</td>
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<tr>
<td>time of day : females/cubs after litter loss</td>
<td>7.814</td>
<td>311.15</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>Julian day : receptive females</td>
<td>8.472</td>
<td>97.64</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>Julian day : females/cubs after litter loss</td>
<td>6.575</td>
<td>57.75</td>
<td>&lt;0.001</td>
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</tbody>
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**Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females**

Movement rate ~ S(time of day) + S(Julian day) + F(age) + F(reproductive state * age) + R(year) + R(ID) + V(reproductive state) (ΔAIC_C = 1.96, ΔAIC_CW = 0.105)

<table>
<thead>
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<tr>
<td>time of day : receptive females</td>
<td>7.913</td>
<td>554.66</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>time of day : females/cubs after litter loss</td>
<td>7.814</td>
<td>326.64</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day : receptive females</td>
<td>8.472</td>
<td>97.66</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day : females/cubs after litter loss</td>
<td>6.563</td>
<td>57.83</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

**Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females**

Movement rate ~ S(time of day) + S(Julian day) + F(reproductive state * age) + R(year) + R(ID) + V(reproductive state) (ΔAIC_C = 1.96, ΔAIC_CW = 0.105)

<table>
<thead>
<tr>
<th>Variable</th>
<th>β</th>
<th>se</th>
<th>t</th>
<th>p</th>
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<tr>
<td>receptive females * age</td>
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<tr>
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<td>554.66</td>
<td>&lt;0.001</td>
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<tr>
<td>time of day : females/cubs after litter loss</td>
<td>7.814</td>
<td>326.64</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day : receptive females</td>
<td>8.472</td>
<td>97.66</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day : females/cubs after litter loss</td>
<td>6.563</td>
<td>57.83</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>
**Prediction 3: comparing movement rates between females/cubs after litter loss and receptive females**

Movement rate ~ $S$(time of day) + $S$(Julian day) + $F$(reproductive state * age) + $R$(year) + $R$(ID) + $V$(reproductive state) ($\Delta$AIC$_C$ = 1.60, AIC$_C$/p = 0.126)

<table>
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<th>$\beta$</th>
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<td>time of day : females/cubs after litter loss</td>
<td>7.814</td>
<td>311.11</td>
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<td>Julian day : receptive females</td>
<td>8.472</td>
<td>97.67</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Julian day : females/cubs after litter loss</td>
<td>6.552</td>
<td>57.84</td>
<td>&lt;0.001</td>
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</tr>
</tbody>
</table>
Paper III
Making the best of a bad situation: resource selection in a risky landscape

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**Running headline:** Resource selection in a risky landscape
Summary

1. Antipredator behavior can vary in space and time and among different sex and age classes, according to predation risk. In large carnivores, predation is often intraspecific and related to infanticide, which can be a male reproductive strategy (i.e. sexually selected infanticide, SSI). Because infanticide can be a strong selective force, female counterstrategies to infanticide have evolved.

2. One possible female counterstrategy to infanticide is to alter resource selection in space and time to avoid potentially infanticidal conspecifics. Although spatiotemporal avoidance would be an obvious strategy, evidence for it in the literature is scarce.

3. We evaluated spatiotemporal avoidance of infanticide in the brown bear, a large polygamous carnivore and seasonal breeder. Because we expect SSI in our study population in Scandinavia, we predict that differences in resource selection are strongest between (I) females with cubs-of-the-year and adult males, and (II) during the mating season. Therefore, we quantified the differences in resource selection among adult males, lone adult females, and females with cubs-of-the-year, based on GPS-relocation data (2006-2010). We evaluated responses to land cover, terrain ruggedness, and human-related variables of each reproductive class to understand their resource selection and potential infanticide avoidance behavior.

4. We found support for prediction I and II and found that females with cubs-of-the-year selected their resources, in contrast to adult males, in less rugged landscapes, in relative close proximity to certain human-related variables, and in more open habitat types during the mating season. Females with cubs-of-the-year markedly shifted their resource selection after the mating season, towards a pattern more similar to that of their conspecifics.

5. Differential resource selection among reproductive classes of bears in our study system is probably partly explained as a female counterstrategy to SSI, in which females with cubs-of-the-year alter their resource selection to avoid infanticidal males. In species exhibiting SSI, female avoidance of infanticidal males is probably more common than observed or reported, and may come with a fitness cost when facing the ‘food or safety’ antipredator dilemma.

Keywords: infanticide, reproductive strategy, risk effects, risk factor, sexual conflict, *Ursus arctos*
Introduction

Predation is a strong selective force that can directly affect an individual’s fitness through its or its offspring’s death (Lima & Dill 1990). Predation can also indirectly affect an individual’s fitness due to costs associated with antipredator behavior and predation risk (Brown & Kotler 2004; Creel & Christianson 2008). Risk effects can play an important role by affecting foraging decisions, such as selection of feeding habitat or activity budgets (Lima & Bednekoff 1998; Brown, Kotler & Bouskila 2001).

Female reproductive success is partly determined by offspring survival (Main 2008). Females should thus favor trade-offs that minimize offspring predation without compromising their own survival (Main 2008; Singh et al. 2010). Life history theory predicts that females without dependent offspring optimize their body condition and fecundity by selecting areas with high-quality food resources and low predation risk (Noordwijk & Jong 1986; Partridge & Harvey 1988). Because predation risk may be size dependent, selection for optimal resources may differ between the sexes in size-dimorphic species (Bowyer 2004). Offspring predation risk may cause sexual segregation in a species, with females separating from males as a reproductive strategy. This may cause females to select habitat to avoid males to maximize offspring safety. Sexual segregation has predominantly been studied in group-living ungulates, such as bighorn sheep (Ovis canadensis) and red deer (Cervus elaphus) (Bowyer 2004; Main 2008).

In large predators, female reproductive success should be less affected by interspecific than intraspecific predation, such as infanticide (Rode, Farley & Robbins 2006). Infanticide can be an adaptive male reproductive strategy when males gain mating opportunities by killing unrelated dependent young (i.e., sexually selected infanticide, SSI) (Hrdy 1979). This shortens the time to the victimized female’s next estrus and a perpetrating male may sire her next litter (Trivers 1972). SSI is common in size-dimorphic species with a polygamous mating system (van Schaik 2000) and occurs during the mating season in seasonal breeders (Bartos & Madlafousek 1994; Zedrosser et al. 2009). SSI is linked to male takeovers of female groups or territories (Pusey & Packer 1994; Swenson et al. 1997). Because infanticide influences the evolution of mammalian mating systems (Wolff & Macdonald 2004), female adaptive behaviors to minimize infanticide should be selected for, leading to the evolution of counterstrategies to infanticide (Ebensperger 1998). Such strategies include pregnancy termination, aggression, group defense, multimale mating, territoriality, and avoidance of infanticidal conspecifics (Agrell, Wolff & Ylönen 1998; Ebensperger 1998). Avoiding infanticidal conspecifics is an obvious counterstrategy, but definitive evidence is rare, and
mainly involves group-living species (Ebensperger & Blumstein 2007) such as lions (*Panthera leo*) (Pusey & Packer 1994) and Hanuman langurs (*Presbytis entellus*) (Hrdy 1979).

The brown bear (*Ursus arctos*) is a solitary, size-dimorphic carnivore with a polygamous mating system (Steyaert *et al.* 2012a). Mortality in cubs-of-the-year (< 1 year old; hereafter termed ‘cubs’) varies from 4 - 66% (Miller 1990; Sæther *et al.* 1998) among populations.

Infanticide occurs mainly during the mating season (Zedrosser *et al.* 2009). Female counterstrategies to infanticide in brown bears include direct defense (Craighead, Sumner & Mitchell 1995), promiscuity and multiple paternity (Bellemain, Swenson & Taberlet 2006), selecting escape habitat (Pearson 1975; Swenson 2003), elusiveness (Dahle & Swenson 2003b), and avoidance of sites with high infanticide risk (clumped food resources) (Wielgus & Bunnell 1995; Ben-David, Titus & Beier 2004; Rode, Farley & Robbins 2006). Evidence for SSI in the brown bear has been documented (Swenson *et al.* 1997; Bellemain, Swenson & Taberlet 2006), but also contested (Miller, Sellers & Keay 2003; McLellan 2005).

Many brown bear populations live in human-dominated landscapes and humans can affect bear behavior and life history (Swenson *et al.* 1997; Zedrosser *et al.* 2011). Bears are expected to avoid humans, because bear mortality is predominantly human-caused (Nielsen *et al.* 2004; Bischof *et al.* 2009). This restricts optimal resource selection, especially for females with cubs (hereafter termed ‘females/cubs’), which have to cope with two risk factors, i.e., humans and infanticide. The intensity of these risk factors changes over time; human disturbance is highest during the day and during periods of intense recreation or hunting (Ordiz *et al.* 2011), whereas the infanticide risk is highest during the mating season (Zedrosser *et al.* 2009).

We test whether spatiotemporal segregation occurs as a counterstrategy to SSI in a nonsocial carnivore, the brown bear, and in an environment where food sources are relatively evenly distributed over a human-dominated landscape. First, we assess whether intraspecific segregation occurs among three reproductive classes (adult males ≥ 5 years), lone adult females (≥ 5 years, hereafter termed ‘lone females’), and females/cubs), and whether segregation behavior is consistent with the sexual selection hypothesis to explain infanticide. We predict that spatiotemporal segregation is (I) more pronounced between females/cubs and adult males than between adult males and lone females or between females/cubs and lone females, and (II) more pronounced during the mating season than during the postmating season. Secondly, we assess the patterns in resource selection by the reproductive classes to better understand potential infanticide avoidance behavior. Therefore, we assess the
spatiotemporal behavioral responses of each reproductive class in relation to land cover, terrain ruggedness, and human disturbance.

**Methods**

The study was conducted in an intensively managed boreal forest in south-central Sweden (~61°N, 15°E), with a dense network of logging roads (0.7 km/km²) and few high-traffic roads (0.14 km/km²) (Martin *et al.* 2010). The human population density is low, with few settlements and isolated houses (mainly holiday cabins) (Martin *et al.* 2010). Human presence is most pronounced during summer and fall, and mainly related to hunting and berry picking (Ordiz *et al.* 2011). Brown bear population density is about 30 individuals/1000 km² (Bellemain *et al.* 2005) and the population is intensively hunted (21 August until 15 October) (Bischof *et al.* 2009).

**Location data**

We modeled resource selection based on locations from individual bears monitored with GPS (Global Positioning System) collars (GPS Plus, Vectronic Aerospace GmbH) during 2006-2010. See Arnemo *et al.* (2011) for details on capture and handling. The GPS collars delivered 1 position every 30 minutes, with an average fix rate of 94.2%. We removed GPS fixes with dilution of precision values ≥ 5 to increase spatial accuracy. This reduced the average fix success rate to 73.4%. We used the year a bear was monitored as the sample unit (bear-year = one bear followed for one year), and obtained data from the three reproductive classes. We defined the operational study area as the 95% kernel density estimated range of all GPS locations.

For every bear-year we sampled availability using random points, equal to the number of GPS points. We sampled availability in the operational study area, based on the principle that every individual could physically reach every site within this area (i.e., Manly’s design type II (Manly *et al.* 2002)) and randomly assigned every data point to a training or validation dataset with a 50% probability. We divided the data into the mating season (1 May – 15 July) and the postmating season (1 August – 1 October), with a 2-week break between (16 July – 31 July) for a clear separation between them. We further divided the data into 8 3-hour intervals to cover diurnal variance in bear behavior (1, 00:00-2:59; 2, 3:00-5:59; 3, 6:00-8:59; 4, 9:00-11:59; 5, 12:00-14:59; 6, 15:00-17:59; 7, 18:00-20:59; 8, 21:00-23:59).
Spatial landscape data

We derived spatial landscape data from three sources, i.e. topographical map tiles (National Land Survey of Sweden, www.lantmateriet.se), a digital elevation model (DEM, 50*50m pixel size, National Land Survey of Sweden, www.lantmateriet.se), and Resourcesat1-IRS-P6-LISS3 satellite imagery (23.5*23.5m, imagery captured on 2 and 7 June 2007, available free at www.lantmateriet.se). We processed the satellite images with Erdas Imagine 9.1 (LeicaGeosystems 2010), and used ArcGIS 9.2 (ESRI) to derive data from the DEM and topographical maps.

Land cover – We obtained land cover types through a supervised classification with a maximum likelihood classifier of the satellite imagery (87% overall user’s accuracy) (Steyaert et al. 2012b). We considered the land cover types ‘bog’, ‘young dense forest’, ‘young open forest’, and ‘older forest’ as potential bear habitat for further analysis.

NDVI – We derived a Normalized Difference Vegetation Index (NDVI) map of the study area from the satellite imagery. The NDVI is a spectral vegetation index based on the reflectance of land cover features of red and near-infrared electromagnetic energy, and is commonly used as a proxy for vegetation density (Pettorelli et al. 2005).

Terrain characteristics – We used the DEM to derive terrain ruggedness indices and slope steepness for each 50*50m pixel in the study area. We adapted the terrain ruggedness index (TRI) of Riley et al. (1999), using variation in altitude for each cell relative to the 8 adjacent cells, the maximum observed altitude in the study area, and the slope aspect, steepness, and curvature to determine an index of terrain ruggedness (refer to Steyaert et al. 2012b for a detailed description). We categorized the TRI pixel values into four quartiles (class 1, least rugged, to 4, most rugged). Because behavioral responses to terrain ruggedness may vary with spatial scale (Mårell & Edenius 2006), we created a second terrain ruggedness index on the landscape scale (TRI1000). We calculated the average TRI for each pixel with a moving window, using all surrounding pixels within a 1000-m radius, and categorized the resulting map into the same four quartiles.

Water bodies – Water can affect the distribution of terrestrial wildlife (Main 2008). We derived the Euclidean distance to the closest creek (< 3 m wide) and larger water bodies for each 25*25 m pixel from the topographical maps.

Human disturbance – Humans may have a profound impact on the distribution, population size and structure, and behavior of wildlife (Festa-Bianchet & Apollonio 2003). We therefore selected human infrastructures, i.e. settlements, buildings, paved roads (termed ‘roads’),
unpaved forest roads (termed ‘forest roads’), and trails, from a topographical map. We derived the Euclidean distance to each of these for all 25*25 m pixels in the study area.

Data analysis

We used logistic generalized linear mixed models with a logit link function and a Markov Chain Monte Carlo algorithm to model brown bear resource selection (Hadfield 2010). Models were run with 65,000 iterations, a burnin of 15,000, a thinning interval of 50, and an Inverse Whiskart prior. We used availability/use as the binary response variable, and a linear combination of the landscape variables as the explanatory variables. We included individual ‘bear ID’ and ‘year’ as random factors. We tested for collinearity among model variables with a Spearman Rho correlation test. We removed the variable ‘Slope’ from further analysis, because it correlated highly (0.606, p <0.001) with TRI.

We formulated two candidate models *a priori* (Burnham & Anderson 2002), i.e., a global model including all variables and a reduced model containing only the variables we believed to be the strongest predictors of brown bear resource selection (Table 1). We selected the most parsimonious candidate model based on the Deviance Information Criteria (DIC) (Hadfield 2010). We used the potential scale reduction factor (PSRF) diagnostic to assess model convergence, based on the variance within and between duplicate Markov chains (Brooks & Gelman 1998). Model convergence is reached when PSRF values approach 1. We used the ‘MCMCglmm’ (Hadfield 2010) and the ‘coda’ package (Plummer et al. 2010) to model resource selection with R2.12.0 for all analyses (R Development Core Team 2009).

We assessed the responses of the different reproductive classes towards the ordinal categorical and the continuous model variables by plotting the parameter estimates and their respective 95% Highest Posterior Density (HPD) intervals during the mating and the postmating season and each diurnal interval. We considered a response as significant if the 95% HPD interval did not contain 0. We ranked the nominal land cover classes according to their parameter estimates by reproductive class, season, and diurnal interval and assigned an ordinal score (1, low – 4, high) to each rank. We tested whether the categories of bears selected for certain land cover types during both seasons with a Friedman Rank Sum test and used two-tailed permutation tests with 1000 iterations to identify the difference between mean rank scores of the land cover types.

We created resource selection maps for each reproductive class, diurnal interval, and season, based on the modeling results and the spatial data layers (Boyce *et al.* 2002). The
pixel values of these maps indicate the relative probability that the pixel will be selected by
an individual of a given class during a given period of time (Boyce et al. 2002).

We assessed the relationships between resource selection of adult males, lone females, and
females/cubs with Pearson correlation tests after accounting for spatial autocorrelation in the
resource selection maps (Legendre 1993). We used semivariograms with a Gaussian fit to
determine the level of spatial autocorrelation in each resource selection map. We used the
average semivariogram range as the threshold distance for spatial independency between map
locations and used this distance as the minimum distance between points that were randomly
sampled within the study area. For each point, we extracted resource selection values for each
resource selection map and used Pearson product-moment correlation tests to assess
segregation in resource selection among reproductive classes. We used Wilcoxon Signed
Rank tests on the paired (by diurnal interval) correlation coefficients to test for differences in
resource selection among the classes. We used the ‘automap’ package (Hiemstra et al. 2009)
in R to assess spatial autocorrelation in resource selection maps.

We used the resource selection maps and the validation location dataset to validate the
predictive accuracy of the resource selection models (Boyce et al. 2002), correlating the area-
adjusted frequency of occurrence of relocation data in the validation dataset with predicted
resource selection maps. High correlation coefficients indicate that pixels with a high
predicted relative probability of selection are selected, compared to their availability, and thus
indicate good model predictive accuracy (Boyce et al. 2002). For all analyses, we considered
$\alpha = 0.05$ as the threshold level for statistical significance.

Results

Model evaluation

We modeled resource selection with data from 90 bear-years from 51 individuals, including
17 males (35 bear-years) and 34 females (55 bear-years), 17 of which had given birth at least
once during the study period (21 bear-years). The operational study area encompassed 2,937
km². We obtained 431,703 bear locations; the average number used in a training data set was
6,275 (range: 2,173 - 8,783; Appendix S1).

The global models performed better than all reduced models (Appendix S1), and were
selected for further analyses. The PSRF approached 1 for each selected model (Appendix
S1). Model validation showed that the area-adjusted frequency of occurrence correlated
strongly ($0.881 < \rho < 0.999$) and significantly ($0.05 < \rho < 0.001$) with the predicted resource
selection maps for all diurnal intervals, reproductive classes, and both seasons (Appendix S1).

Correlates in resource selection
Locations on resource selection maps became spatially independent on average at 3,443.6 m; we therefore added this distance to our sampling criteria for sampling random points to compare correlation in resource selection levels among reproductive classes. We extracted values from each resource selection map from 128 spatially independent random points. Examples of resource selection maps are presented in Appendix S2.

During the mating season, correlations between the resource selection of females/cubs and adult males were significantly negative during night (00:00 – 2:59, Pearson correlation coefficient (R) = -0.478, p < 0.001; 3:00 – 5:59, R = -0.281, p = 0.001; 18:00 – 20:59, R = -0.293, p < 0.001; 21:00 – 23:59, R = -0.234, p = 0.007) (Fig. 1). Positive correlations were found during the intervals from 9:00 – 11:59 (R = 0.447, p < 0.001) and 12:00 – 14:59 (R = 0.679, p < 0.001), and no differences were evident between 6:00 – 8:59 (R = 0.140, p = 0.1) and 15:00 – 17:59 (R = 0.144, p = 0.105). After the mating season, resource selection correlations between females/cubs and adult males were always strongly and significantly positive (p < 0.001), with correlation coefficients between 0.147 and 0.759, except between 00:00 and 2:59, when no difference was found (R = -0.158, p = 0.075) (Fig. 1). Resource selection correlations between adult males and lone females were always significantly positive and varied between 0.196 (p = 0.027, 00:00 – 2:59, mating season) and 0.846 (p < 0.001, 9:00 – 11:59, postmating season). Resource selection correlations between females/cubs and lone females were mostly positive during both seasons (Fig. 1). Mean resource selection correlation (μc) between females/cubs and adult males was lower during the mating season (μc_mating = 0.0155) than the postmating season (μc_post-mating = 0.467, V = 1, p = 0.021), and lower than the resource selection correlation between adult males and lone females (μc = 0.418, V = 0, p = 0.014) and females/cubs and lone females (μc = 0.378, V = 1, p = 0.021) during the mating season. Also during the postmating season, the resource selection correlation between females/cubs and adult males (μc = 0.468) was lower than between adult males and lone females (μc = 0.718, V = 0, p = 0.014), but not between females/cubs and lone females (μc = 0.594, V = 16, p = 0.834). The resource selection correlation between the mating and the postmating season differed significantly between adult males and lone females (μc_mating = 0.418, μc_post-mating = 0.718, V= 2, p = 0.030), but not
between females/cubs and lone females ($\mu_{\text{mating}} = 0.418$, $\mu_{\text{post-mating}} = 0.594$, $V = 7$, $p = 0.142$).

**Responses to landscape variables**

To facilitate interpretation, we report and discuss our results based on graphical representations of the modeling results (Fig 2 and Appendix S3 and S4). Parameter estimates of fixed effects, their 95% HPD intervals, and the MCMC-simulated p-values are available upon request.

Terrain ruggedness – Local-scale selection for terrain ruggedness was similar for all reproductive classes during both seasons. All reproductive classes always selected for the most rugged terrain during the mating season (Appendix S3). During the postmating season, all reproductive classes selected for the most rugged terrain during nocturnal hours (Appendix S3). At the landscape scale during the mating season, adult males selected for the most rugged terrain, there was no apparent selection by lone females, but females/cubs showed a marked and consistent selection against rugged landscapes (Appendix S3). During the postmating season, all reproductive classes selected for the most rugged terrain (Appendix S3).

Distance to buildings and settlements – During the mating season, adult males were further from buildings than random, there was no apparent selection by lone females, but females/cubs were generally closer to buildings than random (Appendix S3). After the mating season, all classes were farther from buildings than random (Appendix S3). However, all reproductive classes generally selected for areas close to settlements during the mating season. During the postmating season, adult males selected areas near settlements, lone females showed no selection, but females/cubs avoided settlements (Appendix S3).

Distance to trails, forest roads and roads – During the mating season, adult males selected for areas closer to trails, forest roads, and roads, especially during night (Appendix S3). Lone females avoided roads and selected areas closer to trails during night, but forest roads had no apparent effect (Appendix S3). Females/cubs generally avoided areas close to trails, forest roads, and roads. During the postmating season, all reproductive classes were farther from forest roads and trails than random, especially during daytime (6:00 – 8:59, 9:00 – 11:59 and 12:00 – 14:59). Roads were generally avoided by adult males and lone females, whereas they had no apparent effect on females/cubs (Appendix S3).

NDVI – Adult males and lone females showed a bell-shaped diurnal trend in their selection of areas with high NDVI values, peaking at midday during both seasons (Fig. 2).
Females/cubs did not show this pattern during the mating season and parameter estimates for NDVI values were generally lower than for the other reproductive classes. The response to NDVI was more similar among reproductive classes during the postmating season, showing selection for areas with high NDVI values during daytime, but not during nighttime. However, the peak of selection by females/cubs was not as pronounced as for adult males and lone females (Fig. 2).

Land cover types – Adult males and lone females did not select land cover types uniformly during the mating season (adult males, Friedman $\chi^2 = 16.35$, df = 3, p < 0.001; lone females, Friedman $\chi^2 = 13.95$, df = 3, p = 0.002). Both classes preferred young dense forest above the other land cover types during all diurnal intervals (see Appendix S4 for post-hoc results). During the postmating season, adult males and lone females showed no clear preference for any land cover type (adult males, Friedman $\chi^2 = 3.15$, df = 3, p = 0.369, adult females, Friedman $\chi^2 = 3$, df = 3, p = 0.391). Females/cubs selected for young dense forest and older forest during the mating season (Friedman $\chi^2 = 20.25$, df = 3, p < 0.001; Appendix S3), and young open and young dense forest during the postmating season (Friedman $\chi^2 = 15.75$, df = 3, p = 0.001; Appendix S4).

Distance to creeks and larger water bodies – Creeks and larger water bodies generally did not affect resource selection by adult males and lone females during the mating season (Appendix S3), but females/cubs significantly avoided them during four of the eight diurnal intervals (Appendix S3). During the postmating season, creeks and larger water bodies were generally avoided by all reproductive classes (Appendix S3).

**Discussion**

Resource selection by brown bears in our study system varied seasonally, diurnally, and among reproductive classes. Differences were greatest between adult males and females/cubs (supporting prediction I) and during the mating season (supporting prediction II). We suggest that differential resource selection among reproductive classes was a consequence of sex-specific reproductive strategies, with females/cubs adapting their resource selection during the mating season to avoid potentially infanticidal males.

Spatiotemporal infanticide avoidance strategies have been suggested in some species. Female Hanuman langurs and gorillas (*Gorilla gorilla*) with dependent young may disperse to avoid infanticide by males (Hrdy 1979; Robbins *et al*. 2009). Setiewan *et al*. (1996) suggested that orangutan (*Pongo pygmaeus*) females with neonates avoided congregated food sources, because they may attract potentially infanticidal conspecifics. Female beluga whales
(Delphinapterus leucas) with calves reside in open waters near the mainland apparently to avoid interspecific predation and infanticidal males (Loseto et al. 2006). Female Alpine marmots (Marmota marmota) may reduce pup mortality after a male takeover by moving their neonates to safer areas (Coulon et al. 1995). In carnivores, female lions with dependent offspring may avoid infanticidal males by becoming temporary nomads (Packer & Pusey 1983). Also in other brown bear populations, females with dependent offspring have been suggested to reduce infanticide risk by avoiding conspecifics (Wielgus & Bunnell 1994; Ben-David, Titus & Beier 2004).

Avoiding males as an infanticide counterstrategy in bears
Females/cubs likely assess their environment for the occurrence of potentially infanticidal individuals, maybe using food availability and human presence as cues. Females/cubs may avoid congregated food sources, such as salmon streams, salt marshes, and garbage dumps, to avoid infanticide (Craighead, Sumner & Mitchell 1995; Rode, Farley & Robbins 2006), resulting in a trade-off between nutrition and cub safety (Mattson & Reinhart 1995; Ben-David, Titus & Beier 2004). Pearson (1975) and Swenson et al. (2001) suggested that females/cubs minimize infanticide risk by selecting the poorest habitats, such as alpine tundra and high-altitude rocky areas. Females/cubs have also been suggested to associate with humans to avoid aggressive males (Nevin & Gilbert 2005a; Rode, Farley & Robbins 2006).

We found that resource selection by different reproductive classes was a complex and multiscaled spatiotemporal mechanism, where females/cubs responded differently to landscape characteristics than the other classes, especially compared with adult males during the mating season. During this season, females/cubs selected the least rugged terrain on the landscape scale, avoided trails, forest roads and roads, and selected areas relatively close to buildings. Also, they showed no diurnal trend in selection for patches with high NDVI values. Adult males, in contrast, selected the most rugged terrain on the landscape scale and areas close to all types of roads during the mating season. They avoided buildings and showed a strong diurnal pattern in selection for patches with high NDVI values.

Our finding that all categories selected areas closer to settlements during the mating season is counterintuitive (Woodroffe 2000). To examine this more closely, we plotted the area-adjusted frequency of occurrence (AAFO) of GPS positions for bears of all categories within a 5-km radius (divided into 500-m bands) around settlements (Fig. 3). AAFO values >1 indicate that an area unit is used more than expected. During the mating season, AAFO values for females/cubs exceeded 1 and peaked at 500-1000 m from settlements, but adult
males avoided settlements closer than 1500 m (Fig. 3). For lone females, AAFO values fluctuated around 1, until approximately 3000 m from settlements, after which they exceeded 1. After the mating season, AAFO values for females/cubs exceeded 1 from distances around 3500 m from settlements and for lone females and adult males at approximately 1000 and 1500 m from settlements, respectively (Fig. 3). Thus, during the mating season, females/cubs used areas close to settlements (500-1000m) more than expected, whereas adult males and lone females avoided these areas. During the postmating season, bears of all reproductive classes avoided settlements, and this effect was strongest for females/cubs.

**Temporal changes in segregation**

Spatiotemporal variation in predation risk allows testing hypotheses related to predation risk, detecting the risk origin, and measuring the magnitude of risk effects (Lima & Bednekoff 1998; Creel & Christianson 2008). We found that resource selection by the reproductive classes showed a seasonal shift, probably due to changing physiology, food availability, human presence, and infanticide risk. The differences in resource selection were greatest between females/cubs and adult males during the mating season, which supports the hypothesis that females/cubs use a male avoidance strategy to minimize SSI risk. Other explanations for nonparental infanticide (i.e., predation, removing competitors, and pathology (Hrdy 1979)) do not require this seasonal component. After the mating season, females rarely enter estrus (Steyaert et al. 2012a) and infanticide is no longer a male reproductive strategy (Bartos & Madlafousek 1994; Zedrosser et al. 2009). As expected, differences in resource selection between females/cubs and adult males were less pronounced during the postmating season.

Nocturnal behavior in the brown bear is often suggested to result from human activity (Swenson 1999). In our study area, bear behavior was closely linked to human disturbance (Martin et al. 2010; Ordiz et al. 2011) and bears showed a period of low activity during daytime (9:00 – 18:00) (Moe et al. 2007). We found a diurnal component in differential resource selection among the reproductive classes. Resource selection was most similar during daytime, suggesting that all bears perceive human disturbance as a threat then. Only females/cubs preferred older forests during nighttime and crepuscular hours, when bear activity peaks (Moe et al. 2007) and human disturbance is low (Martin et al. 2010). We suggest that females/cubs perceive conspecifics as a greater threat than humans at these times and therefore select habitats that facilitate escape, such as older forest types, with more large trees that cubs can climb to escape potential perpetrators (Swenson 2003). Also, in older
forest, females/cubs may detect potential perpetrators earlier by sight and possibly also by olfaction (Swenson 2003).

Landscape cues and refugia

It is commonly accepted that animals can assess predation risk and behave accordingly. Therefore, animals can use landscape features or daylight as cues to evaluate risk (Brown & Kotler 2004; Creel & Christianson 2008). Our results suggest that females/cubs perceive SSI risk as a greater threat than human presence during the mating season and alter their resource selection using landscape characteristics as cues for the occurrence of potentially infanticidal males. For example, we found that adult males made extensive use of all types of roads during the mating season, perhaps to cover large distances when roaming for mates (Dahle & Swenson 2003a). Females/cubs avoided all types of roads during the mating season, likely to avoid infanticidal males. They used areas 500-1000 m from settlements more than expected, but only during the mating season. This zone was avoided by adult males and lone females. Also, females/cubs selected areas relatively close to single buildings only during the mating season, whereas these were avoided by adult males. These results suggest that females/cubs used areas close to humans (but not road infrastructure) as safety refuges. This is in accordance with McLellan and Shackleton (1988), Rode et al. (2006), and Nevin and Gilbert (2005b), who suggested that females with dependent offspring may associate with humans to avoid infanticide by males. The use of humans as a shield against predation has also been reported for North American ungulates (Berger 2007; Muhly et al. 2011).

Proximate mechanisms

In addition to male avoidance as a counterstrategy for SSI, also proximate mechanisms may explain differential resource selection among the reproductive classes. The resource selection correlation between adult males and lone females was, albeit positive and significant, low during nighttime during the mating season. We speculate that this reflects the sexual difference in the strength of sexual selection. Competition for mates is typically greater among males than females (Shuster & Wade 2003), with males trading feeding for mate acquisition (Andersson 1994; Mysterud, Langvatn & Stenseth 2004). For example, males of the extremely size-dimorphic northern elephant seal (Mirounga angustirostris) can lose up to one third of their body mass during the mating season (Deutsch, Haley & Le Boeuf 1990), and male moose (Alces alces) stop feeding during the rut (Mysterud, Solberg & Yoccoz 2005). Thus, although male brown bears probably invest more in mate acquisition than
feeding, females can probably invest more in feeding and optimizing their body condition during the mating season. This probably leads to segregation in resource selection. During the postmating season, resource selection was more similar among reproductive classes, suggesting that they follow a similar resource selection strategy, i.e. hyperphagia to store fat reserves for hibernation and avoiding humans.

During spring and early summer, cub mobility may restrain maternal movement patterns (Dahle & Swenson 2003b), possibly contributing to different resource selection between females/cubs and other reproductive classes. Some of our results support this; females/cubs selected the least rugged landscapes only during the mating season, when cubs are least mobile. The relation between terrain ruggedness and cub mobility is intuitive, but there is no plausible biological relationship between cub mobility and other significant model variables. For example, females/cubs selected areas relatively close to buildings and settlements during the mating season. We found no strong collinearity between variables that could be related to cub mobility (i.e., terrain ruggedness on the local or landscape scales) with other model variables, such as land cover type, distance to buildings and settlements, road structures, and NDVI. Dahle and Swenson (2003b) attributed seasonal shifts in females/cubs’ home range sizes to their secretive behavior during the mating season, when the risk for SSI is high (Zedrosser et al. 2009), and the less secretive behavior after the mating season.

Presuming that cubs can restrict maternal movements, females should select suitable areas before giving birth (during hibernation). This implies that infanticide avoidance should also operate during den-site selection. In an Alaskan brown bear population, males selected dens at low altitudes relatively close to caribou (Rangifer tarandus) calving grounds, whereas females selected higher altitudes and steeper terrain (Libal et al. (2011). They attributed this den site segregation to a female reproductive strategy, reducing infanticide risk from adult males.

**Safety comes with costs**
Perceived predation risk alters prey’s behavior (Brown, Kotler & Bouskila 2001), irrespective of whether predation is inter- or intraspecific (Nevin & Gilbert 2005b). These behavior-mediated effects can affect prey population fitness through restricted resource selection, induced habitat change, elevated stress, etc. (Brown, Launde & Gurung 1999; Creel et al. 2005). In the brown bear, one effect of infanticide risk is reduced consumption of high-quality foods (Mattson & Reinhart 1995; Ben-David, Titus & Beier 2004; Rode, Farley & Robbins 2006). Mattson and Reinhart (1995) showed that females consuming cutthroat
trout (*Oncorhynchus clarki*) at spawning streams were less fecund than females that avoided spawning streams, and explained this by high intraspecific predation risk where bears aggregated. Infanticide can thus also increase the ecological costs for females through behavior-mediated effects (Mattson & Reinhart 1995; Janson & Van Schaik 2000).

**Conclusion**
Our results suggest that differential resource selection among reproductive classes of brown bears was partly a consequence of a female counterstrategy to avoid SSI. We found that resource selection is a complex mechanism, varying spatiotemporally and among reproductive classes. We suggest that individuals use landscape cues to assess their environment and the risk factors therein and select their resources accordingly.

In species exhibiting SSI, female avoidance of infanticidal males may be more common than reported, because proximate and ultimate causes of sex-specific behavioral strategies are difficult to disentangle (Ebensperger & Blumstein 2007; Singh et al. 2010). Therefore, we suggest that fitness effects of infanticide avoidance behavior be studied to provide ultimate explanations. Given that the rate of infanticide can depend on the rate of hunting of males (Swenson et al. 1997) and that infanticide risk can affect resource selection and mediate other behaviors, we suggest that more research be directed towards the cascade that may flow from hunting, through infanticide, and towards female fitness and their reproductive costs.

**Acknowledgements**
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**References**


Figures

Figure 1: Correlation in resource selection among reproductive classes of brown bears. The Spearman correlation coefficients and their respective 95% confidence intervals are given for correlation in resource selection between adult males (≥ 5 years) and females with cubs-of-the-year (●), between lone adult females (≥ 5 years) and females with cubs-of-the-year (X), and between lone adult females and adult males (■) during 8 3-hour intervals in the mating and postmating seasons in central Sweden during 2006-2010.

Figure 2: Diurnal and seasonal responses of brown bears to the Normalized Difference Vegetation Index (NDVI). Parameter estimates and their 95% highest posterior density intervals are shown for adult males (≥ 5 years, ●), adult lone female (≥ 5 years, ■), and females with cubs-of-the-year (X), during 8 3-hour time intervals during the mating and postmating seasons in central Sweden during 2006-2010.
Figure 3: Area-adjusted frequency of occurrence (AAFO) of brown bears in relation to distance to settlements. AAFO values for adult males ($\geq 5$ years, ---), adult lone female ($\geq 5$ years, —) and female brown bears with cubs-of-the-year (—) within a 5-km area (10* 500m wide buffer zones) around settlements in the study area, fitted with spline smoothers, during the mating and postmating season in central Sweden during 2006-2010. Values $> 1$ indicate that a given buffer area was used more relative to its availability.
Table 1: Model specification for two *a priori* candidate models of resource selection by brown bears in central Sweden, 2006-2010.

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<td>Reduced</td>
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Supporting Information

Appendix S1. Model diagnostics of the resource selection models.

Model diagnostics of brown bear resource selection models for adult males (≥ 5 years), lone adult females (≥ 5 years), and females with cubs-of-the-year during the mating and the postmating seasons in central Sweden (2006-2010). The global model was always selected as the most parsimonious. The ‘psrf’ indicates the Gelman diagnostic for model convergence, N = sample size for each specific model, ‘ts’ indicates the diurnal interval, \( \rho \) = the Spearman Rho correlation coefficient between the area-adjusted frequency of bear positions and the binned resource selection probability class for each model, and \( p = \) the p value of the Spearman Rho correlation between the area adjusted frequency of bear positions and the binned resource selection probability class for each model. \( \Delta DIC \) indicates the difference in DIC values between the two candidate models.

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Appendix S2. Examples of resource selection maps.

Details of resource selection maps of brown bears; adult males (A), females with cubs-of-the-year (B) and lone adult females (C) during the mating season and the postmating season (D, E, F, respectively) between 03:00 and 5:59. Water bodies are marked blue, light tones indicate high relative probabilities of use.
Appendix S3: Graphical representations of the modeling results.

Graphical representations of the modeling results. Parameter estimates and their 95% highest posterior density intervals of the continuous and ordinal categorical model variables for adult male (≥ 5 years, ●), adult lone female (≥ 5 years, ■) and female brown bears with cubs-of-the-year (x), during 8 3-hour time intervals during the mating and postmating seasons in central Sweden during 2006-2010. Parameter estimates, 95% Highest Posterior Density intervals, and MCMC-simulated p-values for each variable in for each of the 48 model are available on request.
**Appendix S4: Rank scores and post hoc comparisons of bear responses towards land cover types**

Rank scores and post hoc comparisons of bear responses towards land cover types.

A. Rank scores (1-4) for the land cover types ‘Bog’, ‘Young open forest’, ‘Young dense forest’, and ‘Older forest’ for adult male, lone female, and female brown bears with cubs-of-the-year during 8 3-hour diurnal intervals in the mating and postmating seasons in central Sweden from 2006-2010. μ and σ denote the mean and the standard error for each land cover type per season and reproductive class, respectively. Gray cells identify the response of a habitat type that significantly (α = 0.05) contributed to resource selection at a given diurnal interval for a given reproductive class.

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B. Mean rank scores for land cover types (B = bog, YO = young open forest, YD = young dense forest, O = older forest) per season and brown bear reproductive class (adult males (white bars), lone females (black bars), and females with cubs-of-the-year (gray bars)) in central Sweden from 2006-2010. The whiskers represent the mean + 1 standard error for a given class/land cover type. Characters (a, b, and ab) indicate significant (α = 0.05) differences between mean scores.

C. Post-hoc test results

Adult males: young dense forest always received the highest score (4) during all diurnal intervals, and was ranked significantly higher than young open forest (μ = 2.38, σ = 0.52, p < 0.001), older forest (μ = 2.13, σ = 0.99, p < 0.001), and bogs (μ = 1.5, σ = 0.76, p < 0.001).

Lone females: young dense forest was the highest ranked land cover type (μ = 3.88, σ = 0.35) during the mating season, and ranked higher than the other land cover types (young open forest: μ = 2.50, σ = 0.93, p = 0.005; older forest: μ = 2.0, σ = 0.93, p < 0.001, bogs: μ = 1.63, σ = 0.74, p < 0.001).

Females with cubs-of-the-year: We found no significant differences between rank scores of young dense forest (with the highest rank μ = 3.63, σ = 0.52) and older forest (μ = 3.25, σ = 0.71, p = 0.442), but both were ranked higher than young open forest (μ = 2.13, σ = 0.25, p_{\text{older forest}} = 0.005, p_{\text{young dense forest}} = 0.001), and bogs (μ = 1.00, σ = 0.00, p_{\text{older forest}} < 0.001, p_{\text{young dense forest}} < 0.001). During the postmating season, young open forest received the
highest score ($\mu = 3.38$, $\sigma = 0.52$), but was not significantly different from young dense forest, which was ranked as the second highest land cover type ($\mu = 3.25$, $\sigma = 0.52$, $p = 0.999$). Young open forest was then preferred above older forest, but not above young dense forest ($\mu = 2.25$, $\sigma = 0.71$, $p_{\text{young open forest}} = 0.013$, $p_{\text{young dense forest}} = 0.074$). Bogs were always the least preferred land cover class by females/cubs during the postmating season ($\mu = 1.13$, $\sigma = 0.35$, $p_{\text{all classes}} < 0.001$).
Paper IV
Fecal spectroscopy: a practical tool to assess diet quality in an opportunistic omnivore

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Key words: diet quality, feces, field exposure, near-infrared spectroscopy, NIRS, omnivore, Ursus arctos

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Abstract

Fecal indices of dietary quality can provide useful knowledge about the general ecology of a species, but only if measurements are accurate and the results are interpreted with caution. Here, we evaluated the potential of near-infrared spectroscopy (NIRS) as an analytic tool to derive fecal indices of dietary quality in an omnivorous monogastric species with a wide dietary range, the brown bear (Ursus arctos). We also tested the effects of field exposure on fecal constituents (i.e., nitrogen, lignin, crude fiber (CF), ether extracts (EE), acid detergent fiber (ADF), neutral detergent fiber (NDF), ash, and dry matter (DM)), which are commonly used to as fecal indices of dietary quality. We collected 172 fecal samples from 45 GPS-marked brown bears in south-central Sweden between May and October 2010. For each sample, we recorded maximum field exposure time (h) and canopy cover (%). We used multivariate partial least squares regression with a segmented cross validation procedure to calibrate the NIRS method. We obtained very good ($r^2 \geq 0.9$) NIRS validation results for fecal nitrogen content and NDF, and good ($0.7 \leq r^2 < 0.9$) results for lignin, CF, EE, ADF, and ash. Validation results for DM were poor ($r^2 = 0.29$). We found that field exposure time negatively affected fecal nitrogen content, especially during the first 40 hours of exposure. Because CF and NDF are strongly negatively correlated with fecal nitrogen content, concentrations of these two components increase as a consequence of field exposure. Fecal EE content appeared to be stable under field conditions. Our conclusions are twofold. First, NIRS can be an accurate, fast, and inexpensive analytic tool to evaluate certain fecal indices of dietary quality, including for omnivorous species. Second, fecal indices of dietary quality can be affected by field exposure and can vary among individual animals. Ignoring individual variance and field exposure effects on fecal indices of dietary quality may cause bias in research findings.
Introduction

Information derived from feces can provide valuable knowledge about a species’ general ecology (Putman 1984). Feeding and nutrition takes a prominent place in ecology. Evaluating dietary composition, quantity, and quality is, however, extremely difficult and often controversial, because the actual dietary intake of a wild mammal is almost always unknown (Putman 1984; Kohn & Wayne 1997). Dietary composition of fecal samples is commonly assessed using visual estimation methods (for a methodological review see Klare et al. 2011) or more recently also with genetic techniques, such as DNA-barcoding (Valentini et al. 2009). The analysis of diet quality is often carried out with stable isotope analysis on tissue samples (Crawford et al. 2008; Blanco-Fontao et al. 2010) and with standard chemical analyses on feces (e.g. the Kjeldahl extraction method (Pritchard & Robbins 1990; Gad & Shyama 2011)). These qualitative methods are very valuable in ecological research, but are relatively expensive, time consuming, as well as technically relatively complicated (Givens & Deaville 1999; Dixon & Coates 2009).

Near-infrared spectroscopy (NIRS) is a nondestructive, fast, accurate, and inexpensive technique to estimate the chemical content and composition of analytes (Cen & He 2007). The interactions (i.e., absorption, reflection, or transmittance) among electromagnetic radiation at given wavelengths and a given analyte yield a ‘spectral signature’, which can be recorded with a spectrometer. In combination with reference samples of known content and multivariate statistics, spectral signatures can be used to identify and predict certain characteristics of analytes (Næs et al. 2001). When applied to the ~ 700 – 2500 nm part of the electromagnetic spectrum, this method is referred to as NIRS (Cen & He 2007).

NIRS is routinely applied in various fields of research, such as food science (Næs et al. 1996; Cen & He 2007), clinical and pharmaceutical research (Pellicer & Bravo 2011), and animal husbandry (Givens & Deaville 1999). In animal husbandry, NIRS has often been applied to fecal samples, because there appears to be a strong correlation between the chemical composition of forage and feces derived from that forage (Dixon & Coates 2009). Fecal NIRS has, for example, been used to estimate diet quality, diet composition and digestibility, ecological impacts of grazing, and parasite burden (for a review on the use of fecal NIRS in herbivores, refer to Dixon & Coates 2009). Commonly used fecal constituents to derive indices of dietary quality include nitrogen, crude fiber (CF), ether extracts (EE), acid detergent fiber (ADF), neutral detergent fiber (NDF), lignin, and dry matter (DM) (Pritchard & Robbins 1990; Leslie et al. 2008; Dixon & Coates 2009). Although fecal NIRS has proven its potential in wildlife research, it has rarely been used, and if so, almost
exclusively in herbivores. For example, fecal NIRS was used to evaluate the dietary quality of free-ranging red deer (Cervus elaphus) and roe deer (Capreolus capreolus) (Kamler et al. 2004), white-tailed deer (Odocoileus virginianus) (Showers et al. 2006), and African elephants (Loxodonta africana) (Greyling 2004), as well as to differentiate between feces of red deer and fallow deer (Dama dama) (Tolleson et al. 2005) and between the sexes in African elephants (Greyling 2004).

NIRS calibrations are generally less accurate to predict the chemical composition of compound materials compared to raw materials (Givens & Deaville 1999). Because omnivores presumably have a wider dietary niche than herbivores, and can consume plant as well as animal material, it is expected that NIRS calibrations perform less well for omnivores than for herbivores. Fecal NIRS has nevertheless been applied to omnivores, such as domestic pigs (Sus scrofa domesticus) in controlled conditions (Zijlstra et al. 2011) and humans (Rivero-Marcotegui et al. 1998). However, there are no studies that apply fecal NIRS to omnivores in the wild.

The use of fecal constituents as indices of dietary quality has been debated and criticized, especially with respect to unstable constituents, such as nitrogen (Hobbs 1987; Wehausen 1995 cf. Leslie and Starkey 1987, Leslie et al. 2008). In addition to e.g., diet selection, seasonality, and individual variation, also environmental exposure (e.g. to sunlight, precipitation, insect activity, etc.) and sampling design (e.g. sample freshness) can cause variation in the fecal composition (Putman 1984; Leite & Stuth 1994). Ultimately, this variation can cause bias in research findings. Crucial information that is needed to account for variation in fecal composition is the time and place of defecation and the identity of the defecating individual. Information on defecation time, place, and identity of the defecating individual can only be obtained by direct observation or by tracking individuals with spatiotemporally highly accurate tracking devices, such as GPS (Global Positioning System).

Our goal was to assess the suitability of NIRS to obtain fecal indices of dietary quality in an omnivorous carnivore, based on fecal samples collected in the wild. We used the brown bear (Ursus arctos), an opportunistic omnivore, as our model species. We also evaluated the effects of field exposure time and intensity on the various fecal constituents, based on feces of GPS-marked brown bears.

**Material and methods**

We collected fecal samples from free-ranging brown bears carrying GPS-GSM (Global System for Mobile Communications, Vectronic Aerospace GmbH) collars in south-central
Sweden between May and October 2010. Refer to Martin et al. (2010) for a detailed study area description and to Arnemo et al. (2006) for bear capture and handling details. Brown bears are opportunistic feeders and their diet shifts seasonally according to forage quality and availability (Mattsson 1997; Dahle et al. 1998). In our study area bears feed mainly on graminoids, forbs, ant species (*Formica* spp. and *Camponotus herculeanus*), and moose calves (*Alces alces*) during spring and early summer (Dahle et al. 1998). During late summer and autumn, bears feed mainly on berries, i.e. blueberry (*Vaccinium myrtillus*), crowberry (*Empetrum nigrum hermaphroditum*) and cowberry (*Vaccinium vitis-idaea*) (Dahle et al. 1998).

The GPS collars were scheduled to provide 1 location every 30 minutes. We visited sites where individual bears had stayed ≥ 1.5 hours at a cluster site, i.e. at least 3 consecutive GPS locations within a radius of 30 m. We collected fecal samples at cluster sites only if no observations or signs (e.g. tracks of different size, multiple day beds, etc.) indicated that other bears might have been present at the same cluster site. For each sample, we recorded the maximum field exposure time (i.e. the time in hours from when the bear entered the cluster site until the time a sample was collected) and canopy cover (% cover, measured with a spherical forest densiometer (Lemmon 1956)) as measures of duration and intensity of field exposure. We avoided collecting soil and debris with a sample. After collection, samples were homogenized, dried at 60º C in an oven until a moisture content < 5% (measured with HP-9034C wood moisture content meter), and stored dry in a closed container at room temperature until further processing. For further analysis we reground each sample with an IKA M20 universal grinder (particle size < 1 mm), and subdivided each sample into a reference sample and a prediction sample. We used standard lab procedures (Kjeldahl, Weender and detergent fiber analysis) to obtain measures of fecal constituents (nitrogen, ADF, NDF, lignin, ash, CF, EE, DM) from each reference sample (Nehring 1960; Naumann & Bassler 1976; van Soest et al. 1991). ADF, NDF, lignin, ash, EE, CF and nitrogen were measured relative to the fecal DM content (% of fecal DM). DM content was measured (%) relative to oven dried sample weight. For each prediction sample, we obtained spectral information in the 780-2740 nm range with an MPA Multi Purpose FT-NIR spectrometer (Bruker Optik GmbH) with a helium-neon probe. We scanned each prediction sample three times, and calculated the arithmetic mean of the three spectra per sample to obtain an optimal homogenized spectrum per sample. Thus, for each fecal sample, we obtained reference values for the fecal constituents with the standard laboratory procedures, as well as spectral information with NIRS. We calculated the standard error of the method (S_{ref}) for
each constituent for which we obtained duplicate measurements in the laboratory analysis to evaluate how much the error of the NIRS method was explained by error in the reference methods (Næs et al. 2001). $S_{ref}$ is calculated according to Equation 1, where $s_i$ is the standard deviation of the duplicate measurements, \( I \) the total number of samples that were analysed and \( N \) is the number of duplicate measurements per sample.

$$S_{ref} = \sqrt{\frac{\sum_{i=1}^{I} s_i^2}{IN}}$$ [Equation 1]

We used partial least squares regression (PLSR) with a NIPALS algorithm for multivariate calibration on the 935-2670 nm spectral range (Næs et al. 2001), and considered 2nd derivative with Savitzky-Golay smoothing and Extended Multiplicative Signal Correction (EMSC) for spectral preprocessing. Spectral preprocessing methods normalize the spectra and aim to minimize overall scaling effects (e.g. measurement inaccuracy) and to facilitate detection of ‘real’ variation among the spectra (Næs et al. 2001). We used segmented cross validation to validate the calibration models, with each segment assigned to a unique ‘bear ID’ (‘leave-one-bear-out’ cross validation). We evaluated model quality for each of the fecal constituents, based on the coefficients of determination ($r^2$; $r^2 < 0.7 = \text{poor}$, $0.7 < r^2 < 0.9 = \text{good}$, $r^2 > 0.9 = \text{excellent}$ (Shenk and Westerhaus 1996)), the number of model factors, and the root mean square errors of the cross validation (RMSECV) (Næs et al. 2001). We visually evaluated outliers in the reference and predicted concentrations of fecal constituents with predicted versus reference plots. We occasionally removed outliers to improve model fit (maximum 2.9% of all records, Table 1). Assuming normality and no bias, values of $2 \times \text{RMSECV}$ around the prediction delineate its 95% confidence region (Næs et al. 2001). We used Unscrambler® 10.1 software (Camo software AS.) for the multivariate calibration and validation.

We evaluated the effects of field exposure time and canopy cover on the fecal constituents (in % DM) with linear mixed-effect regression models. We used the reference values of each fecal constituent as the response variable. For each model, we included ‘bear ID’ as a random factor and considered all possible combinations of ‘canopy cover’, ‘exposure time’, and the interaction term ‘canopy cover * exposure time’ as fixed effects (8 combinations, including a null model). We evaluated the most parsimonious model for each fecal constituent based on Akaike’s Information Criteria scores for small sample sizes ($\text{AIC}_C$) and $\text{AIC}_C$ weights (Burnham & Anderson 2002). We used the ‘lme4’ package (Bates & Maechler 2010) for
statistical modeling and generated p-values for the fixed effects of the regression models with a Markov Chain Monte Carlo algorithm (package ‘LMERConvenienceFunctions’ (Tremblay 2011)) in R 2.12.0 (R Development CoreTeam 2009). We considered α = 0.05 as the threshold level for statistical significance.

Results

We collected 172 fecal samples from 45 GPS-marked bears between 10 May and 22 September 2010. Mean field exposure time of the feces was 46.3 h (range: 13 h -104 h) and mean canopy cover at the collection sites was 75.7% (range: 0 % - 100 %). The reference values for each fecal constituent, as extracted by the standard chemical laboratory analysis, are summarized in Table 2.

NIRS calibration

We developed PLSR calibration models to predict the content of nitrogen, lignin, ash, CF, and ADF, based on EMSC preprocessed spectra. We used Savitzky-Golay 2nd derivative preprocessed spectra to predict the fecal content of EE and NDF. We used unprocessed spectra to develop a calibration equation to predict fecal DM content, because preprocessing methods did not improve the calibration results (Table 1). The optimal number of PLS factors varied from 5 (DM) to 15 (ADF) among the models (Table 1). The number of removed outliers varied from 0 (DM) to 5 (CF and Ash) among the models (Table 1). The NIRS-predicted values of the fecal constituents corresponded well with the reference values ($r^2 > 0.84$, all RMSECV between 0.78 and 4.13) (Figure 1, Table 1), with the exception of the predicted values for DM. The model to predict fecal DM performed poorly ($r^2 = 0.29$). NIRS validation diagnostics for all models are summarized in Table 1.

Field exposure

The most parsimonious models to evaluate the effect of field exposure (time and canopy cover) on the fecal content of nitrogen, lignin, ADF, NDF, ash, and CF only contained ‘exposure time’ as a fixed factor. Field exposure time significantly and negatively affected the fecal content of nitrogen ($β = -0.067$, $t = -2.856$, $p = 0.005$), and positively affected the fecal content of CF ($β = 0.08$, $t = 3.068$, $p = 0.003$) and NDF ($β = 0.149$, $t = 3.022$, $p = 0.003$). Field exposure time had no apparent effect on fecal content of lignin ($β = -0.010$, $t = -0.383$, $p = 0.702$), ADF ($β = 0.072$, $t = 1.773$, $p = 0.078$), or ash ($β = -0.076$, $t = -1.873$, $p = 0.063$) (Table 3). Fecal composition varied among individual bears, especially with regard to
fecal NDF (mean = 33.78 % DM, random effect $\sigma^2 = 22.934$) and ash content (mean = 10.22 % DM, random effect $\sigma^2 = 11.793$) (Table 3). Fecal EE content was best explained by the null model, suggesting that exposure time and intensity did not affect EE in fecal samples (Table 3). We validated each most parsimonious model with residual-versus-fit plots (Zuur et al. 2009). We found no trends in the residual-versus-fit plots, suggesting that no model assumptions were violated.

Discussion

The NIRS calibrations for fecal indices of dietary quality for the omnivorous brown bear showed a quality comparable to NIRS calibrations for herbivore feces as reported in the literature (see Dixon & Coates 2009 for a review). Dixon and Coates (2009) reported coefficients of determination between 0.58 - 0.94 for nitrogen, 082 - 0.94 for lignin, 0.76 - 0.94 for NDF, 0.79 - 0.97 for ADF, and 0.74 - 0.97 for ash. The coefficients of determination obtained in our study fell within the reported ranges and were $> 0.84$, with the exception of DM. According to the criteria proposed by Shenk and Westerhaus (1996), we obtained excellent calibration results ($r^2 > 0.9$) for nitrogen and ADF, good precision ($0.7 < r^2 < 0.9$) for NDF, ash, lignin, CF, and EE, but poor calibration results for fecal DM content. The measurement errors of the laboratory analyses ($S_{ref}$) were relatively low and explained between 10.9 % (CF) and 15.4 % (ADF) of the RMSECV of the NIRS multivariate calibration.

The use of fecal indices of dietary quality has been heavily debated, because factors such as weather, insect activity, and exposure time can affect fecal composition, and thus ultimately research findings (Putman 1984; Jenks et al. 1990; Robbins et al. 1991; Leslie et al. 2008). Especially indices based on fecal nitrogen (e.g., crude protein and correlated variables such as CF and NDF) may be unreliable, because nitrogen compounds can dissolve from feces with water or as volatile ammonia (Putman 1984; Leslie et al. 2008). Relatively dry feces, such as pellets of white-tailed deer and goats (Capra spp.) have been reported to be relatively stable under field conditions (2-3 weeks) with respect to the nitrogen content (Jenks et al. 1990; Dixon & Coates 2009). However, Dixon and Coates (2009) reported that moister feces (such as brown bear feces) can be expected to be less stable under field conditions. Our results show that exposure time negatively affected the nitrogen content in fecal samples of brown bears (approximately 0.07 ($\beta$) ± 0.023 ($\sigma$) % was lost per hour exposed in the field, Table 3). We plotted the nitrogen content of the reference samples against the field exposure...
time and it seems that nitrogen loss is most apparent during the first 40 hours of field exposure (Figure 2). Because CF and NDF are closely related with nitrogen (Pearson’s product-moment correlation test CF – nitrogen: correlation coefficient = -0.61, p < 0.001; NDF – nitrogen: correlation coefficient = -0.60, p < 0.001), we could thus also expect a significant effect of field exposure time on CF and NDF. Canopy cover was never included in the models evaluating the stability of fecal constituents, which suggests that canopy cover per se is a poor proximate for exposure intensity. We also found that fecal constituents (especially NDF and ash) can vary considerably among individuals.

Our results show that NIRS can be an accurate tool for the prediction of fecal constituents in omnivorous species with a wide dietary range. Some fecal constituents are, however, affected by the time of exposure to climatic conditions in the field, and may also vary among individual animals. It is therefore advisable to control for these factors in a statistical analysis of fecal constituents as indices of dietary quality.

Acknowledgements - We thank the 2010 field crew of the Scandinavian Brown Bear Research Project for their help in collecting and processing fecal samples. We thank W. Gregor and the Research Institute of Wildlife Ecology (FIWI) in Vienna, Austria, for their generous help and assistance in conducting the Kjeldahl extractions and providing the NIRS equipment. S. Steyaert was funded by the Austrian Research Council, project number P20182. The Scandinavian Brown Bear Research Project was funded by the Swedish Environmental Protection Agency, the Norwegian directorate for Nature Management, the Norwegian Research Council, World Wildlife Fund (WWF) Sweden and the Swedish Association for Hunting and Wildlife Management. This is paper xxx of the Scandinavian Brown Bear Research Project.

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Tables

Table 1: Validation results of near-infrared spectroscopic (NIRS) calibration models to predict the content of nitrogen, lignin, crude fiber (CF), neutral detergent fiber (NDF), acid detergent fiber (ADF), ether extracts (EE), ash, and dry matter (DM) in 172 fecal samples of brown bears, collected between May and October 2010 in central Sweden. ‘Prep.’ stands for the type of spectral preprocessing (EMSC = Extended Multiplicative Scatter Correction, 2^ND = second derivative). ‘# outliers’ indicates the number of outliers that were removed to obtain the models. ‘# factors’ indicates the number of partial least square factors that were included in the models. ‘RMSECV’ = root mean square error of the cross validation. ‘r^2’ = the coefficient of determination. ‘Reference r^2’ = the range of coefficients of determination for NIRS models as reported in the literature review by Dixon and Coates 2009.

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<th>#</th>
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Table 2: Reference values (%) of nitrogen, lignin, crude fiber (CF), neutral detergent fiber (NDF), acid detergent fiber (ADF), ether extracts (EE), ash and dry matter (DM) in brown bear feces, collected in south-central Sweden between May and October 2010. DM is expressed in % relative to the weight of oven dried feces. The other constituents are expressed as % relative to DM content. ‘SD’ = standard deviation and ‘Sref’ = standard error of the method.

<table>
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<td>6.32</td>
<td>0.282</td>
</tr>
<tr>
<td>CF</td>
<td>18.86</td>
<td>36.67</td>
<td>5.42</td>
<td>0.210</td>
</tr>
<tr>
<td>NDF</td>
<td>34.25</td>
<td>68.84</td>
<td>10.85</td>
<td>0.571</td>
</tr>
<tr>
<td>ADF</td>
<td>33.38</td>
<td>49.31</td>
<td>8.93</td>
<td>0.431</td>
</tr>
<tr>
<td>EE</td>
<td>5.03</td>
<td>12.51</td>
<td>2.07</td>
<td>na</td>
</tr>
<tr>
<td>Ash</td>
<td>10.12</td>
<td>47.65</td>
<td>8.75</td>
<td>na</td>
</tr>
<tr>
<td>DM</td>
<td>91.94</td>
<td>99.71</td>
<td>1.33</td>
<td>na</td>
</tr>
</tbody>
</table>
Table 3: Outputs of the most parsimonious models to evaluate the effect of field exposure time and intensity on fecal constituents (nitrogen, lignin, crude fiber (CF), neutral detergent fiber (NDF), acid detergent fiber (ADF), ether extracts (EE), ash; in % relative to fecal dry matter content DM) in brown bear feces (collected during May-October 2010, central Sweden) as predicted with near-infrared spectroscopy (NIRS). ‘$\beta$’ = parameter estimate, ‘$\sigma$’ = standard error, ‘t’ = test statistic, ‘p’ = p value and ‘$\sigma^2$’ indicates the variance of the random component (Bear ID). ‘$wAIC_c$’ = Akaike’s weight for each most parsimonious regression model.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Field exposure time</th>
<th>Bear ID</th>
<th>$wAIC_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\beta$</td>
<td>$\sigma$</td>
<td>$t$</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>-0.067</td>
<td>0.023</td>
<td>-2.856</td>
</tr>
<tr>
<td>Lignin</td>
<td>-0.012</td>
<td>0.027</td>
<td>-0.383</td>
</tr>
<tr>
<td>CF</td>
<td>0.08</td>
<td>0.026</td>
<td>3.068</td>
</tr>
<tr>
<td>NDF</td>
<td>0.149</td>
<td>0.049</td>
<td>1.773</td>
</tr>
<tr>
<td>ADF</td>
<td>0.072</td>
<td>0.041</td>
<td>3.022</td>
</tr>
<tr>
<td>EE</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ash</td>
<td>0.076</td>
<td>0.041</td>
<td>-1.873</td>
</tr>
</tbody>
</table>

Superscript * indicates the variance of the random component (Bear ID). ‘$wAIC_c$’ = Akaike’s weight for each most parsimonious regression model.

Field exposure time was the only fixed variable that was included in the most parsimonious model to evaluate fecal content of nitrogen, lignin, CF, NDF, ADF and ash. Fecal EE content was best explained by the null model. Each fecal constituent was treated separately as a response variable in a mixed effect regression model.
Figures

Figure 1: Concentrations (%) of nitrogen, lignin, crude fiber (CF), neutral detergent fiber (NDF), acid detergent fiber (ADF), ether extracts (EE), ash, and dry matter (DM) predicted by Near-Infrared Reflectance Spectroscopy plotted against reference concentrations based on laboratory extractions (Kjeldah, Weender and detergent fiber analysis) in feces of brown bears collected in central Sweden between May and October 2010. DM is expressed as % relative to the weight of oven-dried feces, whereas the other components are measured in % relative to the fecal DM content. Refer to Table 1 for statistical details. The diagonal line represents perfect linear correlation (x=y).
Figure 2: Nitrogen content (in % of fecal dry matter (DM), derived with the Kjeldalh nitrogen extraction method) in brown bear feces plotted against the time (h) a fecal sample was exposed to field conditions. The data were fitted with a LOESS smoother (—) to facilitate interpretation.
Coping with sexually selected infanticide: a food-or-safety trade-off?

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Abstract

Predation risk is an important selective force and strategies to avoid it should be selected for. Risk effects emerge when individuals face a trade-off between selecting optimal resources and minimizing predation risk. Risk effects are also expected to emerge for intraspecific predation such as infanticide. We investigated this trade-off in relation to sexually selected infanticide (SSI) in the brown bear (Ursus arctos), our model species. Strong evidence for SSI in brown bears exist, and trade-offs in resource selection in relation to SSI risk have been suggested. We hypothesized that females with cubs-of-the-year experience a dietary cost as a consequence of altered resource selection to avoid of SSI. In species with strong sexual selection, males are expected to prioritize mate acquisition above maintaining body condition during the mating season. We evaluated our hypothesis in a Scandinavian population, and used fecal crude fiber content (FCF) of GPS-marked lone females, females with cubs-of-the-year and adult males as a proxy for diet quality. We predicted that 1) during the mating season, females with cubs-of-the-year had diets of lower quality than a) lone females, but b) of similar quality than adult males. We predicted that 2) during the postmating season, females with cubs-of-the-year had diets of a) at least similar quality than lone females, and b) of similar or lower diet quality than adult males. We used mixed-effect regression models to test our predictions, and controlled for several factors that could affect FCF content (e.g. age, processing time). We found that diet quality was strongly related to reproductive status, during both the mating and the postmating season. We found that the diet quality of females with cubs-of-the-year was significantly lower during the mating season than that of lone females, and significantly higher during the postmating season. Diet quality of adult males did not differ from that of lone females and females with cubs-of-the-year during both seasons. We suggest that females with cubs-of-the-year experienced a nutritive cost as a risk effect of SSI, and probably compensate for that cost during the postmating season, by selecting high quality diets. We suggest that risk effects of SSI can add to the female costs of reproduction.

Key words: brown bear, diet quality, predation, risk effects, risk regime, sexually selected infanticide
**Introduction**

Predation is a strong selective force and strategies to minimize predation risk should be selected for (Lima and Dill 1990; Brown et al. 1999). Antipredator adaptations include traits that reduce detection (e.g. cryptic behavior), promote escape (e.g. grouping for vigilance), and hamper handling success (e.g. armor) by predators (Vermeij 1982). Individuals that are more successful in avoiding predation have higher potential for survival and reproduction (Lind and Cresswell 2005). Although antipredator adaptations have an obvious fitness advantage, they can also be costly (Brown and Kotler 2004). For example, many species reduce predation risk by altering their selection for resources in space and time, by trading off optimal resources for safety (Pianka 1976; Lima and Bednekoff 1998; Brown and Kotler 2004; Houston et al. 2011). Because these trade-offs are directly related to fitness (Stearns 1989), prey can incur a significant fitness cost due to predation risk (Creel and Christianson 2008). In mammals, vulnerability to predation is highest during the first year of life (Lind and Cresswell 2005). Therefore, the trade-off between seeking food or safety is expected to be strongest among females with dependent offspring, which need to meet high nutritional requirements, safety, as well as to maximize their reproductive output (Gittleman and Thompson 1988; Main 2008). For example, in many ungulate species, females and their dependent young segregate from males as a female reproductive strategy and sometimes select for poor quality habitats, but with low predation risk (Bowyer 2004; Ruckstuhl 2007; Main 2008).

Animals respond rapidly to changing regimes of predation risk (Lima and Bednekoff 1998; Brown and Kotler 2004). If predation risk is predictable in time (e.g. a season, night/day), animals are expected to feed at the lowest possible rates to meet energetic requirements for bridging the risk period, irrespective of the actual risk (i.e. the risk spreading theorem) (Houston et al. 1993). After a predictable period of high risk, animals can compensate for the energetic cost of reduced feeding during the period of high risk, by e.g., feeding more intensively or selecting higher quality foods (Lima and Bednekoff 1998; Carrascal and Polo 1999; Cruz-Rivera and Hay 2000). Risk factors can be identified by relating behavior with temporal variation in risk (Lima and Bednekoff 1998; Brown and Kotler 2004).

Sexually selected infanticide (SSI) is a form of intraspecific predation in which mating opportunities, rather than prey consumption, is the perpetrators’ goal. The SSI hypothesis requires that (i) males kill conspecific but unrelated dependent offspring, (ii) the victimized
mother enters estrus shortly after offspring loss, and (iii) the perpetrating male has a high probability to sire the victimized mother’s next offspring (Hrdy 1979). SSI is common among polygamous mammals with lactational anestrus and in which lactation lasts longer than gestation (van Schaik 2000). SSI has mostly been documented in primates, carnivores and rodents (Hausfater and Hrdy 1984; van Schaik and Janson 2000). In seasonal breeders, SSI can only be beneficial for males when committed during mating season and when females rapidly reenter estrus (Bartos and Madlafousek 1994; Swenson and Haroldson 2008). Because SSI has an obvious fitness cost for females, various counterstrategies for SSI have evolved, including multi-male mating, pregnancy termination, territoriality, grouping, and spatiotemporal avoidance (Agrell et al. 1998; Ebensperger 1998). Evidence for spatiotemporal avoidance to reduce SSI risk is extremely rare (Ebensperger and Blumstein 2007), but suggestive evidence has been provided for e.g., orangutans (*Pongo pygmaeus*) (Setiawan et al. 1996), gorillas (*Gorilla gorilla*) (Stokes et al. 2003), lions (*Panthera leo*) (Packer and Pusey 1983) and brown bears (*Ursus arctos*) (Wielgus and Bunnell 1995). Analogous with interspecific predation, a food-or-safety trade-off in resource selection by females with dependent offspring is expected in species with SSI. However, evidence for this trade-off in relation to SSI has not yet been documented.

Here, we evaluate the food or safety trade-off in relation to SSI theory in our model species, the brown bear. Brown bears are size-dimorphic nonsocial large carnivores with strong evidence for SSI (Swenson et al. 1997; Bellemain et al. 2006). Brown bears are polygamous and have a mating season that lasts from spring to early summer (Steyaert et al. 2012). Suggestive evidence exists that females/cubs alter their resource selection in space and time to reduce the risk for SSI (Wielgus and Bunnell 1995, Steyaert et al. submitted).

We hypothesized that females with cubs-of-the-year (hereafter ‘females/cubs’, ≥ 5 years, accompanied by cubs-of-the-year) trade food for safety to reduce the risk for SSI. In species with strong sexual selection, such as the brown bear, males often prioritize competition for mates over maintaining body condition during the mating season (Mysterud et al. 2004). We compared diet quality of females/cubs, lone females (≥ 5 years), and adult males (≥ 5 years) between the mating and the post mating season to evaluate the hypothesis. We predicted that 1) during the mating season, females with cubs-of-the-year had diets of lower quality than a) lone females, but b) of similar quality than adult males. We predicted that 2) during the postmating season, females with cubs-of-the-year had diets of a) at least similar quality than
lone females, and b) of similar or lower diet quality than adult males, because of the male body size advantage for resource competition (Craighead et al. 1995).

Methods

Study area and species
Our study was conducted in Dalarna and Gävleborg counties in south-central Sweden (61°30’ N, 15°00’ E), in an intensively managed boreal forest ecosystem. The study area encompasses ~13,000 km², and the bear density is ~30 individuals/1000 km² (Bellemain et al. 2005). The bear population is intensively hunted during autumn (21 August until quotas are filled), but family groups, i.e. females accompanied with young irrespective of their age, are protected (Bischof et al. 2008). Refer to Martin et al. (2010) for a detailed study area description.

Brown bears are size dimorphic, with adult males up to 2.2 times the size of adult females (Schwartz et al. 2003). Infanticide is common in brown bears (Craighead et al. 1995; Schwartz et al. 2003) and has been suggested as the most important source of natural mortality in some populations (Swenson 2003). Infanticide is almost exclusively committed by males during the mating season (Bellemain et al. 2006; Zedrosser et al. 2009). Strong support for SSI in the brown bear exists (Swenson et al. 1997; Swenson et al. 2001; Bellemain et al. 2006), but is contested (Miller et al. 2003; McLellan 2005). Females use various strategies to reduce the risk of infanticide, including direct defense (Craighead et al. 1995), promiscuity (Bellemain et al. 2006), and spatiotemporal avoidance of conspecifics (Mattson and Reinhart 1995; Wielgus and Bunnell 1995; Ben-David et al. 2004; Steyaert et al. unpublished data B, C). In our study area, food sources are relatively evenly distributed over the landscape and bears do not aggregate. During spring, bears feed mainly on graminoids, forbs, insects, and ungulates (moose (Alces alces) calves and carrion). Summer diet comprises mostly forbs, insects, and some moose. During hyperphagia in autumn, bears feed almost exclusively on berries (bilberry (Vaccinium myrtillus), cowberry (V. vitis idaea), and crowberry (Epetrum spp.)) (Dahle et al. 1998).

Diet quality and data collection
Dietary intake of wild and elusive mammals is extremely difficult to estimate in the field (Putman 1984). However, the chemical composition of forage and feces derived from that
forage correlate strongly (Dixon & Coates 2009). Therefore, measures derived from feces can serve as proxies for diet quality (Putman 1984; Leslie et al. 2008; Dixon and Coates 2009). The digestive efficiency of brown bears is similar to those of obligate carnivores (Bunnell and Hamilton 1983; Clauss et al. 2010), and bears are not adapted to digest coarse forage efficiently (Bunnell and Hamilton 1983). Therefore, we used fecal crude fiber content (FCF, in % dry fecal matter (% DM)), i.e. the undigested residue of plant material in feces after extraction with solvents, acid detergents, and dilute alkali (Williams and Olmstead 1935), as a proxy for diet quality. High FCF values indicate low diet quality, because fiber is difficult to digest for bears (Clauss et al. 2010, Clauss personal communication), and diets consisting of plant material are less energetic and contain less protein than animal-based diets (Pritchard and Robbins 1990; Clauss et al. 2010).

We collected feces from free-ranging adult males, females/cubs and lone females marked with GPS-GSM collars (Global System for Mobile Communications, Vectronic Aerospace GmbH) during the mating season (1 May – 15 July) and postmating season (1 August – 30 September) of 2010. Refer to Arnemo et al. (2011) for bear capture and handling details. The GPS collars were scheduled to provide 1 location every 30 minutes. We continuously monitored cub survival during the study period with surveys from helicopters, direct observations from ground, and from signs of cubs (e.g. tracks, feces, and scratch marks on trees) collected at clusters of their mothers’ GPS positions (hereafter ‘cluster sites’, minimum 3 consecutive GPS positions within a 30-m radius circle). We visited cluster sites of individual bears to collect fecal samples. We never visited a cluster site within 24 hours after a bear had left (> 500 m) the site, and aimed collect one sample per bear per week. To assure assigning the correct bear ID to each sample, we only collected feces if no signs (e.g. tracks, feces, and scratch marks on trees) suggested that other bears might have been present at the same cluster site. To control for possible effects of field exposure on FCF content, we recorded the maximum time that a sample could have been exposed to field conditions (i.e. time (in hours) from when the bear entered a cluster site until the time a sample was collected, hereafter ‘time in the field’) and canopy cover (% cover, measured with a forest densiometer (Lemmon 1956)) as measures of duration and intensity of field exposure. We used near infrared spectroscopy (NIRS) to determine FCF content in each sample. We used partial least square regression for multivariate calibration after Extended Multiplicative Signal Correction of spectra, and obtained a coefficient of determination of 0.88 ($r^2 >0.90$ is considered excellent (Shenk and Westerhaus 1996)). Refer to Steyaert et al. (in press) for a
description of the method, NIRS calibration, and validation. During the NIRS preprocessing stage, we oven-dried each sample at 60°C until the fecal moisture content was < 5%. For every sample, we recorded the drying time in the oven (hereafter ‘drying time’, in hours) to control for potential effects of the drying process on FCF content.

Statistical analysis
We used linear mixed-effect regression models to test our predictions with FCF content as the response variable. We included bear ID as a random component because of repeated FCF measures per bear. We considered ‘reproductive state’, ‘canopy cover’, ‘time in the field’, ‘canopy cover * time in the field’, and ‘drying time’ for inclusion in the most parsimonious model. We also considered ‘bear age’ and the interactions of ‘bear age * reproductive state’ for inclusion in our models, because younger and smaller individuals may be less experienced and have lower competitive abilities than older ones (Paitz et al. 2007; Zedrosser et al. 2009), and this may affect reproductive classes differently. We used second-order bias-corrected Akaike’s Information Criteria (AIC) model difference values ($\Delta$AIC$_C$), model weights ($\text{AIC}_C$), and evidence ratios ($E_{D}$) for model selection (Burnham and Anderson 2002). We report results of candidate models with $\Delta$AIC$_C$ values < 2. We considered an $\alpha = 0.05$ threshold level for statistical significance for evaluation model term effects (Zuur et al. 2009).

We created separate models for each season because of the nature of the hypotheses and technical reasons.

We evaluated each prediction by running all possible (n = 128) combinations of model terms, with the expectation that ‘reproductive state’ would be included as a significant variable in the top ranked model ($\Delta$AIC$_C = 0$). We visually validated the most parsimonious models by evaluating residual versus fitted plots (Zuur et al. 2009). We used the ‘lme4’ (Bates and Maechler 2010) and ‘MuMIn’ (Barton 2012) packages in R 2.12.0 (RDevelopmentCoreTeam 2009) for statistical analysis.

Results
We obtained FCF measurements of 491 ($N_{\text{mating season}} = 312$, $N_{\text{postmating season}} = 179$) fecal samples collected from 30 individuals, including 12 lone females (234 samples), 11 adult males (135 samples), and nine females/cubs (122 samples). Average time between two samples collected from the same bear was 7.5 days. Four of the nine females/cubs
experienced litter loss during the mating season. Two females/cubs lost their entire litter (one and three cubs respectively) due to infanticide during the mating season. We classified these two females as ‘lone females’ after they lost their litter. We recorded partial litter loss (one cub survived) due to infanticide by a GPS-marked male in one case, and one female lost one cub due to unknown reasons. No litter loss occurred during the postmating season.

During the mating season, the most parsimonious model to evaluate the FCF content in bear feces contained ‘reproductive state’, ‘drying time’, ‘time in the field’ and ‘canopy cover’. The three highest ΔAIC<sub>C</sub> - ranked models included ‘reproductive state’ as a model term, and the evidence ratio between the most parsimonious model (ΔAIC<sub>C</sub> = 0, AIC<sub>CW</sub> = 0.747) and the first model that did not include ‘reproductive state’ (model rank 4, ΔAIC<sub>C</sub> = 9.18, AIC<sub>CW</sub> = 0.051) was 14.7 (Table 1). During the mating season, feces of females/cubs contained more crude fiber than feces of lone females (β = 2.709, σ = 1.147, t = 2.362, p = 0.019), and there was no significant difference between FCF content in feces from adult males and lone females (β = 0.367, σ = 1.251, t = 0.294, p = 0.769) (Table 2, Figure 1). We found no significant difference in FCF content between females/cubs and adult males (β = 2.34, σ = 1.34, t = 1.756, p = 0.082; after exchanging ‘lone females’ with ‘adult males’ as the reference level). ‘Drying time’ significantly affected FCF content (β = -0.031, σ = 0.007, t = -0.044, p <0.001). ‘Canopy cover’ and ‘time in the field’ did not strongly affect FCF content (canopy cover, β = -0.026, σ = 0.014, t = -1.906, p = 0.058; time in the field, β = 0.006, σ = 0.009, t = 0.671, p = 0.503) (Table 2).

During the postmating season, the most parsimonious model included ‘reproductive state’, ‘time in the field’ and ‘canopy cover’ as model terms. The 12 highest ΔAIC<sub>C</sub> - ranked models included ‘reproductive state’ as a model term. The evidence ratio between the highest ranked model (ΔAIC<sub>C</sub> = 0, AIC<sub>CW</sub> = 0.217) and the first model that did not include ‘reproductive state’ (ΔAIC<sub>C</sub> = 5.64, AIC<sub>CW</sub> = 0.012) was 16.6 (Table 3). During the postmating season, feces of females/cubs contained less crude fiber than feces of lone females (β = -4.374, σ = 2.153, t = -2.032, p = 0.044), and feces of lone females and of adult males did not differ in FCF content (β = -0.933, σ = 1.472, t = -0.634, p = 0.527) (Table 4). Canopy cover had a significant effect on FCF content (β = 0.030, σ = 0.012, t = 2.564, p = 0.011), but no effect was found for ‘time in the field’ (β = 0.001, σ = 0.015, t = 0.086, p = 0.931) (Table 4). We found no significant difference in FCF content between females/cubs and adult males during the postmating season (β = -3.44, σ = 2.197, t = 1.566, p = 0.119; after exchanging ‘lone females’ with ‘adult males’ as the reference level). During the postmating season, four other
models had $\Delta AIC_c$ scores $\leq 2$ (Table 3). The results of these models were similar as the results of the most parsimonious model; feces of females/cubs contained more crude fiber than feces from lone females ($p < 0.043$, except in the 5th ranked model, $p = 0.051$) (Appendix 1), and FCF content did not differ between adult males and lone females ($0.469 < p < 0.556$). We found no apparent trends in the fitted versus residual plots for either prediction, suggesting that no model assumptions were violated.

**Discussion**

The diet quality of bears in our study system varied across seasons and reproductive classes. We found support for prediction 1a, 1b, and 2a, i.e., during the mating season, feces of females/cubs had higher FCF content than feces of lone females but not higher than adult males, and the diet quality of females/cubs was higher than that of lone females. We found no support for prediction 2b, i.e., that adult males did not have a better quality diet than females/cubs and lone females during the post mating season. Our results support previous findings, i.e., that females/cubs alter their resource selection to reduce the risk for SSI (Steyaert et al. unpublished data), and suggest that avoiding SSI in space and time comes with a nutritive cost. Because this nutritive cost was only apparent during the mating season, our results suggest that the sexual selection hypothesis explains infanticide in our study system.

FCF is a coarse measure for diet quality, and provides no information about the actual intake or dietary composition. Because FCF is a proxy for diet quality, results must be interpreted cautiously and remain suggestive. Pritchard and Robbins (1990), Clauss (2010), and Bunnell and Hamilton (1983) show that digestibility of foods is directly related to diet composition in bears, and found no differences in digestibility of foods between the sexes, species, and taxonomic groups of carnivores. Additional fine-scaled qualitative methods, such as fecal DNA barcoding (Valentini et al. 2009), would improve our understanding of the foraging ecology of various reproductive classes of bears and the mechanisms behind them.

Trade-offs between selecting good quality resources and predation risk have been documented in many species of several clades, both with experimental research designs and under field conditions. One appealing example is the effect of the reintroduction of wolves (*Canis lupus*) on elk (*Cervus elaphus*) behavior in the Greater Yellowstone Ecosystem. In the presence of the newly introduced predator, elk started to avoid their preferred foraging habitats and used more often the protective cover of forests (Creel et al. 2005). The
reintroduction of wolves affected also aggregation behavior as well as foraging behavior, and ultimately the physiology and demography of the resident elk population Creel et al. (2007). Similar examples are common in the literature, and almost exclusively support the hypothesis that animals tradeoff between food and safety, and that indirect effects of predation risk cause fitness effects (see Lima and Dill 1990; Lima and Bednekoff 1998; Brown et al. 2001; Brown and Kotler 2004; Creel and Christianson 2008).

Risk effects of infanticide avoidance are rare in the literature. Loseto et al. (2006), for example, suggested that in beluga whales (Delphinapterus leucas), female groups with calves adapted their habitat selection partly to avoid infanticide by males; and female orangutans with offspring were suggested to avoid concentrated food sources, such as fruit trees, to avoid infanticide by males (Setiawan et al. 1996). Risk effects of infanticide are probably bests studied in the brown bear, and relate to segregation among different reproductive classes of bears (Wielgus and Bunnell 1995; Libal et al. 2011). Proximate and ultimate causes of segregation are, however, difficult to disentangle (Sih and McCarthy 2002; Ruckstuhl 2007). In bears, segregation is often explained as the consequence of both a female strategy to protect offspring from infanticide, a result of sexual size dimorphism and the related nutritional needs and competitive abilities (Mattson and Reinhart 1995; Ben-David et al. 2004; Nevin and Gilbert 2005b; Rode et al. 2006). Most research on segregation in bears has been conducted in systems with concentrated food sources, such as salmon (Oncorhynchus spp.), salt marshes, and garbage dumps (Craighead et al. 1995; Mattson and Reinhart 1995; Ben-David et al. 2004). Bears congregate at these food sources and local dominance hierarchies develop, which are typically controlled by larger and more aggressive males (Craighead et al. 1995). The risk of infanticide is high at these congregations (Mattson and Reinhart 1995; Ben-David et al. 2004). However, avoiding these concentrated food sources to minimize infanticide risk is costly, because feeding and fat storage is essential for hibernation, cub production, and cub survival (Farley and Robbins 1995; Ben-David et al. 2004; Nevin and Gilbert 2005a). Thus, in systems with concentrated foods, an obvious trade-off exists between infanticide risk and nutrient intake (Rode et al. 2006).

In our study system, no concentrated food sources occur and segregation in resource selection among various reproductive classes is less obvious. Previous research in our study system suggested, however, that females/cubs adopt an elusive life-style (Dahle and Swenson 2003) and select their resources in a spatiotemporally different or inverse way than adult males and lone females to avoid SSI (Steyaert et al. submitted). For example, females/cubs
selected for the least rugged landscapes, more open habitat types, and areas relatively close to human settlements during the mating season, whereas adult males selected for the most rugged terrain, the densest habitats, and areas relatively far from human settlements (Steyaert et al. unpublished data). After the mating season, when the risk for SSI declines, resource selection among various reproductive classes converged (Steyaert et al. unpublished data), and females/cubs avoided areas in close proximity to human infrastructures, and selected for denser habitat types and for the most rugged landscapes (Steyaert et al. unpublished). The change in the diet quality of females/cubs probably reflects the seasonal shift in their resource selection, and its pattern corresponds with the expected food-of-safety trade-off under a changing SSI risk regime.

In our study system, the risk regime changes drastically throughout the year, and differently affects various reproductive classes. During the postmating season, females/cubs are freed from the risk of SSI, and human hunting becomes a major risk factor for all classes of bears except family groups (Bischof et al. 2008). At the onset of the hunting season, adult males and lone females abruptly become more nocturnal (Ordiz et al. in press.). Females/cubs also adjust their movement patterns, but much less than adult males and lone females. Also Martin (2009) showed that females/cubs are much more day-active during hyperphagia. We suggest that the observed patterns in diet quality during the postmating season are probably explained by compensatory foraging of females/cubs in the absence of SSI, and that the risk effect of hunting constrains foraging efficiency of adult males and lone females. Because we did not find differences in diet quality during the mating and the postmating season between lone females and adult males, we suggest that size dimorphism, related nutritive needs, and competitive abilities are less likely to cause segregation in resource selection in our study system, and perhaps in general in a systems with relatively evenly distributed foods.

Cubs are highly altricial at birth, and females/cubs stay longer in the den and around the den site than other reproductive classes and move less than lone females (Friebe et al. 2001). Movement rates of females/cubs and lone females average approximately 0.2 km/h and 0.45 km/h during the mating season, respectively (Steyaert et al. unpublished data). With a movement capacity of 0.2km/h, females/cubs could cover considerable daily distances, and perhaps reach good quality foraging habitat. Nevertheless, they typically adopt an elusive life-style with small home ranges compared to conspecifics (Swenson 2003) and home range sizes of females/cubs were negatively related to population density (Dahle and Swenson 2003). Also, females/cubs that moved more during the mating season have a higher
probability to lose offspring (Steyaert et al. submitted), and offspring loss in our study system is almost exclusively caused by infanticide by males. We suggest that cub mobility is not likely to explain the observed differences in diet quality among reproductive classes and seasons. However, the effect of cub mobility on diet quality of females/cubs cannot be ruled out.

Conclusion

Risk effects of predation have been widely studied during the last three decades, and evidence for the food-or-safety trade-off is accumulating for many species of invertebrates, amphibians, fishes, birds and mammals (see Lima and Dill 1990; Lima and Bednekoff 1998; Brown et al. 2001; Brown and Kotler 2004; Creel and Christianson 2008). Food or safety trade-offs have also been documented or suggested in relation to infanticide. With the exception of few primate species (e.g. orangutan (Setiawan et al. 1996)), infanticide risk effects have almost exclusively been suggested or studied in bears (e.g., Wielgus and Bunnell 1994; Nevin and Gilbert 2005a; Rode et al. 2006), but not in relation to the adaptive significance of infanticide. Our results suggest that females/cubs have a lower diet quality than lone females during the mating season, but not during the postmating season, when the opposite pattern was found. Our results support the hypothesis that infanticide in our study system is an adaptive male reproductive strategy that causes females with dependent offspring to trade food quality for safety.

In the realm of optimal foraging theory, predation, and predation risk, it is not surprising that a food or safety trade-off emerges for intraspecific predation such as infanticide. Temporal variability in the risk of infanticide can, however, be useful to disentangle its functional form. We suggest that a food-or-safety trade-off can be widespread among species in SSI is an important source of offspring mortality. SSI directly affects a female’s reproductive success and largely increases her energetic investment per capita offspring, which most likely is constrained by the risk of SSI. Risk effects of SSI add to the females’ costs of reproduction, but the extent of that cost is not known and needs to be addressed in future research.
Acknowledgements

We thank the 2010 field crew of the Scandinavian Brown Bear Research Project for their help in collecting and processing fecal samples, and especially M. Müller and F. Hütter for processing the samples. The Scandinavian Brown Bear Research Project was funded by the Norwegian Research Council, the Swedish Environmental Protection Agency, the Norwegian directorate for Nature Management, World Wildlife Fund (WWF) Sweden and the Swedish Association for Hunting and Wildlife Management. S. Steyaert and the 2010 fieldwork was funded by the Austrian Research Council, project number P20182.

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Hrdy SB (1979) Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology 1:13-40


Table 1. Model structure of the 10 top-ranked models from all (128) possible combinations of 7 potential model variables (intercept not shown) to evaluate fecal crude fiber content in brown bear feces, collected during the 2010 mating season in central Sweden. Inclusion of a variable in a model is indicated with a ‘+’. We used second-order bias-corrected AIC differences (relative to the most parsimonious model, ΔAIC_C), weights (AIC_CW), and evidence ratios (E_I) as model diagnostics.

<table>
<thead>
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<th>Rank</th>
<th>Model variable</th>
<th>Model Diagnostics</th>
</tr>
</thead>
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<td>Age + Canopy cover + Time in the field + Drying time + Reproductive state</td>
<td>0 0.747 1.0</td>
</tr>
<tr>
<td>2</td>
<td>Canopy cover + Time in the field + Drying time + Reproductive state</td>
<td>4.073 0.097 7.7</td>
</tr>
<tr>
<td>3</td>
<td>Age * Reproductive state + Canopy cover * Time in the field</td>
<td>4.117 0.095 7.8</td>
</tr>
<tr>
<td>4</td>
<td>+ + + +</td>
<td>5.377 0.051 14.7</td>
</tr>
<tr>
<td>5</td>
<td>+ + + +</td>
<td>9.18 0.008 98.5</td>
</tr>
<tr>
<td>6</td>
<td>+ + +</td>
<td>13.04 0.001 678.6</td>
</tr>
<tr>
<td>7</td>
<td>+ + + +</td>
<td>15.43 0.000 2242.7</td>
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<td>8</td>
<td>+ + + + +</td>
<td>17.04 0.000 5014.1</td>
</tr>
<tr>
<td>9</td>
<td>+ + + +</td>
<td>17.12 0.000 5218.7</td>
</tr>
<tr>
<td>10</td>
<td>+ +</td>
<td>18.28 0.000 9320.8</td>
</tr>
</tbody>
</table>
Table 2. Results of the most parsimonious regression model to evaluate fiber content in feces of GPS-marked adult males, females with cubs-of-the-year (females/cubs), and lone female brown bears that were collected during the 2010 mating season in central Sweden. The reference levels for comparison for the categorical variables ‘Reproductive state’ and ‘Season’ are ‘Lone females’ and ‘Mating season’, respectively. ‘CL’ indicate the 2.5 % lower and 97.5 % upper confidence limit, calculates as $\beta \pm 1.96 \times \sigma$.

<table>
<thead>
<tr>
<th></th>
<th>$\beta$</th>
<th>$\sigma$</th>
<th>2.5% CL</th>
<th>97.5% CL</th>
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<td>0.671</td>
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<tr>
<td>Drying time</td>
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<td>0.007</td>
<td>-0.044</td>
<td>-0.017</td>
<td>-4.350</td>
<td>&lt;0.001</td>
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<tr>
<td>Reproductive state</td>
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<td></td>
<td></td>
<td></td>
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<td>Adult males</td>
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<td>Females/cubs</td>
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<td>1.147</td>
<td>0.461</td>
<td>4.957</td>
<td>2.362</td>
<td>0.019</td>
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</table>
Table 3. Model structure of the 15 top-ranked models from all (128) possible combinations of 7 potential model variables (intercept not shown) to evaluate fecal crude fiber content in brown bear feces, collected during the 2010 postmating season in central Sweden. Inclusion of a variable in a model is indicated with a ‘+’. We used second-order bias-corrected AIC differences (relative to the most parsimonious model, ΔAIC\(_C\)), weights (AIC\(_CW\)), and evidence ratios (E\(_I\)) as model diagnostics.

<table>
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</tr>
<tr>
<td>15</td>
<td>+</td>
<td>+</td>
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Table 4. Results of the most parsimonious regression model to evaluate fiber content in feces of GPS-marked adult males, females with cubs-of-the-year (females/cubs), and lone female brown bears that were collected during the 2010 postmating season in central Sweden. The reference levels for comparison for the categorical variables ‘Reproductive state’ and ‘Season’ are ‘Lone females’ and ‘Mating season’, respectively. ‘CL’ indicate the 2.5 % lower and 97.5 % upper confidence limit, calculates as $\beta \pm 1.96 \times \sigma$.

<table>
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<tr>
<th></th>
<th>$\beta$</th>
<th>$\sigma$</th>
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<th>97.5% CL</th>
<th>t-value</th>
<th>p-value</th>
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</tr>
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<td>Canopy cover</td>
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<td>0.007</td>
<td>0.052</td>
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<td>Time in the field</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult males</td>
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<td>-3.818</td>
<td>1.952</td>
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<td>-8.593</td>
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Figure 1. Mean fiber content (%DM) in brown bear feces of lone females (LF), adult males (AM), and females with cubs-of-the-year (FWC) that were collected in central Sweden in 2010 during the mating season (black) and the postmating season (grey). Whiskers indicate the 95% confidence interval around the estimate.
**Supplementary material**

Appendix 1. Candidate models with $\Delta \text{AIC}_C$ values $\leq 2$. Models with $\Delta \text{AIC}_C$ values $\leq 2$ were obtained only for prediction 2, to evaluate the effect of reproductive state (lone females, adult males, females/cubs) on the fecal crude fiber content in brown bear feces during the 2010 postmating season in central Sweden.

<table>
<thead>
<tr>
<th>Model variable</th>
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<td>20.713</td>
<td>14.201</td>
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<td>0.008</td>
<td>0.052</td>
<td>2.709</td>
<td>0.007</td>
</tr>
<tr>
<td>Reproductive state</td>
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<td>-3.820</td>
<td>1.914</td>
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<tr>
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<td>Females/cubs</td>
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Rank 2  $\Delta \text{AIC}_C = 0.128$  $\text{AIC}_C = 0.204$  $E_D = 1.1$

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<th>97.5% CL</th>
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<td>0.113</td>
<td>0.910</td>
</tr>
<tr>
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<td>0.862</td>
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<tr>
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<td>Adult Adult male</td>
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<td>3.234</td>
<td>-8.670</td>
<td>4.008</td>
<td>-0.721</td>
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<tr>
<td></td>
<td>Females/cubs</td>
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<tr>
<td>Reproductive state * Age</td>
<td>Adult Adult male</td>
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<td>0.432</td>
</tr>
<tr>
<td></td>
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Rank 3  $\Delta \text{AIC}_C = 1.231$  $\text{AIC}_C = 0.118$  $E_D = 1.9$

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<tr>
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<tr>
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<tr>
<td>Reproductive state * Age</td>
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Rank 4  $\Delta \text{AIC}_C = 1.276$  $\text{AIC}_C = 0.115$  $E_D = 2.0$

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<td>Females/cubs</td>
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<td>-0.019</td>
<td>-1.968</td>
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</table>

Rank 5  $\Delta \text{AIC}_C = 1.655$  $\text{AIC}_C = 0.095$  $E_D = 2.3$
Paper VI
Brown bear conservation and the ghost of persecution past

Andreas Zedrosser\textsuperscript{a,b,*}, Sam M.J.G. Steyaert\textsuperscript{a,b}, Hartmut Gossow\textsuperscript{a}, Jon E. Swenson\textsuperscript{b,c}

\textsuperscript{a} Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Post Box 5003, NO-1432 Ås, Norway
\textsuperscript{b} Department of Integrative Biology and Biodiversity Research, Institute for Wildlife Biology and Game Management, University of Natural Resources and Life Sciences, Vienna, Gregor Mendel Str. 33, A-1180 Vienna, Austria
\textsuperscript{c} Norwegian Institute for Nature Management, NO-7485 Trondheim, Norway

**ABSTRACT**

Large carnivores, such as brown bears, are focal species for conservation efforts. Historically, brown bears were persecuted in Europe for centuries before their gradual elimination from much of Western Europe. In contrast, large carnivore populations in North America were eradicated within two centuries in the east and within a few decades in the west. After a change towards conservation-oriented management in the 20th century, many bear populations are again increasing on both continents. Europe is seemingly less suited (i.e. higher human densities, greater habitat alteration and landscape fragmentation) than in North America, however bears seem to respond faster to conservation measures in Europe. We analyzed ecological and historical factors that may affect differences in reproductive allocation (mean litter size in relation to mean adult female body mass) and help explain why different brown bear populations react differently to conservation measures. The results indicated that mean litter size increased significantly with mean adult female body mass and a long persecution history. Our results suggest that high and long-term rates of nonelective harvesting can change life-history traits of large mammals, as has also been shown by modeling, but only has been documented for morphological traits. Incidentally, this “ghost of persecution past” may have helped some brown bear populations to be more productive and therefore to respond more positively to protective management policies than populations with short exploitation histories.

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1. Introduction

People and large carnivores have been in conflict throughout their common history (Linnell et al., 2001; Woodroffe, 2000). In contrast to other large mammals, such as ungulates, carnivores were not killed primarily for consumption, but to prevent them from killing livestock, other wildlife, or people. Emperor Charlemagne was the first to establish a dedicated large carnivore hunting corps around 800 AD (Boitani, 1995), but it took many centuries to gradually eliminate large carnivores from Western Europe (Frank and Woodroffe, 2001). In contrast, the technology of poison, traps, and firearms eradicated large carnivores from much of eastern North America in two centuries, and organized predator control programs eliminated them from most of the American West within a few decades (Frank and Woodroffe, 2001). A shift in the management paradigm towards more conservation-oriented management has occurred in the 20th century, and today many large carnivore populations are again on the increase in North America and Europe (e.g. Boitani, 2000; Breitenmoser, 1998; Linnell et al., 2001; Schwartz et al., 2006b; Servheen et al., 1998; Swenson et al., 2000; Woodroffe, 2000). The present conservation challenges regarding large carnivores include their large area requirements and predatory behavior (Linnell et al., 2001; Nowell and Jackson, 1996), as well as their comparatively low population densities and slow life histories. Especially small populations of large carnivores are very vulnerable to stochastic events and the loss of key individuals (Linnell et al., 2005).

Large carnivore conservation today must take place on different ecological stages. In North America the focus of recovery is mostly aimed at protected, remote, and wilderness areas, whereas conservation in Europe must be achieved in a cultural landscape with high human densities, where protected areas are comparatively small, and remote or wilderness areas are virtually nonexistent (Frank and Woodroffe, 2001; Linnell et al., 2001; Woodroffe, 2000). For example, Woodroffe (2000) has suggested that population declines of brown bears (\textit{Ursus arctos}) in North America occurred at critical historical human population densities of 4.2 people/km\textsuperscript{2}. Today, with modern management, several populations of brown bears are increasing again in North America in association with a mean human population density of...
5.8 people/km² (Linnell et al., 2001). In Europe brown bear populations are increasing as well, however at mean human population densities >80 people/km² (Linnell et al., 2001). Despite the fact that European bears live in areas that are seemingly less suited (i.e. higher human densities, higher habitat alteration, higher landscape fragmentation), they seem to be able to tolerate more human pressure and respond faster to conservation activities than North American populations. For example, brown bear population growth rates of 14% and 16% annually have been documented in Europe (Sæther et al., 1998), whereas the highest population growth rates documented in North America are considerably smaller; 8.5% in British Columbia, Canada (Hovey and McLellan, 1996), and 4.2–7.6% in the Greater Yellowstone Ecosystem (Harris et al., 2007; Schwartz et al., 2006a).

Herein we asked the question whether these apparently different patterns in populations of the brown bear may be related to differences in reproductive allocation, and if so, which ecological and historical factors are important. Several factors can affect the life history and reproductive allocation of a species. Density-dependence is a key concept in population dynamics (Bonenfant et al., 2009; Clutton-Brock et al., 1996), and it affects several life history parameters. As population density increases, the body mass of large mammals typically declines, affecting individual performance traits, such as age of first reproduction and juvenile survival (e.g. Bonenfant et al., 2009; Zedrosser et al., 2006). Density-dependent changes in life history characters are thought to occur at population levels close to the carrying capacity (Fowler, 1981). Habitat quality and changing food conditions due to density independent environmental fluctuations have also been reported to influence life history traits and consequently population dynamics in large mammals (Forchhammer et al., 2001; Lindstrom and Kokko, 2002). Food availability differs among years and thus affects growth patterns of subadult individuals and ultimately their adult size. Effects of fluctuating food conditions on life-history parameters have been found repeatedly in ungulates (e.g. Albon et al., 1987; Skogland, 1989; Post et al., 1997; Festa-Bianchet et al., 2000) as well as in large carnivores (e.g. Dahle et al., 2006; Derocher and Stirling, 1995; Derocher and Wiig, 2002; Zedrosser et al., 2006).

Interspecific competition among carnivores can limit spatial distributions, constrain habitat selection, reduce prey encounter rates, reduce food intake, and increase mortality rates (Creel et al., 2001). The usual direction of the relationship between two carnivore species is that large carnivores commonly affect the distribution, demography, and population dynamics of medium-sized carnivores, which in turn limit smaller carnivores (Creel et al., 2001). For example, the distribution and population size of coyotes (Canis latrans) in Yellowstone National Park has decreased as a result of the reintroduction of wolves (Canis lupus) (Berger and Gese, 2007). However, smaller carnivores can also potentially limit larger species, when there is extensive dietary overlap, their density is higher, and when they are more efficient using a low density of the same food resource.

We chose the brown bear as model species for our evaluation, because it is, to our knowledge, the only large carnivore species of worldwide distribution with published data on litter size and adult female body mass in a quantity and quality sufficient for statistical analysis, as well as documented differences in persecution history between areas (i.e. Europe and North America). We focus on litter size in relation to adult female body size as a measure of reproductive allocation. An allochronic approach, i.e. quantifying phenotypic change through time within a population (Hendry et al., 2008), would have been best suited to find evidence supporting the hypothesis of human-induced life history changes. Obviously, no such historic records exist for brown bears. Instead, evolutionary change is commonly inferred using synchronic approaches, i.e. comparing phenotypic differences between populations that have a common ancestry (Hendry et al., 2008, and references therein). For the purposes of our analysis we define evolutionary change as change in phenotypic traits.

We aim to evaluate the differences in reproductive allocation of brown bear populations in relation to population density, body mass, and juvenile survival of brown bears. For example, Mattson et al. (2005) suggested that the American black bear (Ursus americanus) body mass was estimated by summing the average adult body mass (≥5 years) April–July weight and the average August-November weight and dividing by 2 (McLellan, 1994; Stringham, 1990). In our own study populations (northern and southern Sweden) body mass was estimated by averaging spring body mass of adult females captured in the course of our study. To obtain comparable weight estimates, the mean spring weights in populations where bears only were weighed in spring were multiplied by 1.28 to obtain an estimate of the annual mean mass. This correction factor is based on populations where bears were weighed in both seasons (McLellan, 1994; Stringham, 1990). Female body mass was log-transformed in the analysis to obtain a better model fit.
Table 1
Data used to analyze the relative degree of female reproductive allocation in brown bear populations. Continent refers to the geographic location of the population (NA = North America, EU = Europe, A = Asia); NDVI is the mean normalized difference vegetation index around the center location of each study area for the months May–July in the years 2000–2005; density is the reported population density in bears/1000 km²; salmon refers to whether populations have access to spawning salmon as food source; persecution refers to length of persecution by modern man (long: >500 years; short: <150 years); black bear = presence (Yes) or absence (No) of sympatric black bear populations; mean female mass = mean adult female body mass in kg, and \( N \) = sample size of adult females used to calculate mean adult female mass; mean litter size = mean number of cubs per litter, and \( N \) = sample size of litters used to calculate mean litter size. The column “reference” indicates the source(s) of the data.

<table>
<thead>
<tr>
<th>Population</th>
<th>Continent</th>
<th>NDVI</th>
<th>Density</th>
<th>Salmon</th>
<th>Persecution</th>
<th>Black bear</th>
<th>Mean female mass</th>
<th>( N )</th>
<th>Mean litter size</th>
<th>( N )</th>
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</tr>
</thead>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
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<td>Admiralty Island</td>
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<td>0.320</td>
<td>419(^a)</td>
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<td>Short</td>
<td>No</td>
<td>169(^b)</td>
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<td>32</td>
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<td>No</td>
<td>Short</td>
<td>No</td>
<td>154(^c)</td>
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<td>71</td>
<td>Miller et al. (1997), Reynolds (1997)</td>
</tr>
<tr>
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<td>Short</td>
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<td>256(^d)</td>
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<td>46</td>
<td>Miller et al. (1997), Miller et al. (2003)</td>
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<td>Denali National Park</td>
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<td>No</td>
<td>Short</td>
<td>Yes</td>
<td>125(^e)</td>
<td>65</td>
<td>2.10</td>
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<td>2.20</td>
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<td>Short</td>
<td>Yes</td>
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<td>16</td>
<td>2.20</td>
<td>26</td>
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<td>551</td>
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<td>Short</td>
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<td>Yes</td>
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<td>121(^l)</td>
<td>35</td>
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<td>No</td>
<td>202(^m)</td>
<td>16</td>
<td>2.50</td>
<td>29</td>
<td>LeFevre et al. (1987), McLellan (1994)</td>
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<td>Yes</td>
<td>170(^n)</td>
<td>23</td>
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<td>Short</td>
<td>Yes</td>
<td>110(^o)</td>
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<td>1.80</td>
<td>6</td>
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<td>Middle Susitna</td>
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<td>0.460</td>
<td>21(^r)</td>
<td>No</td>
<td>Short</td>
<td>Yes</td>
<td>170(^s)</td>
<td>50</td>
<td>2.09</td>
<td>91</td>
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<td>Short</td>
<td>No</td>
<td>103(^u)</td>
<td>31</td>
<td>1.59</td>
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<td>Short</td>
<td>No</td>
<td>116(^v)</td>
<td>35</td>
<td>2.00</td>
<td>6</td>
<td>Nagy et al. (1983a)</td>
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<tr>
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<td>No</td>
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<td>No</td>
<td>142(^w)</td>
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<td>119</td>
<td>Yukolv, F., pers. com.; Mordosov (1993)</td>
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<tr>
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<td>0.641</td>
<td>93</td>
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<td>Short</td>
<td>No</td>
<td>102(^x)</td>
<td>17</td>
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<td>13</td>
<td>Mano and Tsutoba (2002), Hokkaido Institute of Environmental Sciences (2000)</td>
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<td>No</td>
<td>124(^y)</td>
<td>36</td>
<td>2.30</td>
<td>18</td>
<td>Nagy et al. (1983b)</td>
</tr>
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<td>No</td>
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<td>35</td>
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<td>Short</td>
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<td>135(^a)</td>
<td>63</td>
<td>2.00</td>
<td>102</td>
<td>Blanchard (1987), Mattson et al. (2005), Schwartz et al. (2006b)</td>
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<td><strong>Populations with long persecution history</strong></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<td>Dinara</td>
<td>EU/Slovenia, Croatia</td>
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<td>No</td>
<td>128(^b)</td>
<td>67/</td>
<td>2.39</td>
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<td>No</td>
<td>132(^d)</td>
<td>81</td>
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<td>No</td>
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<td>31</td>
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<td>No</td>
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<td>2.40</td>
<td>33</td>
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</tr>
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<td>EU/Sweden</td>
<td>0.592</td>
<td>29</td>
<td>No</td>
<td>Long</td>
<td>No</td>
<td>117(^g)</td>
<td>59</td>
<td>2.30</td>
<td>55</td>
<td>Stoen et al. (2006), Swenson et al. (2001b)</td>
</tr>
<tr>
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<td>EU/Spain</td>
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<td>Long</td>
<td>No</td>
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<td>12</td>
<td>2.26</td>
<td>23</td>
<td>Fernandez Gil (2009), Naves et al. (1999),Wiegand et al. (1998)</td>
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</tbody>
</table>

\(^{a}\) Mean of two estimates in Miller et al. (1997).

\(^{b}\) Spring and fall body mass divided by 2.

\(^{c}\) Spring body mass multiplied by 1.28.

\(^{d}\) Total number of bears divided by area occupied by bears.

\(^{e}\) Hunter-killed females in fall.

\(^{f}\) Data extracted from Hilderbrand et al. (1999).

\(^{g}\) Estimate derived from 2 study areas close by Sellers and Aumiller (1994b).

\(^{h}\) Estimate based on captured bears (Stringham, 1990).

\(^{i}\) Mean of 2 estimates given in Tobey (2001).
We used a linear model to analyze the relative degree of reproductive allocation (i.e., litter size while controlling for female mass) in six populations that experienced long persecution in Europe with 22 populations with a short period of persecution in North America and Asia. The six populations with long persecution history are considered genetically independent based on geographic distances and genetic data (Manel et al., 2007; Tammeleht et al., 2010). We have evaluated potential correlations among the variables with the variance inflation factor following the method proposed by Zuur et al. (2009). We selected the best model in a backward elimination procedure, choosing predictor variables according to their p-values; an α level of 0.05 was considered statistically significant. The statistical software R 2.12.0 (R Development Core Team, http://www.r-project.org) was used in all analyses.

We used NDVI as a predictor of habitat quality and productivity (Pettorelli et al., 2005). The Global Land Cover Facility provides time series of NDVI, covering the entire world in biweekly and continental-wide mosaics since 1986. The spatial resolution (pixel size) of these NDVI layers is 8 km × 8 km. The data originate from imagery recorded by the Advanced Very High Resolution Radiometer Sensors on board the National Oceanic and Atmospheric Administration satellites (Pinzon et al., 2005; Tucker et al., 2005). NDVI layers for Eurasia and North America were downloaded from http://glc.fiumiaci.umd.edu/data/gimms/ (accessed September 2010). We placed the center locations of each study area (based on the study area descriptions) in large and unfragmented areas suitable for bears (i.e., we avoided placing the center points in e.g. large open water bodies or glaciers). Because the populations used in this analysis were studied at different points in time from the 1970s until after the turn of the millennium, we were not able to calculate NDVI values for all studies exactly at the time they were carried out. We therefore calculated the mean NDVI per pixel across all layers of the months May–July for the years 2000–2005 with Erdas Imagine software. We imported this averaged NDVI layer into ArcGIS 9.3.1, and assigned “NoData” to all water to avoid bias because of its default value. We then smoothed the averaged layer with a moving window approach to calculate the mean NDVI for each pixel within a radius of 17.845 km around a given pixel (this radius approximates an area of 1000 km², and fully or partially contains 32.8 km × 8 km pixels). This radius was chosen because an area of 1000 km² covers the home ranges of several adult females, and because the density measure we used was expressed in bears/1000 km² (see below). We then extracted the NDVI-value of the pixel corresponding to each study area center location.

Hilderbrand et al. (1999) found that body size of female brown bears increased with protein intake, and there is evidence that increased consumption of vertebrates by brown bears is negatively correlated with NDVI (Bojarska and Selva, in press). We therefore compared the difference in NDVI-values between populations with long and short persecution histories with parametric statistics.

Population density can have pronounced effects on life history traits and reproduction (e.g. Bonenfant et al., 2009; Clutton-Brock et al., 1996). We therefore controlled for the effect of population density in our analysis. Data was obtained from published sources (Table 1), however, due to a variety of methods used in the derivation of the density estimates, comparisons must be interpreted cautiously. Population density was log-transformed in the analysis to obtain a better model fit.

Individuals in bear populations with access to spawning salmon as a food source are on average larger and heavier than bears in populations without access to spawning salmon (Hilderbrand et al., 1999). Because access to spawning salmon is highly correlated with population density (all populations with >100 individuals/1000 km² had access to spawning salmon (Table 1) (Spearman’s rho = 0.668, p < 0.001; variance inflation factor = 5.251, Zuur et al. (2009)), we considered whether or not a population had access to spawning salmon only to subsample populations for analysis, and not as variable in the analysis itself.

We evaluated the effect of sympatric black bears (as a binary variable absence/presence), because they might compete with brown bears (Mattson et al., 2005). All variables were included as separate variables into the model. In addition, we included interactions between mean female body mass and all other variables into our analysis.

3. Results

All variables had variance inflation factors <2 and accordingly are used in the model (Zuur et al., 2009). The final model on reproductive allocation of female brown bears contained only two variables and suggested that litter size increased significantly with mean adult female body mass and that brown bear populations with a long history of persecution produced significantly more offspring relative to their body mass than those with a short history of persecution (Table 2, R² model a = 0.57; Fig. 1). The following variables and interactions tested were not significant and were removed from the analysis in this order: log(population density) × NDVI, β = 0.027, p = 0.942; log(mean adult female body mass) × NDVI, β = 0.679, p = 0.678; log(mean adult female body mass) × factor(presence/absence of black bears), β = 0.244,

<table>
<thead>
<tr>
<th>Variable</th>
<th>β</th>
<th>S.E.</th>
<th>T</th>
<th>p</th>
<th>R²</th>
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</tr>
<tr>
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<td>4.337</td>
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</tr>
<tr>
<td>Short persecution history</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Long persecution history</td>
<td>0.435</td>
<td>0.086</td>
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<td>Model b: Excluding populations with access to salmon</td>
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<td>Log(body mass)</td>
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</table>

Table 2
Results of a linear regression model analyzing the relative degree of female reproductive allocation (mean litter size in relation to mean adult female mass) in brown bear populations. The explanatory variable was mean litter size. The predictor variables available were mean adult female body mass (log-transformed), population density (log-transformed), persecution history (short persecution history: populations with <150 years of persecution; long persecution history: populations with several centuries of persecution), the mean normalized difference vegetation index within a radius of 17.845 km around the center location of each study area for the months May–July for the years 2000–2005, absence or presence of sympatric black bears, and meaningful interactions of these variables. Access to spawning salmon was highly correlated with population density, therefore whether or not a population had access to spawning salmon was used only to subsample populations for analysis, and not as variable in the analysis itself. The sample size in model a (including populations with access to salmon) was 28 populations, and in model b (excluding populations with access to salmon) 21 populations.
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4. Discussion

A species life history is shaped by its physical and ecological environment through the processes of natural selection (Stearns, 1992). Our results showed significant differences in reproductive allocation among populations of brown bears between especially North America and Europe. In addition, females in European brown bear populations also have a shorter mean interlitter interval (2.8 years; data recalculated from Steyaert et al. (in press)) and a younger mean age at primiparity (5.3 years; data recalculated from Steyaert et al. (in press)) than females in North American populations (mean interlitter interval: 3.6 years; mean age at primiparity: 6.9 years; data recalculated from Steyaert et al. (in press)). These life-history differences among bear populations may be a reason why the highest documented reproductive rates for brown bears are from European populations (i.e. 16% in Sweden, Europe (Sæther et al., 1998). Differences in the population growth rates translate also into differences in sustainable hunting rates for the species in North America and Europe. Brown bear populations can sustain a hunting rate of ~10% annually without declining in Europe (Bischof and Swenson, 2009), whereas maximum sustainable hunting mortality has been estimated to be 5.7% in North America (Miller, 1990).

The observed differences in reproductive allocation and other life history traits among brown bear populations may be related to several ecological variables that might differ now or might have differed during the last many millennia since bears colonized North America. Alternative explanations for the observed differences may be related to dietary patterns and energy availability, habitat productivity, population density, as well as historic hunting pressure. In general, the absence of some of these explanatory variables in our results may be partly related to a small sample size and the quality and comparability of the population density estimates (Table 1).

In brown bears there is a strong relationship between population density, habitat productivity, and energy availability (Ferguson and McLoughlin, 2000; Bischof et al., 1999). Meat contains the highest digestible energy and protein content among bear food items (Pelletti et al., 2003; Robbins et al., 2007), and litter size in brown bears varies with the amount of meat (including but not limited to salmon) in the diet (Hilderbrand et al., 1999). Bojarska and Selva (in press) reviewed the global patterns of brown bear diet and found that increased consumption of vertebrates was negatively correlated with NDVI, which they explained by bears compensating the limited availability of vegetal foods by consuming more vertebrates. Our results show that bears with long persecution history (i.e. European populations) live in areas with higher NDVI values than populations with short persecution histories, which suggests lower meat consumption by European populations based on the arguments of Bojarska and Selva (in press). There is in fact evidence from predation studies that North American brown bears are more predatory and consume more meat than European brown bears (e.g. Swenson et al., 2001a; Zager and Beecham, 2006). These results strengthen the support for our hypothesis of the effects of persecution history rather than diet on reproductive allocation in brown bears.

An alternative explanation for the observed patterns of reproductive allocation could be a density-dependent response, as documented for ungulates (Eberhardt, 2002), where harvesting reduces population density and the response to the increased availability of per capita food resources is often an earlier age at first reproduction and a higher reproductive rate.

High levels of centuries-long human persecution may have contributed to an evolutionary life-history change in brown bears, causing females to invest relatively more in reproduction in relation to body mass. Because life-history strategies often involve trade-offs between body growth and reproduction, life-history theory predicts that animals in populations with a high adult mortality rate should prioritize reproduction over body growth to increase the probability of reproducing before death (Stearns, 1992). The duration of persecution of brown bears by humans differed between Europe compared with North America and northern Asia. Europeans conducted extermination campaigns for centuries with primitive weapons and traps; thus the mortality was likely nonselective. Populations declined relatively slowly until effective firearms became available in the 1800s (Curry-Lindahl, 1972;
Swenson et al., 2000). In North America south of Canada, brown bear populations collapsed rapidly during 1850–1920 and most remnant populations disappeared during 1920–1970, due to persecution by settlers with modern weapons (Frank and Woodroffe, 2001; Mattson and Merrill, 2002). In much of northern North America and in northern Asia, settlers arrived later and in smaller numbers, and brown bear populations have remained large over vast areas (Servheen et al., 1999). Aboriginal North Americans may have truncated the expansion of the brown bear to the east and competed with them at salmon spawning streams (Mattson and Merrill, 2002), however no organized extermination efforts were carried out as in Europe. In fact, although some tribes had bear-hunting cults or made a sport of killing brown bears (Schul- lery, 2002), historical accounts suggest that North American aboriginals had only a minor effect on brown bear mortality, due to fear, respect, or taboos on killing and/or eating them (Hallowell, 1926; Storer and Tevis, 1955).

Evidence is accruing suggesting that phenotypic evolution probably is occurring in exploited populations as a result of selective harvesting, although its genetic basis has rarely been demonstrated (Allendorf et al., 2008; Law, 2003). There is growing evidence from wild animal populations of human-induced selection on morphology (Hendry et al., 2008) and life-history traits (Darimont et al., 2009), the latter especially from commercially exploited fish populations (Hutchings and Fraser, 2008). In large mammals, only effects on morphological traits have been documented; selective phenotype-based harvest of high-quality big-horn sheep (Ovis canadensis) rams over 5 generations depleted genes that conferred rapid early body and horn growth (Coltman et al., 2003). Also, Jachmann et al. (1995) suggested that tusklessness in female African elephants (Loxodonta africana) increased due to selective illegal ivory hunting.

Several authors have warned of potential selective effects of sport harvest of individuals with large horns or antlers (e.g. Coltman et al., 2003; Festa-Bianchet, 2003). Modeling suggests that random harvest of red deer (Cervus elaphus) also alters female reproductive strategies, with higher harvest rates causing lower body mass at primiparity (Proaktor et al., 2007). Although the heritability of life-history traits is lower than that of morphological traits (Mousseau and Roff, 1987), it is large enough to cause evolutionary change under selective exploitation (Law, 2003). In fish, experimental size-selective harvesting of populations has shown evolutionary effects on somatic growth and population productivity (Conover and Munch, 2002) and life-history traits of fish can change rapidly when under strong selection (Reznick et al., 1990).

Our results suggest that human-caused selection may have altered natural evolutionary processes of large mammals. Incidentally, this “ghost of persecution past” may have allowed European brown bear populations to survive persecution more easily and subsequently increase with modern enlightened management to reduce mortality. Behavioral traits may also have been subject to human selection. European brown bears are less aggressive to humans (Herrero, 1985; Swenson et al., 1999) and less diurnal (Kaczensky et al., 2006; Moo et al., 2007; Roth and Huber, 1986) than North American bears, which also make them easier for humans to tolerate and conserve. In Europe, wolves, Eurasian lynx, and brown bears (all species with similar persecution histories (Boitani, 2000; Breitenmoser et al., 2000)) also appear to be more tolerant of human disturbance, and all three species have shown the ability to live close to people, even within suburban and urban environments (J.D.C. Linnell, pers. obs., in Linnell et al., 2005).

Conservation of carnivores with a world-wide distribution has to be achieved in different settings and at different paces in different parts of the world. Whereas remote and protected areas in, for example, North America are large enough to support substantial populations of large carnivores, conservation in, for example, Europe must be achieved in a cultural landscape with high human densities (Linnell et al., 2001; Woodroffe, 2000). The “ghost of persecution past” suggested by our results may have inadvertently aided conservation efforts in Europe. However, they should also serve as a warning that humans have the potential to be a major evolutionary force (Darimont et al., 2009). Our results also point out the importance of tailoring the conservation approach to the individual situation, as there is no “one-size-fits-all” approach to conservation problems (Linnell et al., 2005). Conservation models for large carnivores based on knowledge gathered in stable populations in spacious and healthy habitats may not give the correct answer for management and conservation problems in areas with high human densities and/or highly human-influenced landscapes. For example, the abundant brown bear populations in Alaska and the management knowledge achieved working with these populations may offer a great opportunity for developing a model conservation program for brown bears (Servheen et al., 1999), however this model may not be readily applicable to the conservation of other brown bear populations.

Conservation efforts world-wide have focused on preventing the extinction of species and populations (Linnell et al., 2005). Currently, conservation is increasingly moving from species conservation towards the conservation of ecosystem processes, as the modern definitions of biodiversity includes all levels of interactions among species, ecological and behavioral processes, and landscapes (Pyare and Berger, 2003; Redford and Richter, 1999). It may be important in the future also to include evolutionary processes within the definition of biodiversity.

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