

PATTERNS AND MECHANISMS BEHIND THE OCCURRENCE OF BEARS CLOSE TO HUMAN SETTLEMENTS

MØNSTER OG MEKANISMER BAK FOREKOMSTEN AV BJØRNER NÆR BEBYGGELSE

MARCUS ELFSTRÖM

Patterns and mechanisms behind the occurrence of bears close to human settlements

Mønster og mekanismer bak forekomsten av bjørner nær bebyggelse

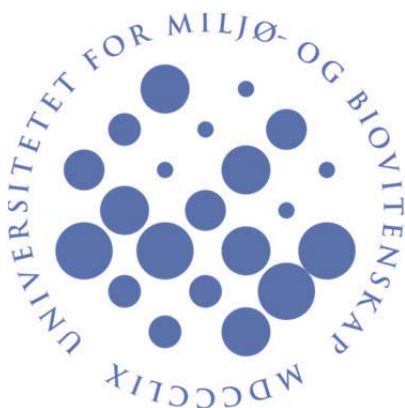
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Summary

Bears near settlements are considered to be a problem, because they may damage property and because people are afraid of them. The most accepted explanation for why some bears occur near settlements is that they associate people with easily accessible foods (i.e. food-conditioning). However, we found a similar composition and quality of the Scandinavian brown bears' diet close to settlements compared to the same when in remote areas. Also, there was no correlation between the occurrence of problem brown bears and food conditions in either southern or northern Europe, and the body condition of problem and nonproblem bears was similar. These results give little support for food search or food shortage to explain the occurrence of problem brown bears near settlements in Europe.

We found further that adult males denned farther from settlements and plowed roads than other categories of brown bears, that problem brown bears are younger than nonproblem bears, and that brown bears are generally younger in areas with higher human density in both southern and northern Europe. Females with young had a diet containing less protein and they showed a lower use of slaughter remains than other brown bear categories in south-central Sweden, supporting the hypothesis that the distribution of predation-vulnerable bears is affected to some degree by a despotic behavior of dominant bears. However, subadult bears showed no dietary deviance from adult males, suggesting no effects from interference competition.

A literature review of brown bears, and American and Asiatic black bears revealed that subadults and females with cubs are overrepresented in areas near settlements in North America, Europe and Japan. This pattern likely occurs because bears are distributed despotically due to interference competition and/or avoidance of aggression or predation, and settlements may function as refuges for predation-vulnerable bears against dominant conspecifics. Thus, we suggested that habituation and food conditioning are proximate

responses, as a result of bears' despotic distribution which is the ultimate mechanism.

Attractant management is important, but failure to consider interactions among bears may lead to only treating the symptoms of habituation or conditioning. Bears seeking refuge near settlements may not be viewed as 'unnatural', but rather as an example of an adaptive behavior to avoid dominant conspecifics, which use habitats farther from people.

Sammanfattning

Björnar nära bebyggelse upplevs som problematiska därför att de kan orsaka skador och för att människor är rädda för dem. Den mest accepterade förklaringen till varför björnar uppehåller sig nära bebyggelse är att de har lärt sig att associera mänsklig aktivitet med lättillgänglig föda (en s.k. födobetingad respons). Men vi fann i Skandinavien en liknande sammansättning och näringsinnehåll i brunbjörnars diet nära bebyggelse jämfört med när samma björnar uppehöll sig i avlägsen terräng. Vi fann heller ingen korrelation mellan antalet problembjörnar och säsongsmässig födotillgång i varken södra eller norra Europa, och konditionsstatus var liknande mellan problembjörnar och övriga brunbjörnar. Dessa resultat indikerar andra bakomliggande orsaker än att problembjörnar primärt skulle söka föda nära bebyggelse eller uppleva en dålig födotillgång i avlägsen terräng.

Vi kan konstatera att vuxna hanar vid övervintring placerar sina iden längre från bebyggelse och plogade vägar än andra kategorier av brunbjörnar, att problembjörnar är yngre än övriga brunbjörnar, och att brunbjörnar generellt är yngre i områden med högre befolkningstäthet i både södra och norra Europa. Dieten hos honor med ungar hade en lägre andel protein, samt ett mindre inslag av slaktrester, jämfört med övriga kategorier av brunbjörn. Detta antyder att björnar som är mer exponerade och känsliga för predation inom arten kan vara påverkade av ett despotiskt beteende från dominanta (predationstoleranta) björnar. Yngre solitära björnar avvek inte i diet från vuxna hanar, och vi kan därmed inte se några hämmande effekter i födosök utifrån konkurrens mellan dessa brunbjörnar.

En litteraturstudie på brunbjörn, svartbjörn, och kragbjörn visade att yngre björnar och honor med ungar är överrepresenterade nära bebyggelse i Nordamerika, Europa och Japan. Denna fördelning av björnar i relation till bebyggelse är sannolikt ett resultat av hämmande konkurrens om resurser och/eller försök att undvika aggression eller predation, där bebyggelse kan fungera som skydd för predationskänsliga individer gentemot dominanta

artfränder. Vi föreslog därför att björnars despotiska beteende är en ultimat mekanism som kan resultera i proximata, såsom habituering och födobetingade responser, hos björnar nära bebyggelse. Ett viktigt inslag för att förebygga förekomsten av närgångna björnar vid bebyggelse är att avlägsna lockande födoämnen. Men det finns en risk att björnförvaltningen endast fokuserar på att hantera symptom av habituering eller födobetingade responser, istället för att även ta hänsyn till interaktioner mellan björnar. Björnar som söker skydd nära bebyggelse behöver inte nödvändigtvis betraktas som ”onaturliga”, utan snarare som ett exempel på ett adaptivt beteende för att undvika dominanta artfränder i avlägsen terräng.

List of papers

Paper I

Elfström, M., Zedrosser, A., Støen O-G., Swenson, J.E. 2013. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review*. *In press*. doi:10.1111/j.1365-2907.2012.00223.x

Paper II

Elfström, M., Swenson, J.E. 2009. Effects of sex and age of den site use by Scandinavian brown bears. *Ursus* 20(2):85–93.

Paper III

Elfström, M., Zedrosser, A., Jerina, K., Støen, O-G., Kindberg, J., Budic, L., Jonozovič, M., Swenson, J.E. Does despotic behavior or food search explain the occurrence of problem brown bears in Europe? *Submitted manuscript*.

Paper IV

Elfström, M., Støen O-G., Zedrosser, A., Warrington, I., Swenson, J.E. 2013. Gut retention time in captive brown bears *Ursus arctos*. *Wildlife Biology*. *In press*. doi: 10.2981/12-121.

Paper V

Elfström, M., Davey, M.L., Zedrosser, A., Müller, M., De Barba, M., Støen O-G., Miquel, C., Taberlet, P., Hackländer, K., Swenson, J.E. Do Scandinavian brown bears approach settlements to obtain high-quality food? *Manuscript*.

Synopsis

... the struggle [for existence] almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers.

Charles Darwin, *On the Origin of Species* (1859)

He who believes in something is lost.

Nikanor Teratologen, *Apsefiston* (2002)

Introduction

People have considered large carnivores a threat to life and property for centuries (Schwartz et al. 2003). The common solution to these problems was the extermination of large carnivores, which started in Europe before the Middle Ages and has continued until the early part of the 20th century (Schwartz et al. 2003). In Scandinavia, the persecution of large carnivores was intensified due to increased livestock depredation by large carnivores after ungulate prey species had been overharvested, during the late part of the 18th century (Schwartz et al. 2003). As human densities increased, carnivores declined or were eliminated in most of their range in both North America and Europe (Woodroffe 2000). However, attitudes towards Nature in Western cultures have changed from emphasizing primarily utilitarian to more intrinsic/naturalistic values and a willingness to conserve wildlife (Messmer and Enck 2012). This resulted in a shift in the management paradigm from persecution to conservation strategies, and large carnivores are now increasing in numbers and in range (Linnell et al. 2001, Enserink and Vogel 2006). However, their return is not welcomed by everyone, because large carnivores can cause problems such as public anxiety, damage to property, and reduced opportunities for ungulate hunters (Naughton-Treves et al. 2003, Røskft et al. 2003, Nilsen et al. 2005, White et al. 2012). In addition, large carnivores are charismatic and few people have a neutral attitude towards them (Gittleman et al. 2001). Thus, policy decisions and management of large carnivores often generate conflicts among a variety of stakeholders, especially conservationists and hunters (Treves and Karanth 2003, Bisi et al. 2007). In order for people and large carnivores to coexist, we need to increase our understanding of the mechanisms behind the occurrence of large carnivores near human settlements. This thesis aims to increase our understanding of such mechanisms.

Large carnivores commonly avoid human activity and settlements (Woodroffe and Ginsberg 1998, Frid and Dill 2002). However when large carnivores do occur close to people

and settlements, it is often interpreted as behavioral responses, such as an increased tolerance of humans and/or an association between humans and attractive foods (Bejder et al. 2009). Stimulus-specific waning of a response, i.e. nonassociative learning not to respond (Immelmann and Beer 1989), can explain increased tolerance towards humans in animals with increasing (benign) encounters with people, and is hereafter called human habituation. Food resources are unconditioned stimuli, i.e. not related with other stimuli, which usually result in the unconditioned response of foraging. Feeding can become conditioned upon an unrelated (conditioned) stimulus, such as human activity or settlements, after repeated association between the unconditioned and conditioned stimuli (Immelmann and Beer 1989); this process is hereafter called food conditioning. These learning processes, human habituation and food conditioning, are common among most organisms (Alcock 1988, Rodríguez-Prieto et al. 2010).

Human habituation and food conditioning can explain why one animal is not wary of humans or often occurs near settlements in contrast to conspecifics, because of earlier exposures to stimuli (or experiences). However, human habituation and food conditioning do not predict that exposures to stimuli will vary among conspecifics (e.g. sex/age or reproductive categories). In contrast to habituation and conditioning, if animals occur near people because they lack cumulative experience of them (Bejder et al. 2009), i.e. are naïve, this would predict younger individuals near human activity and settlements. Subadults may approach people or settlements due to their naivety. However, resource competition and aggression from resident older conspecifics may trigger the dispersal of young (naïve) individuals in several large carnivores, e.g. Florida panthers (*Puma concolor*) (Maehr et al. 2002), Iberian lynx (*Lynx pardinus*) (Ferrerías et al. 2004), and tigers (*Panthera tigris*) (Smith 1993).

Attraction to people or settlements that is presumed to be caused by food-conditioning can also be the result of other mechanisms, such as individual differences in tolerance or searching shelter from predation (Whittaker and Knight 1998, Bejder et al. 2009). Avoidance of settlements by large carnivores creates predator-relaxed habitats for several prey species (Berger 2007, Barber et al. 2009). Ungulates, such as moose (*Alces alces*) and roe deer (*Capreolus capreolus*), have been reported to use areas closer to settlements to avoid predation by carnivores, such as brown bears (*Ursus arctos*) (Berger 2007), wolves (*Canis lupus*) (Rogala et al. 2011), and lynx (*Lynx lynx*) (Basille et al. 2009). In areas with spawning salmon and overlapping distribution of American black bears (*Ursus americanus*) and brown bears, brown bears seem to displace sympatric black bears and exclusively utilize salmon (MacHutchon et al. 1998, Belant et al. 2006, Fortin et al. 2007, Belant et al. 2010).

The brown bear is the largest terrestrial carnivore in Europe, and its presence commonly generates public anxiety (Røskoft et al. 2003, Ericsson et al. 2010, Johansson et al. 2012a, Johansson et al. 2012b). Brown bears usually avoid settlements (Mace and Waller 1996, Nellemann et al. 2007). If settlements are associated with human disturbance (Martin et al. 2010, Ordiz et al. 2011), bears occurring near settlements may be naïve in terms of lacking experience with humans (Blanchard and Knight 1991, McLellan et al. 1999, Kaczensky et al. 2006, Rogers 2011), and/or gaining benefits (e.g. food) to balance the costs of human disturbance. Bears are opportunistic omnivores (Robbins et al. 2004, Bojarska and Selva 2012). If bears have a different diet when near settlements, i.e. human derived foods, this may also be a result of food conditioning; indicating that these bears approach people in search of food (McCullough 1982, Klenzendorf and Vaughan 1999, Gunther et al. 2004, Rogers 2011). Food search near settlements can also occur while avoiding human activity, i.e. without gaining human tolerance (McCullough 1982, McCutchen 1990). On the other hand, bears may also occur near settlements or people without utilizing human-derived foods, because of

an increased tolerance of humans, i.e. human habituation (McCullough 1982). Human habituation and food conditioning may be common responses by bears due to frequent exposures of people and human-derived foods (McCullough 1982, Herrero et al. 2005). However, predation and aggression of conspecific young (especially cubs-of-the-year and yearlings) by older bears, especially males, constitute a common pattern in bears (McLellan 1994, Swenson et al. 1997b, Swenson et al. 2001, McLellan 2005). Thus, human activity or settlements may provide not only food resources, but also refuge for young bears and females with young against dominant conspecifics (Wielgus and Bunnell 1994, Mueller et al. 2004, Steyaert et al. 2013).

In this thesis I analyzed habitat use, foraging behavior and body condition among sex, age and reproductive categories of brown bears in relation to human settlements. I asked the following questions: 1) do some sex, age and reproductive bear categories occur more often near human settlements than others, and if so 2) which mechanisms can explain the likelihoods of occurrence near settlements among sex, age and reproductive categories of bears. I also tested 3) the assumptions based on the paradigm on food search to explain problem bear occurrence near settlements in southern and northern Europe, which included 4) the diet of bears approaching settlements in south-central Sweden.

Objectives and their rationale

Identifying which categories of bears approach settlements and are considered to be problem animals (Papers I, II, III)

If certain sex, age and reproductive categories of bears more often approach people or are involved in incidents, i.e. are considered ‘problem’ animals, there may be alternative explanations than human habituation and food conditioning. Therefore, I reviewed the literature regarding sex, age and reproductive categories of brown bears and black bears

(*U. americanus*, *U. thibetanus*) occurring near human activity and settlements (Paper I); compared den site characteristics among sex, age and reproductive categories of brown bears in relation to roads and settlements in south-central Sweden (Paper II); and compared the age distribution of problem and nonproblem brown bears, also in relation to the density of people in northern and southern Europe (Paper III).

Explaining the likelihoods that different categories of bears occur near settlements

(Paper I)

Human habituation and food conditioning can explain why some bears occur near settlements more often than others. However, mechanisms which account for interactions among conspecifics must be invoked to understand the ultimate and proximate factors explaining the occurrence of bears near settlements, given that there are different likelihoods for occurrence among sex, age and reproductive categories. Therefore, I identified mechanisms to explain bear occurrence near settlements, considering sex, age and reproductive bear categories (Paper I).

Testing the paradigm of food search near people: diet and body condition in relation to settlements and problem bear status (Papers III, IV, V)

I evaluated the assumptions of the paradigm of food search to explain the occurrence of management-killed bears ('problem' bears) in northern and southern Europe (Paper III).

Also, I compared the diet of bears, based on fecal remains, when they were close to and far from settlements in south-central Sweden, and compared the feeding patterns among sex, age and reproductive bear categories (Paper V). To relate movements with diet based on fecal remains, I determined the gut retention time (GRT), i.e. how long it takes for different ingested food items to pass through the digestive tract of brown bears (Paper IV).

Materials and methods

Study area

Our study area for the spatiotemporal analyses of GPS/GSM-equipped brown bears was located in south-central Sweden (~61° N, 15° E), and encompasses ~12,000 km² (Dahle and Swenson 2003). More than 80% of the area consists of intensively managed boreal forest, with Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) as dominating tree species; the remaining area is mainly covered by bogs or lakes (Moe et al. 2007). The forest floor is dominated by lichens, heather (*Calluna vulgaris*), and berries (*Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum*) (Swenson et al. 1999). Elevation ranges between 200 to 1000 meters above sea level (Dahle and Swenson 2003), and the slopes are <8° in >90% of the area (Elfström et al. 2008). The area is sparsely populated, with few settlements and isolated houses (Martin et al. 2010). There are six towns and settlements, ranging from 3,000–11,000 inhabitants, and two major tourist resort areas with cabins (Nellemann et al. 2007) in our study area. 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).

Study populations

The Swedish brown bear population size was estimated at 2970-3670 animals in 2008, distributed over the northern two-thirds of the country (Kindberg et al. 2009, Kindberg et al. 2011). Human density in the bear range is low, although more populated areas occur at the edge of the bear distribution along the eastern coast (Kindberg et al. 2011). In Paper III, we also analyzed data derived from brown bears in Slovenia. Slovenian brown bears occur mainly in and near the Dinaric Mountains, and represent the northwestern part of the Alpine-

Dinaric-Pindos population (Zedrosser et al. 2001). The highest densities of Slovenian bears occur inside a protected area within the Dinaric Range, characterized by low human densities (Kryštufek and Griffiths 2003, Jerina et al. 2013). The Slovenian brown bear population was estimated to be 394-475 animals in 2007 (Skrbinšek et al. 2008).

Capture and handling of bears

This doctoral thesis was part of the ongoing “Scandinavian Brown Bear Research Project” (SBBRP). The SBBRP has studied bears in this area since 1985, and prioritized to follow females and their offspring, although individuals from all sex, age, and reproductive categories of bears occurring in the area are followed continuously. Details for capture and handling of bears are described in Arnemo et al. (2011). All capturing and treatment were approved by the Swedish Environmental Protection Agency and the Ethical Committees of Animal Research in Umeå and Uppsala (Djuretiska nämnderna i Umeå och Uppsala).

Data collection and analyses

In Paper II, den site characteristics were measured by visiting dens used by radiocollared bears, combined with data derived from 1:50,000 Geographical Sweden Data (GSD) maps. We used Pearson χ^2 , analyses of variance, and logistic regressions with backward elimination of factors for statistical analysis of den site characteristics among bear categories.

In Paper III, we analyzed body measurement data of shot bears in Slovenia and Sweden. Age was determined using cementum annuli of an upper premolar of shot bears (Matson et al. 1993). We calculated a body condition index (BCI) as the standardized residuals when regressing the ratio between body mass and body size (front paw width) on Julian date the bear was killed. Residual extractions were carried out separately by country, season, and for subadults and adults. We used ArcView 3.2 and 9.3 (Environmental Systems

Research Institute, Inc., Redlands, California) to extract densities of humans and bears at killing sites of bears. We used linear mixed-effect models (LMM) to analyze BCI and age distribution among bears in relation to densities of bears and people, and generalized linear models to analyze numbers of problem bears in relation to food availability among years. All models were defined *a priori* and most parsimonious models were selected based on Akaike's Information Criteria scores for small sample sizes (AIC_c) and AIC_c weights, by applying the information theoretic approach (Akaike 1973, Burnham and Anderson 2002).

In Paper IV, we analyzed the gut retention time of captive brown bears in Orsa Bear Park Grönklitt, Sweden. Each experiment lasted for 24 hours with bears confined to an area of 400 m², and bears were given an experimental diet of either berries or carcasses. We video-recorded feeding and defecations using light-equipped cameras and recording capability within infrared wavelengths. We analyzed the GRT in relation to diet, activity level, feeding time (midday/midnight), sex, age (subadult/adult), ingested amounts of food, prior food remains processed by the gut, and defecation rate, using LMM. All models were defined *a priori* and most parsimonious models were selected based on AIC_c and AIC_c weights, by applying the information theoretic approach (Akaike 1973, Burnham and Anderson 2002).

In Paper V, we monitored 49 bears during 2010 equipped with GPS/GSM-collars with relocations scheduled at 10- or 30-minute intervals (VECTRONIC Aerospace GmbH, Berlin, Germany). We used fecal remains to estimate diet quality of bears (Steyaert et al. 2012). Diet composition was analyzed based on the genetic metabarcoding approach (Taberlet et al. 2012). Nutritive content was analyzed using LMM, and dietary composition using generalized linear mixed-effect models (GLMM). All LMM and GLMM were defined *a priori* and most parsimonious models were selected based on AIC_c and AIC_c weights (Akaike 1973, Burnham and Anderson 2002). When combining nutritive content with dietary

composition, we used detrended correspondence analysis (DCA), and compared the result with that from global nonmetric multidimensional scaling (GNMDS), and used partial canonical correspondence analysis (CCA) to test the diet in relation to settlements while controlling for other factors.

Summary of results

Identifying which categories of bears approach settlements and are considered to be problem animals (Papers I, II, III)

In Paper I, we reviewed studies of habitat use by different sex, age and reproductive categories of bears, with focus on the brown bear, but also considered American and Asiatic black bears. We found a common pattern, with subadult bears (i.e. young, sexually immature individuals) being more common near human activity and settlements in North America, Europe, and Japan (Dau 1989, Garshelis 1989, McLean and Pelton 1990, Mattson et al. 1992, McLellan et al. 1999, Pease and Mattson 1999, Clark et al. 2002, Schwartz et al. 2006, Hristienko and McDonald 2007, Nellemann et al. 2007, Izumiyama et al. 2008, Kishimoto 2009, Krofel et al. 2012) (Figure 1). We confirmed the same pattern in the den site locations of Scandinavian brown bears in relation to human activity in Paper II, and in problem and nonproblem brown bears in relation to density of people in northern and southern Europe in Paper III. These results are summarized in more detail below. In addition, McLellan and Shackleton (1988), Nevin and Gilbert (2005b), Rode et al. (2006b), and Steyaert et al. (2013) reported that female brown bears with young occur more often near human activity than adult males or lone adult females.



Figure 1. A 2-year-old male brown bear near a settlement in south-central Sweden in June 2009. This bear is equipped with a GPS/GSM collar by the Scandinavian Brown Bear Research Project for our study of bears' diet in relation to settlements (Paper V). A despotic distribution best explained unequal distribution among sex, age and reproductive status of bears near settlements (Paper I). (Photo by Claes Henning, 2009)

Nellemann et al.(2007) reported that younger Scandinavian brown bears are near settlements during the nondenning period. Because of different energetic and ecological conditions during winter, we tested whether den site characteristics differed among sex, age and reproductive categories of brown bears in Scandinavia in Paper II. We compared 391 winter dens used by 114 individual bears in relation to types of den, topography within 5 m, forest composition within 50 m, and the distances to the nearest settlements and roads within 10 km. In general, denning characteristics of adult males differed the most from other bear categories; e.g. adult males used nest dens more than other types of den compared to pregnant females or females with cubs (Figure 2).



Figure 2. Examples of den sites used by GPS/GSM collared brown bears in our study area during the winter 2008/2009. A) a den dug out under a tree and used by a female which gave birth. B) a den composed of a bed of branches (i.e. nest den) on the ground which was used by an adult male. (Photos by Marcus Elfström)

Degree of human activity influenced the differences in den locations among bear categories in relation to human infrastructure. Adult males denned farther (i.e. $> 2 \text{ km} \pm 1 \text{ (SE)}$, $p \leq 0.001$ using post hoc Tukey test) from plowed roads than all other bears (Figure 3). Premature abandonment of dens was more common closer to plowed roads ($\beta = -0.52$, 1 df, $p = 0.005$). We also found that adult males denned farther (i.e. $2 \text{ km} \pm 1 \text{ (SE)}$, $p < 0.05$ using post hoc Tukey test) from settlements than subadult bears. However, we found no differences related to reproductive status among adult females.

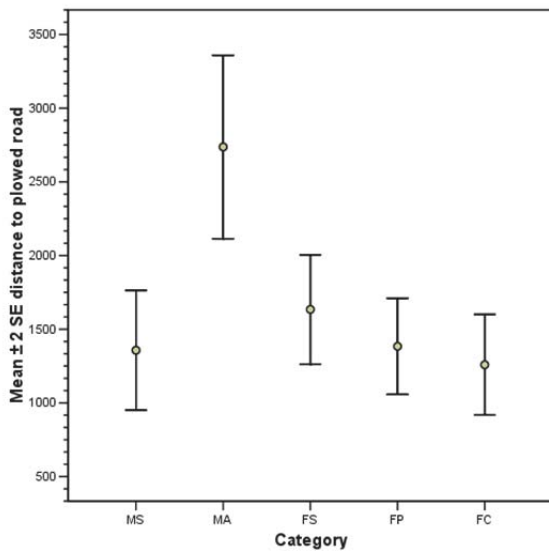


Figure 3. Mean distance (m) from brown bear dens to the nearest plowed road by sex, age and reproductive categories in south-central Sweden, 1986–2003. Adult males (MA) were significantly different from all other sex-age categories: subadult males (MS), subadult females (FS), pregnant females (FP), and females with cubs (FC), post hoc Tukey test: $p = 0.001$, $p = 0.002$, $p = 0.001$, and $p = 0.001$, respectively. *Figure is reprinted from Paper II.*

In Paper III, we compared the age distribution of hunter-killed nonproblem bears ($n = 1,896$), management-killed problem bears ($n = 149$), and bears shot in self defense during hunting ($n = 47$), between 1990 and 2010. If a despotic behavior among bears (i.e. food-competition/predation avoidance) explained the age distribution, we expected that problem bears would be younger than nonproblem bears, and bears in general would be younger with increasing human density. However, if only food-search explained bear occurrence near settlements, we predicted no relation between age of bears and problem bear status or human density. Younger bears seem to leave their diurnal resting sites earlier than older individuals when approached by people (Moen et al. 2012). Therefore, we predicted that bears shot in self defence would be older than nonproblem bears.

Problem bears were $1.6 \text{ years} \pm 1.2 \text{ (SE)}$ younger, but bears shot in self defense were $4.2 \text{ years} \pm 1.3 \text{ (SE)}$ older than nonproblem bears, and bears in general were younger with increasing human density (Figure 4). We suggested that younger bears are less competitive, more vulnerable to predation, and lack human experience, compared to adults.

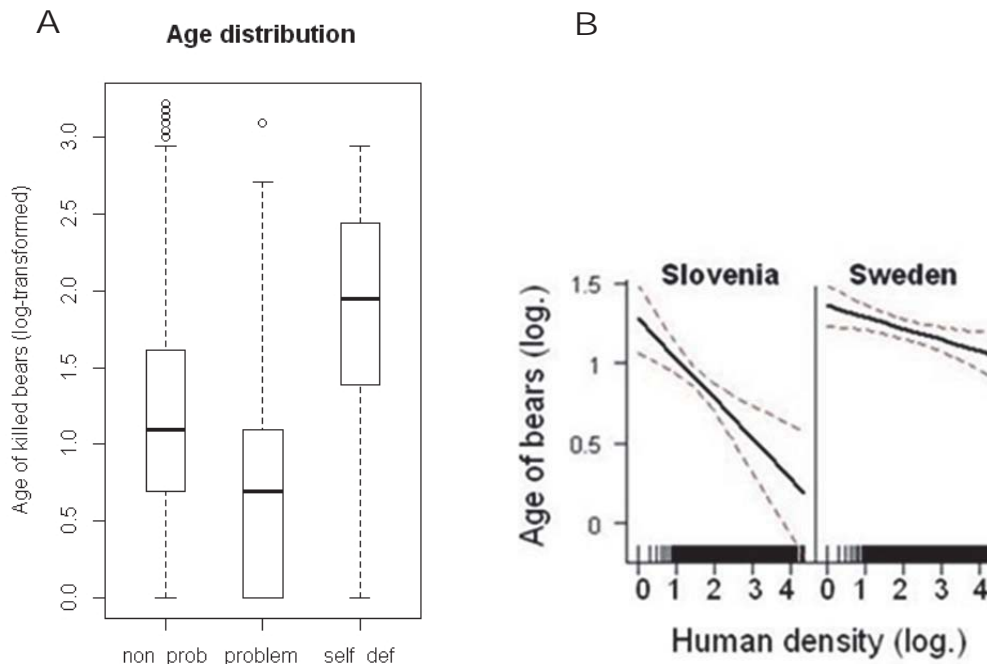


Figure 4. Age distribution among 1,896 hunter-killed nonproblem bears, and 149 management-killed problem bears in Slovenia and Sweden, and 47 Swedish bears shot in self defense, between 1990 and 2010. A) boxplots (i.e. median, 1st and 3rd quartiles and range) of age of bears in relation to problem bear status. B) separate effects, and 95% confidence intervals, on age distribution in relation to human density among shot bears, based on the linear mixed model with highest support ($\Delta AIC_c=0.00$, $AIC_c w=0.98$), *reprinted from Paper III*.

Variables are log transformed.

Explaining the likelihoods that different categories of bears occur near settlements

(Paper I)

Habituation and food-conditioning are examples of nonassociative and associative learning processes, respectively, as a result of frequent exposure to stimuli. These mechanisms can explain why some animals occur more often in an area than others, based on individuals' earlier experiences (Whittaker and Knight 1998, Bejder et al. 2009). However, habituation and conditioning poorly explain any unequal distribution of sex, age, or reproductive

categories of a species. We therefore concluded that the documented differences in age, sex, and reproductive categories of bears in relation to human activity and settlements cannot be explained only by considering habituation or sensitization, such as food conditioning, and, therefore, these mechanisms are proximate.

Younger bears can occur near settlements because they are naïve in terms of lacking experience of people (Blanchard and Knight 1991, Kaczensky et al. 2006). Naivety is more common when individuals disperse from natal areas. However, dispersal occurs because of interactions among bears, including inbreeding avoidance (Zedrosser et al. 2007), and aggressive behavior from resident conspecifics (Støen et al. 2005, Støen et al. 2006). We therefore concluded that the occurrence of young, naïve bears near settlements is a proximate mechanism, because their habitat use is a result of interactions with conspecifics. However, human-caused mortality also can explain why younger bears are near settlements, if bears have lower survival near people (Mattson et al. 1992, Mueller et al. 2004). Separating human-induced mortality from adult bears' avoidance of settlements is therefore important to explain the difference in age in relation to settlements. The common pattern of predation-vulnerable individuals (younger bears and females with young) occurring closer to settlements compared to dominant/predation-tolerant individuals (adult males and lone adult females) can best be explained by a despotic distribution among conspecifics. We therefore suggested that despotic distribution is the ultimate mechanism causing the proximate mechanisms of habituation, conditioning, and ultimately explaining the occurrence of young naïve bears near settlements.

Attractant management is important to counteract food conditioning and reduce the numbers of 'problem' bears. However, we concluded that failure to consider the despotic distribution of bears may lead to only treating the symptoms, e.g. habituation and conditioning. We suggested that the type of bear observed near a settlement can indicate the

underlying mechanisms behind their occurrence. Large, solitary bears near settlements suggest an attractive area (e.g. high food availability/quality and low disturbance), because these individuals seem to dominate in high-quality habitats, and we suggest that attractant management be prioritized in such areas in order to reduce bear-related problems. On the contrary, if females with young and/or subadult (i.e. smaller) individuals are more often reported near a settlement, this indicates a low-quality habitat, considering the despotic behavior of dominant conspecifics. Attractant management may therefore be less successful in reducing bear occurrence, because these predation-vulnerable individuals may focus on avoiding dominant conspecifics in remote areas.

Testing the paradigm of food search near people: diet and body condition in relation to settlements and problem bear status (Papers III, IV, V)

Understanding the underlying mechanisms behind bear occurrence near settlements and, thereby, the causes behind why some individuals are considered as ‘problem’ animals is of fundamental importance within large carnivore management. In Paper III, we asked whether food availability among years and body condition of bears in relation to densities of bears and people could explain the occurrence of ‘problem’ bears (i.e. animals killed by managers near settlements), by considering not only food search, but also interactions among bears.

We compared a body condition index (BCI) among hunter-killed nonproblem bears (n=1,279), management-killed problem bears (n=124), and bears shot in self defense during hunting (n=30), between 1990 and 2010. We compared patterns between Slovenia and Sweden, i.e. areas with and without the use of supplemental feeding. We evaluated two hypotheses. The food-search/food-competition hypothesis (I) predicted a different BCI in problem bears (because of either failure to find food in remote areas or because of exploiting

large amounts/high quality of human-derived foods near settlements) than nonproblem bears, higher BCI with increasing human density, and more problem bears during periods of lower food availability (calculated from the mean seasonal BCI of nonproblem bears). If food competition occurs, the BCI should be lower with increasing bear density. The safety-search/naivety hypothesis (II) predicted similar BCI between problem/nonproblem bears, no relation between BCI and human density, and no relation between number of problem bears and food availability.

We found no difference in BCI between problem and nonproblem bears (Figure 5), no relation between BCI and human density, and no relation between problem bear occurrence and seasonal food availability. The lack of difference in BCI in relation to human density and problem bear status support the safety-search/naivety hypothesis; that searching safety from conspecifics in combination with naivety (lack of human experience) best explain bear occurrence near settlements in Europe. BCI was negatively related with bear density in Sweden, whereas no correlation was found among Slovenian bears (Figure 5). This pattern may be due to the use of supplemental feeding, reducing food competition, and the high bear harvest rates in Slovenia compared to Sweden. BCI did not differ between bears shot in self defense and nonproblem bears. We therefore suggested that reasons other than food shortage probably explain why bears are involved in encounters with people or involved as problem bears near settlements.

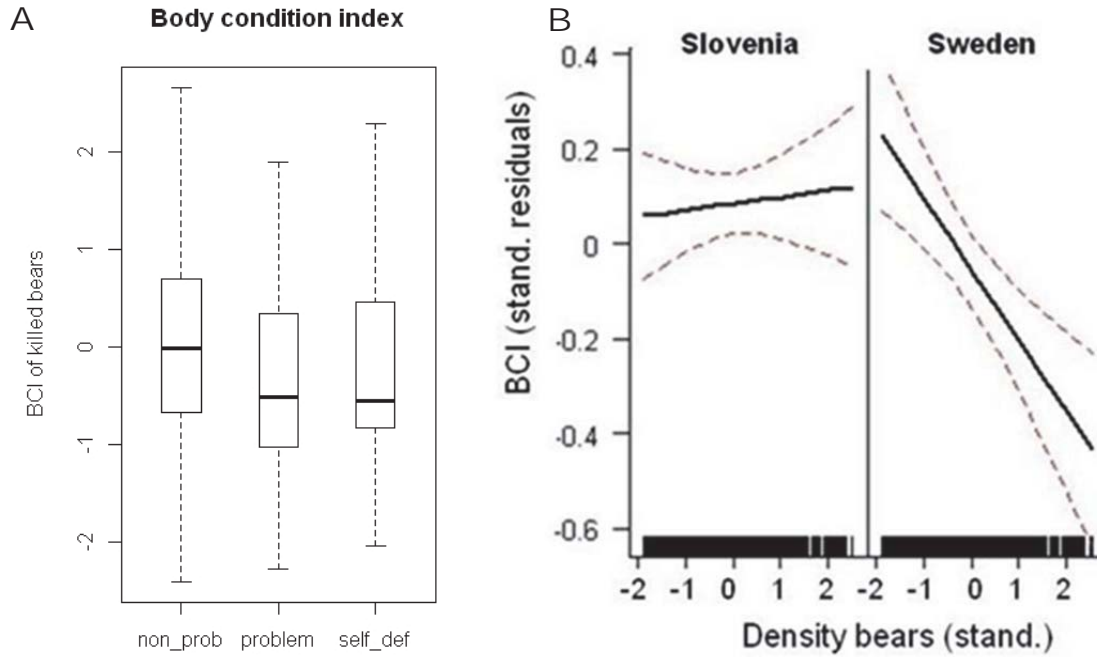


Figure 5. Body condition index (BCI) among 1,279 hunter-killed nonproblem bears, and 124 management-killed problem bears in Slovenia and Sweden, and 30 Swedish bears shot in self defense, between 1990 and 2010.

A) boxplots (i.e. median, 1st and 3rd quartiles and range) of BCI in relation to problem bear status. B) separate effects, and 95% confidence intervals, on BCI in relation to standardized density of bears among shot bears, based on the linear mixed model with highest support ($\Delta AIC_c=0.00$, $AIC_c w=0.64$), *reprinted from Paper III*.

Density of bears was calculated differently between Slovenia and Sweden.

In our study of brown bear diet in relation to bear movements near settlements (Paper V), we had to relate relocations of GPS-collared bears to the origin of their fecal remains, because diet was based on fecal samples. Knowledge of the gut retention time (GRT) would allow us to define a time frame during which defecations occur in relation to feeding patterns, i.e. uniting fecal samples with spatiotemporal data. Therefore, we analyzed the GRT for important food items, i.e. berries and meat, by Scandinavian brown bears in Paper IV. We expected a shorter GRT for berries than meat, because digestibility and fiber

content differ between these food items (Pritchard and Robbins 1990), in combination with a possible laxative function of berries (Jaric et al. 2007).

We experimentally measured the GRT on 6 captive brown bears, by feeding them either a mixture of berries (*Vaccinium myrtillus* and *V. vitis-idea*) or animal carcasses (either *Rangifer tarandus*, *Oryctolagus cuniculus*, *Sus scrofa domestica*, *Bos taurus*, or *Equus ferus caballus*). We analyzed the GRT in relation to diet, activity level, feeding time (midday/midnight), sex, age (subadult/adult), ingested amounts of food, prior food remains processed by the gut, and defecation rate, while controlling for bear identity.

Median GRT (1st and 3rd quartiles) when 50% of all feces containing the experimental food had been defecated was 5:47 (4:36 – 7:03, N=20) hours:minutes for a berry diet, and 14:30 (10:09 – 16:57, N=20) hours:minutes for a meat diet. We also documented median GRT for first and last defecations containing experimental food. Only the diet explained variation in GRT, with a meat diet having a 6:26 ± 1:56 (SE) hours:minutes longer GRT than a berry diet, based on 39 experiments.

We found no support for food shortage to explain problem bear occurrence in Sweden and Slovenia (Paper III). However, bears may still be under the influence of food conditioning, because of a different and high-quality diet near settlements. Therefore, in Paper V, we analyzed the dietary composition and quality of brown bears in relation to settlements to test the current paradigm of food as the key role behind bears occurring close to settlements. We predicted a different and higher-quality diet when an individual bear was near settlements than when the same bear was in a remote area, i.e. the food-search hypothesis.

We analyzed fecal remains of bears during a minimum period of 24 hours, after GPS/GSM-equipped bears were and had been relocated <150 m from settlements (Figure 1), which overlaps the GRT periods we reported in Paper IV. The 150-m cut-off was based on

reported bear movements between scheduled relocations and maximum distances between residential houses and their garbage bins. Remote areas were defined as relocations >600 m from settlements, which corresponds to a 95% habitat use among the studied bears. In addition, we analyzed the diet of bears within 48 hours prior to a settlement visit, provided no bear relocations had occurred within the <150-m radius from settlements. Fecal nutritive content was analyzed based on near infrared spectroscopy (NIRS), and dietary composition on the DNA metabarcoding approach. By combining nutritive data based on NIRS with data of dietary items based on DNA metabarcoding, we could account for any differences in dietary constituents when analyzing bears' diet quality based on fecal remains.

We analyzed 120 fecal samples based on 36 bear visits close to settlements from 21 individuals (33 feces from 5 adult males, 14 from 3 females with cubs-of-the-year, 11 from 3 females with yearlings, 37 from 2 lone adult females, and 25 from 9 subadult males and females), after 36 approaches close to settlements (28 prior-to-visit-to-a-settlement feces, 51 near-settlement feces, 41 remote feces). Median (1st and 3rd quartiles) duration of a bear visit near settlements was 30 (10 and 230) minutes, based only on relocations occurring within 150 m from the settlements and, thus, are considered as minimum values for the lengths of the bears' visits.

Among the brown bears' most common food items, we identified berries (*V. vitis idea*, *V. myrtillus*, *Empetrum* spp.), ants (*Camponotus* sp, *Formica* spp.) and moose (*Alces alces*), which is similar to earlier studies of diet from central Sweden and our study area (Dahle et al. 1998, Swenson et al. 1999, Rauset et al. 2012). In addition, we identified a number of presumed settlement-associated items, including a variety of cereals (*Avena* sp., *Hordeum vulgare*, *Triticum aestivum*, *Malus* sp.), domesticated animals (*Bos* sp., *Ovis* sp., *Sus scrofa*) and nonnative plant species (*Musineon vaginatum*, *Areca triandra*, *Cannabis sativa*).

We found no significant difference in the bears' dietary composition or quality between settlements and remote areas, <1.9% of the dietary composition was associated with settlements, and, thus, no support for the food-search hypothesis to explain bear occurrence near settlements (Figure 6). However, bears more often ingested pig remains (*Sus scrofa*) within 48 hours prior to a settlement visit and while occurring >150 m from any settlements than compared to when using settlements or remote areas (Figure 7).

Subadults did not differ from adult males in diet or fecal nutritive quality, suggesting no effects from interference competition. The fecal nutritive quality of females with cubs-of-the-year was not different and diet composition was in general not different from adult males. However, females with yearlings had 5.1 ± 2.9 (SE)% lower fecal protein content than adult males. Sample sizes of sex, age, and reproductive categories were generally small. If we combined females with cubs-of-the-year with females with yearlings, we found that females accompanied by young less often exploited pig remains compared to other bears. This suggests that the distribution of predation-vulnerable bears may be affected to some degree by despotic behavior of dominant bears.

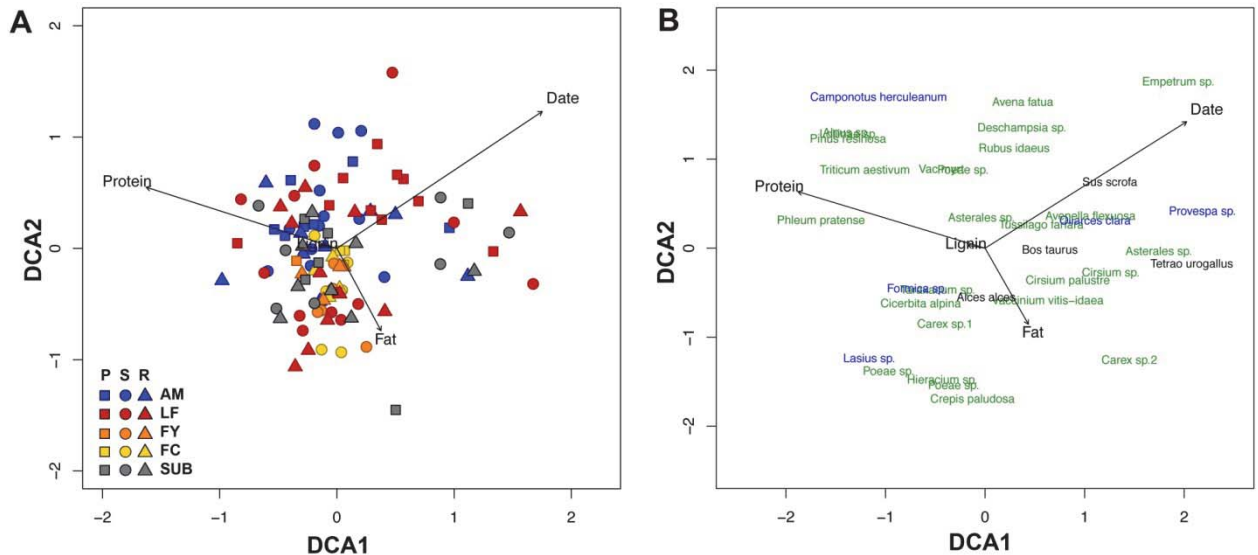


Figure 6. Detrended correspondence analysis of diet composition and quality based on 106 fecal samples from different sex, age and reproductive categories of brown bears before and when they were near settlements, or used remote areas in south-central Sweden 2010. Dietary composition A) shown in relation to settlements and bear categories, and B) shown in relation to common food items. Diet quality is based on near infrared spectroscopy and diet composition is based on the DNA metabarcoding approach. Categories are defined as follows: P-prior to settlement visits, S-settlements, R-remote areas, AM-adult males, LF-lone parous females, FY-females with yearlings, FC-females with cubs, SUB-subadult females and males. *Figure is reprinted from Paper V.*



Figure 7. Example of a dump site for slaughter remains of pigs and cattle, at a roadside >500 m from settlements within our study area in south-central Sweden, exploited repeatedly during a period of several weeks by GPS/GSM-equipped brown bears, especially adult males, during 2009. (Photos by Marcus Elfström)

Discussion

Identifying which categories of bears approach settlements and are considered to be problem animals

Based on a literature review, we have identified a common pattern in North America, Europe and Asia of a different likelihood of occurrence of black and brown bears near settlements based on sex, age, and reproductive categories. We concluded in Paper I that bears near human activity and settlements were younger, and that females accompanied by their offspring were more often near settlements or humans than adult males or lone adult females. We identified a similar pattern; with adult males farther from settlements than other brown bears during the critical period of winter denning in Sweden in Paper II, and that brown bears are younger in areas with higher human density, whereas problem bears are younger than nonproblem bears in both Sweden and Slovenia in Paper III. Thus, the different habitat use by European brown bears, which we reported in Papers II and III, confirmed the common view reported from other areas regarding certain types of individuals, especially predation-vulnerable bears, being overrepresented near human activity and settlements.

Explaining the likelihoods that different categories of bears occur near settlements

A despotic distribution, can explain why predation-vulnerable subadults and females accompanied by offspring occur in lower-quality habitats and closer to settlements compared to adult males and lone adult females. The theory of despotic distribution is not novel to describe interactions among black bears or brown bears (Beckmann and Berger 2003, Libal et al. 2011), and several authors have described social dominance behavior, different habitat use, and intraspecific predation among bears (Herrero 1983, Craighead et al. 1995). All this evidence supports a despotic distribution among individuals. However, we are not aware of

any effort to distinguish ultimate and proximate mechanisms behind bear occurrence near settlements.

Individual learning responses, e.g. waning or sensitization of a stimuli, can explain why some individuals behave differently towards humans. Albert and Bowyer (1991) concluded that human habituation was particularly advantageous for subadults and females with young, because they would avoid dominant conspecifics, which also would imply different adaptability for learning among different sex, age, and reproductive categories of conspecifics. However, we concluded that human habituation or food conditioning poorly predicted different habitat use among sex, age, and reproductive categories of conspecifics, because different exposures to stimuli are required before different learning responses can occur (Paper I). Therefore, we concluded that a despotic distribution was an ultimate mechanism, which may result in the proximate mechanisms of habituation, conditioning, or naivety.

Scandinavian brown bears spend half their life hibernating in winter dens and females give birth there. Winter dormancy can result in 20-40% weight loss (Kingsley et al. 1983), and therefore bears' choice of den location is probably important in order to avoid disturbance and conserve energy. Earlier studies from our study area reported that females with cubs have the longest and males the shortest denning periods (Friebe et al. 2001), and that human disturbance and human activity may influence den abandonment and den site selection (Swenson et al. 1997a, Elfström et al. 2008). Premature (i.e. midwinter) den abandonment by females after giving birth may be extra costly, in terms of reproductive success, if newborn cubs are exposed to thermal and energetic stress (Linnell et al. 2000). Young cubs are also especially vulnerable for infanticidal males after den emergence in the spring. Therefore, den site characteristics may differ among sex, age and reproductive bear categories for both energetic reasons and risks for midwinter disturbance and predation

during spring. We did not test whether choice of den site location was influenced by other bears in the area. However, Libal et al. (2011) reported that adult female brown bears, not separated by reproductive status, seem to avoid denning near adult males in Alaska. In Paper II, we considered reproductive status of adult females (i.e. lone and pregnant or accompanied by young when entering the den) when comparing denning characteristics, and found no differences related to reproductive status among female Scandinavian brown bears. Thus, although requirements for shelter and security against disturbance and predation may be larger for females that will give birth after entering the den, compared to females accompanied by yearlings or older offspring, we found no such effects in den site characteristics. Linnell et al. (2000) suggested that females that give birth during denning may be more tolerant to disturbance, because premature den abandonment can result in lower reproductive success. However, the different advantages of human tolerance by sex, age, and reproductive categories of bears, as suggested by Linnell et al. (2000) and Albert and Bowyer (1991), require considerations of intraspecific interactions, rather than only focus on habituation or conditioning, to explain habitat use and human tolerance among bears. We found that adult males denned farther from plowed roads than other bears, and that these roads probably represent a disturbance, because of greater premature den abandonment near these roads in Paper II, and because bears avoid them when selecting den sites (Elfström et al. 2008).

Human-induced mortality could explain why bears were younger near settlements, if bears there were killed before they reached adulthood (Beeman and Pelton 1976, Rogers et al. 1976, Bunnell and Tait 1985, Mattson et al. 1992, Mueller et al. 2004). However, habitats with high food quality is disproportionately used by dominant/predation-tolerant bears (adult males, lone adult females) compared to predation-vulnerable conspecifics (Storonov and Stokes 1972, Stelmock and Dean 1986, Mattson et al. 1987, Blanchard and Knight 1991,

Mattson et al. 1992, Wielgus and Bunnell 1994, Craighead et al. 1995, Wielgus and Bunnell 1995, Olson et al. 1997, Ben-David et al. 2004, Nevin and Gilbert 2005b;a, Peirce and Van Daele 2006, Rode et al. 2006b). This spatiotemporal difference in habitat use cannot be explained by human-induced mortality, or human habituation and food-conditioning, because these habitats are not necessarily correlated with human activity. We found a similar pattern; with females accompanied by offspring exploiting dump sites for slaughter remains less often compared to other bears in Sweden (Paper V).

Testing the paradigm of food search near people: diet and body condition in relation to settlements and problem bear status

Although we argue that interactions among bears are the ultimate cause behind their occurrence near settlements, food conditioning may still be a common mechanism among bears near people. However, we found no difference in body condition between problem and nonproblem bears, and similar diet composition and quality in relation to distance from settlements, and thus no support for food shortage or food conditioning in Scandinavian brown bears near settlements (Papers III and V). This contradicts all expectations of the paradigm of food-search to explain why bears approach settlements. The reason why Scandinavian bears deviate in comparison with earlier diet studies on American black bears and brown bears from North America and Asia (Gunther et al. 2004, Sato et al. 2005, Greenleaf et al. 2009, Hopkins et al. 2012) may be different ecological conditions, where e.g. many North American bear populations face lower food availability during years of food failure in remote areas, and no choice but to search food closer to settlements (Mattson et al. 1992).

Because we found no difference in bears' diet composition and quality between settlements and remote areas; I) food-search seems not to play a significant role in explaining

why these bears were approaching settlements. Provided that settlements are associated with disturbance costs, approaching young bears II) may be naïve in terms of not yet having recognized these costs if they chose to approach without any obvious trade-off in terms of food. Alternatively, the bears already may have gained cumulative experience of human activity, and as a result they III) have become human habituated and, thus, seem to have gained a higher tolerance of human activities. However, we believe human habituation is not common among brown bears, because their avoidance of human activity (Mace and Waller 1996, Nellemann et al. 2007) suggests that they have a low tolerance of people. Alternatively, if the settlements were not associated with costs (e.g. disturbance), there is no reason to expect a trade-off in terms of food behind approaches of bears near settlements in our study area. We noticed a dense understory vegetation, which reduced the sighting distance to only a few meters, around several settlements approached by bears. However, we did not test whether the sighting distance at settlements visited by bears differed from that at settlements not visited by bears. However, Ordiz et al. (2011) reported that bears in our study area were more reluctant to use open areas (i.e. areas with increasing sighting distance) for daybeds while near settlements. Thus, the settlements that were approached by bears, reported in Paper V, may not have represented a disturbance for the bears, if dense vegetation allowed them to approach people and settlements undetected.

The similar body condition in relation to problem bear status and human density among brown bears in Sweden and Slovenia suggests that other reasons than food shortage explain bear occurrence near settlements (Paper III). An alternative explanation for not finding differences in body condition may be that even well nourished bears can experience hunger. However, we argue that malnourished individuals should experience hunger more often than well nourished ones, and thus a lower body condition among bears near settlements, if hunger was a significant factor.

Management implications

Our results suggest alternative explanations to the current paradigm in bear management that food search is the primary cause why bears occur near settlements. Observations of bears near settlements are typically explained by the public or managers as individuals searching for food, and that these animals risk becoming food conditioned and/or human habituated. The arguments of human habituation and food conditioning are often used without confirmation, and the risk of a bear responding to either one of these mechanisms may be a sufficient reason for removing the animal due to concerns for property damages and human injuries. However, habitat use by bears is influenced by their interactions with conspecifics, independently of human habituation/food conditioning. The human shield theory, i.e. that subadults and/or female brown bears with young approach settlements in order to avoid dominant/aggressive adult male bears, has been suggested by several authors as a reason for bear occurrence near people (Mattson et al. 1987, Mattson 1990, Albert and Bowyer 1991, Wielgus and Bunnell 1994, Olson et al. 1997, Mueller et al. 2004, Nevin and Gilbert 2005b, Rode et al. 2006a, Rode et al. 2006b, Schwartz et al. 2010). The despotic distribution suggests: I) that food conditioning / human habituation is not a prerequisite to explain why predation-vulnerable bears occur near human activity and settlements; II) that settlements may cause a redistribution of bears over the landscape, with predation-vulnerable bears spatiotemporally selecting habitats with higher human activity in order to avoid dominant conspecifics.

One of the biggest problems in bear management is that people are afraid of bears. On the other hand, bears also seem to fear people (Ordiz et al. 2011, Ordiz et al. 2012, Ordiz et al. 2013). However, dominant bears may inflict more fear than people, particularly in the very bears that trigger the fear in people in settlements. Thus, if bears occur close to people in order to avoid dominant conspecifics, such behavior should not be viewed as ‘unnatural’

behavior, because the selection of a predation refuge habitat is an adaptive strategy for vulnerable age and reproductive categories of bears. Although our results suggest that food shortage or food conditioning is not common among Scandinavian brown bears, we acknowledge that actions such as attractant management is important to prevent wildlife-related problems near human settlements, including bears. Our results also suggest that Scandinavian brown bears often exploit illegal dump sites of slaughter remains. This indicates that the practice of illegally dumping slaughter remains outside settlements may be common and that the practice, thus, requires to be addressed properly by the responsible management authorities. Although the occurrence of human habituation or food conditioning may be more common in bears outside Scandinavia, we suggest that bear managers in general also address the ultimate mechanisms of despotic distribution in bears, when dealing with the public's anxiety about bears. An increased understanding of why some bears more often occur in an area compared to conspecifics, may mitigate the public's anxiety, e.g. regarding their view of how 'unnatural' the behavior of these bears really is.

Bears near settlements seem not to represent a 'problem' as long as they are not observed by people and no property damages occur, because human habituation and food conditioning seem to be uncommon among Scandinavian bears. In Paper II, we concluded that habitat use differences among bears are related to human activity, and this result is also supported by the common pattern of bears avoiding human activity and settlements. In Paper III we found no support for food shortage behind problem bear occurrence, and in Paper V we found no support for food conditioning, due to the similar diets in relation to distance from settlements. However, if people want to reduce the likelihood of bear occurrence near settlements, we recommend the removal of dense understory vegetation (Ordiz et al. 2011). This kind of attractant management can be resource demanding, however, the type of bear(s) (i.e. large solitary, or small, and females with young) observed near

settlements may serve as an indicator to which areas to prioritize regarding removing habitat features to prevent the occurrence of problem bears.

Future research perspectives

There are still many questions left to answer in order to increase our understanding of a despotic distribution of bears and their occurrence near settlements. The difference in age of bears in relation to settlements may be, both a result of the avoidance of people by adult bears, and a result of human-induced mortality. Therefore, mortality rates of bears should be documented in relation to settlements, in order to separate the effects of human-induced mortality and avoidance of people by adult bears on the observed age distribution of bears. Human-induced mortality risk among GPS/GSM-equipped bears could be analyzed in relation to their proportional habitat use near settlements. In bear populations expanding towards areas with higher human densities, younger bears may be nearer people because of more dispersing subadults occur near the expansion front. Therefore, it would be important also to analyze the locations of (shot) bears in relation to known expansion fronts.

Dispersing (young) bears may approach people because of naivety. Therefore, the effects of high densities of established bears and/or high human densities could be important to analyze in relation to dispersal routes of young bears when they leave their natal areas. This analysis could reveal how often dispersing bears approach settlements, and document the influence from other bears on dispersal routes. In addition, spatiotemporal GIS analyses of habitat use between subadults and adult males (i.e. predation-vulnerable and predation-tolerant/dominant individuals), e.g. based on resource selection functions, could document the influence of human activity compared with conspecifics.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. B. Petrov, and F. Caski, eds. Proceeding of the Second International Symposium on Information Theory:267-281.
- Albert, D. M., and R. T. Bowyer. 1991. Factors related to grizzly bear-human interactions in Denali National Park. *Wildlife Society Bulletin* 19:339-349.
- Alcock, J. 1988. *Animal behavior: an evolutionary approach*. Fourth edition. 596 pp. Sinauer Associates, Massachusetts, USA.
- Arnemo, J. M., A. Evans, Å. Fahlman, P. Ahlqvist, H. Andrén, S. Brunberg, O. Liberg, J. D. C. Linnell, J. Odden, P. Persson, H. Sand, P. Segerström, K. Sköld, T. H. Strømseth, O.-G. Støen, J. E. Swenson, and P. Wabakken. 2011. *Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx*. Hedmark University College, Evenstad, Norway:14.
- Barber, J. R., K. R. Crooks, and K. M. Fristrup. 2009. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25:180-189.
- Basille, M., I. Herfindal, H. Santin-Janin, J. D. C. Linnell, J. Odden, R. Andersen, K. Arild Høgda, and J.-M. Gaillard. 2009. What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32:683-691.
- Beckmann, J. P., and J. Berger. 2003. Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy* 84:594-606.
- Beeman, L. E., and M. R. Pelton. 1976. Homing of black bears in the Great Smoky Mountains National park. *Ursus* 3:87-95.
- Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing

- wildlife responses to anthropogenic stimuli. *Marine Ecology-Progress Series* 395:177-185.
- Belant, J. L., K. Kielland, E. H. Follmann, and L. G. Adam. 2006. Interspecific resource partitioning in sympatric ursids. *Ecological Applications* 16:2333-2343.
- Belant, J. L., B. Griffith, Y. Zhang, E. H. Follmann, and L. G. Adams. 2010. Population-level resource selection by sympatric brown and American black bears in Alaska. *Polar Biology* 33:31-40.
- Bellemain, E., J. E. Swenson, O. Tallmon, S. Brunberg, and P. Taberlet. 2005. Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears. *Conservation Biology* 19:150-161.
- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465-474.
- Berger, J. 2007. Fear, human shields and redistribution of prey and predators in protected areas. *Biology Letters* 3:620-623.
- Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Myrsetrud, and O. Gimenez. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78:656-665.
- Bisi, J., S. Kurki, M. Svensberg, and T. Liukkonen. 2007. Human dimensions of wolf (*Canis lupus*) conflicts in Finland. *European Journal of Wildlife Research* 53:304-314.
- Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58:41-67.
- Bojarska, K., and N. Selva. 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. *Mammal Review* 42:120-143.

- Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North-American bears. *Arctic* 38:316-323.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. New York, Springer-Verlag.
- Clark, J. E., F. T. van Manen, and M. R. Pelton. 2002. Correlates of success for on-site releases of nuisance black bears in Great Smoky Mountains National Park. *Wildlife Society Bulletin* 30:104-111.
- Craighead, J. J., J. Sumner, and J. A. Mitchell. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959-1992. 517pp. Island Press, Washington D.C., USA.
- Dahle, B., O. Sørensen, J., E. Wedul, H., J. E. Swenson, and F. Sandegren. 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biology* 4:147-158.
- Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* 260:329-335.
- Dau, C. P. 1989. Management and biology of brown bears at Cold Bay, Alaska. Bear-people conflicts: proceedings of a symposium on management strategies. Pages 19-26 in M Bromley, ed. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Elfström, M., J. E. Swenson, and J. P. Ball. 2008. Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* 14:176-187.
- Enserink, M., and G. Vogel. 2006. Wildlife conservation - The carnivore comeback. *Science* 314:746-749.

- Ericsson, G., C. Sandstrom, J. Kindberg, and O.-G. Støen. 2010. Om svenskars rädsla för stora rovdjur, älg och vildsvin. Rapport 2010:1. [Report on people's attitude and fear towards large carnivores, moose and wild boar in Sweden.] [In Swedish] 15 pp. Institutionen för vilt, fisk och miljö, Sveriges Lantbruksuniversitet.
- Ferreras, P., M. Delibes, F. Palomares, J. M. Fedriani, J. Calzada, and E. Revilla. 2004. Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behavioral Ecology* 15:31-40.
- Fortin, J. K., S. D. Farley, K. D. Rode, and C. T. Robbins. 2007. Dietary and spatial overlap between sympatric ursids relative to salmon use. *Ursus* 18:19-29.
- Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:16.
- Friebe, A., J. E. Swenson, and F. Sandegren. 2001. Denning chronology of female brown bears in central Sweden. *Ursus* 12:37-45.
- Garshelis, D. L. 1989. Nuisance bear activity and management in Minnesota. Bear-people conflicts: proceedings of a symposium on management strategies. Pages 169-180 in M. Bromley, ed. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Gittleman, J. L., S. M. Funk, D. W. Macdonald, and R. K. Wayne. 2001. Why 'carnivore conservation'? Pages 1-7 in J.L Gittleman, S.M. Funk, D. Macdonald, R.K. Wayne eds. *Carnivore conservation*. Cambridge University Press 675 pages.
- Greenleaf, S. S., S. M. Matthews, R. G. Wright, J. J. Beecham, and H. M. Leithhead. 2009. Food habits of American black bears as a metric for direct management of human-bear conflict in Yosemite Valley, Yosemite National Park, California. *Ursus* 20:94-101.

- Gunther, K. A., M. A. Haroldson, K. Frey, S. L. Cain, J. Copeland, and C. C. Schwartz. 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992-2000. *Ursus* 15:10-22.
- Herrero, S. 1983. Social behaviour of black bears at a garbage dump in Jasper National Park. *Ursus* 5:54- 70.
- Herrero, S., T. Smith, T. D. DeBruyn, K. Gunther, and C. A. Matt. 2005. From the field: brown bear habituation to people - safety, risks, and benefits. *Wildlife Society Bulletin* 33:362-373.
- Hopkins, J. B., P. L. Koch, C. C. Schwartz, J. M. Ferguson, S. S. Greenleaf, and S. T. Kalinowski. 2012. Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. *Journal of Wildlife Management* 76:703-713.
- Hristienko, H., and J. E. McDonald. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* 18:72-88.
- Immelmann, K., and C. Beer. 1989. A dictionary of ethology. 341pp. Harvard University Press, Cambridge, Massachusetts, USA.
- Izumiyama, S., T. Mochizuki, R. Kishimoto, M. Gotoh, and H. Hayashi. 2008. Elucidation of massive haunt factor to Asiatic black bear depend to rural area capture time and age assesement in the Nagano Prefecture. *Bulletin Shinshu University. Alpine Field Center*. (In Japanese) 6:19-24.
- Jaric, S., Z. Popovic, M. Macukanovic-Jovic, L. Djurdjevic, M. Mijatovic, B. Karadzic, M. Mitrovic, and P. Pavlovic. 2007. An ethnobotanical study on the usage of wild medicinal herbs from Kopaonik Mountain (Central Serbia). *Journal of Ethnopharmacology* 111:160-175.

- Jerina, K., M. Jonožovič, M. Krofel, and T. Skrbinšek. 2013. Range and local population densities of brown bear *Ursus arctos* in Slovenia. *European Journal of Wildlife Research* In press.
- Johansson, M., J. Karlsson, E. Pedersen, and A. Flykt. 2012a. Factors governing human fear of brown bear and Wolf. *Human Dimensions of Wildlife: An International Journal of Animal Ecology* 17:58-74.
- Johansson, M., M. Sjöström, J. Karlsson, and R. Brannlund. 2012b. Is Human Fear Affecting Public Willingness to Pay for the Management and Conservation of Large Carnivores? *Society & Natural Resources* 25:610-620.
- Kaczensky, P., D. Huber, F. Knauer, H. Roth, A. Wagner, and J. Kusak. 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *Journal of Zoology* 269:474-485.
- Kindberg, J., G. Ericsson, and J. E. Swenson. 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. *Biological Conservation* 142:159-165.
- Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* 17:114-123.
- Kingsley, M. C. S., J. A. Nagy, and R. H. Russell. 1983. Patterns of weight gain and loss for grizzly bears in northern Canada. *Ursus* 5:174-178.
- Kishimoto, R. 2009. Status of the 2006 drastic rise of Asiatic black bear (*Ursus thibetanus*) intrusions into residential areas in Nagano Prefecture. Toru Oi, Naoki Ohnishi, Toru Koizumi, Isamu Okochi eds. *FFPRI Scientific Meeting Report 4 "Biology of Bear Intrusions"*. 82pp. Forestry and Forest Products Research Institute, Ibaraki, Japan:35-39.

- Klenzendorf, S., and M. R. Vaughan. 1999. An overview of brown bear management in six European countries. *Ursus* 11:163-178.
- Krofel, M., M. Jonožovič, and K. Jerina. 2012. Demography and mortality of removed brown bears in a heavily exploited population. *Ursus* 23:91-103.
- Kryštufek, B., and H. I. Griffiths. 2003. Anatomy of a human–brown bear conflict. Case study from Slovenia in 1999–2000. In B. Kryštufek, B. Flajšman, H.I. Griffiths, eds *Living with bears, a large European carnivore in a shrinking world* 368pp. Ecological Forum of the Liberal Democracy of Slovenia, Ljubljana, Slovenia:126-153.
- Libal, N., J. Belant, B. Leopold, G. Wang, and P. Owen. 2011. Despotism and risk of infanticide influence grizzly bear den-site selection. *PLoS ONE* 6:1-10.
- Linnell, J. D. C., J. E. Swenson, R. Andersen, and B. Barnes. 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28:400-413.
- Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4:345-349.
- Mace, R. D., and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. *Wildlife Society Bulletin* 24:461-467.
- MacHutchon, G., S. Himmer, H. Davis, and M. Gallagher. 1998. Temporal and spatial activity patterns among coastal bear populations. *Ursus* 10:539-546.
- Maehr, D. S., E. D. Land, D. B. Shindle, O. L. Bass, and T. S. Hoctor. 2002. Florida panther dispersal and conservation. *Biological Conservation* 106:187-197.
- Martin, J., M. Basille, B. Van Moorter, J. Kindberg, D. Allaine, and J. E. Swenson. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology* 88:875-883.

- Matson, G. M., L. Van Daele, E. Goodwin, A. Aumiller, H. V. Reynolds, and H. Hristienko. 1993. A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth. Matson's Laboratory, Milltown, Montana, USA.
- Mattson, D. 1990. Human impacts on bear habitat use. *Ursus* 8:33-56.
- Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Ursus* 7:259-273.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* 56:432-442.
- McCullough, D. R. 1982. Behavior, bears, and humans. *Wildlife Society Bulletin* 10:27-33.
- McCutchen, H. E. 1990. Cryptic Behavior of Black Bears (*Ursus americanus*) in Rocky Mountain National Park, Colorado. *Ursus* 8:65-72.
- McLean, P. K., and M. R. Pelton. 1990. Some demographic comparisons of wild and panhandler bears in the Smoky Mountains *Ursus* 8:105-112.
- McLellan, B. 1994. Density-dependent population regulation of brown bears. In M. Taylor, ed. Density-dependent population regulation of black, brown, and polar bears. 43pp. *Ursus. Monograph Series* 3:15-24.
- McLellan, B. N., and D. M. Shackleton. 1988. Grizzly bears and resource-extraction industries - effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology* 25:451-460.
- McLellan, B. N., F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management* 63:911-920.

- McLellan, B. N. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16:141-156.
- Messmer, T. A., and J. W. Enck. 2012. Human dimension of wildlife use management in D.J. Decker, S.J. Riley, W.F. Siemer (eds) Human dimensions of wildlife management. The Johns Hopkins University Press, Baltimore, US, 286 pages, second edition:203-219.
- Moe, T. F., J. Kindberg, I. Jansson, and J. E. Swenson. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* 85:518-525.
- Moen, G. K., O. G. Stoen, V. Sahlen, and J. E. Swenson. 2012. Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. *Plos One* 7.
- Mueller, C., S. Herrero, and M. L. Gibeau. 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15:35-47.
- Naughton-Treves, L., R. Grossberg, and A. Treves. 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. *Conservation Biology* 17:1500-1511.
- Nellemann, C., O. Støen, J. Kindberg, J. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157-165.
- Nevin, O. T., and B. K. Gilbert. 2005a. Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? *Biological Conservation* 121:611-622.

- Nevin, O. T., and B. K. Gilbert. 2005b. Measuring the cost of risk avoidance in brown bears: Further evidence of positive impacts of ecotourism. *Biological Conservation* 123:453-460.
- Nilsen, E. B., T. Pettersen, H. Gundersen, J. M. Milner, A. Mysterud, E. J. Solberg, H. P. Andreassen, and N. C. Stenseth. 2005. Moose harvesting strategies in the presence of wolves. *Journal of Applied Ecology* 42:389-399.
- Olson, T. L., B. K. Gilbert, and R. C. Squibb. 1997. The effects of increasing human activity on brown bear use of an Alaskan river. *Biological Conservation* 82:95-99.
- Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears *Oecologia* 166:59-67.
- Ordiz, A., O. G. Stoen, S. Saebo, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? *Biological Conservation* 152:21-28.
- Ordiz, A., O. G. Stoen, S. Saebo, V. Sahlen, B. E. Pedersen, J. Kindberg, and J. E. Swenson. 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology* 50:306-314.
- Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. *Ecology* 80:957-975.
- Peirce, K. N., and L. J. Van Daele. 2006. Use of a garbage dump by brown bears in Dillingham, Alaska. *Ursus* 17:165-177.
- Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 68:1645-1651.
- Rauset, G. R., J. Kindberg, and J. E. Swenson. 2012. Modeling female brown bear kill rates on moose calves using global positioning satellite data. *Journal of Wildlife Management* 76:1597-1606.

- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15:161-171.
- Rode, K., S. Farley, and C. Robbins. 2006a. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* 133:70-80.
- Rode, K. D., S. D. Farley, and C. T. Robbins. 2006b. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636-2646.
- Rodríguez-Prieto, I., J. Martín, and E. Fernández-Juricic. 2010. Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology* 64:1937-1945.
- Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, C. J., and M. M. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. *Ecology and Society* 16:16-39.
- Rogers, L. L., C. M. Stowe, E. M. Erickson, L. J. Verme, and J. J. Ozoga. 1976. Characteristics and management of black bears that feed in garbage dumps, campgrounds, or residential areas. *Ursus* 3:169-175.
- Rogers, L. L. 2011. Does diversionary feeding create nuisance bears and jeopardize public safety? *Human-Wildlife Interactions* 5:287-295.
- Røskaft, E., T. Bjerke, B. Kaltenborn, J. D. C. Linnell, and R. Andersen. 2003. Patterns of self-reported fear towards large carnivores among the Norwegian public. *Evolution and Human Behavior* 24:184-198.
- Sato, Y., T. Mano, and S. Takatsuki. 2005. Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan. *Wildlife Biology* 11:133-144.

- Schwartz, C. C., J. E. Swenson, and S. D. Miller. 2003. Large carnivores, moose, and humans: a changing paradigm of predator management in the 21th century. *Alces* 39:41-63.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1-68.
- Schwartz, C. C., S. L. Cain, S. Podrutzny, S. Cherry, and L. Frattaroli. 2010. Contrasting activity patterns of sympatric and allopatric black and grizzly bears. *Journal of Wildlife Management* 74:1628-1638.
- Skrbinšek, T., M. Jelenčič, H. Potočnik, P. Trontelj, and I. Kos. 2008. Analiza medvedov odvzetih iz narave in genetsko-molekularne raziskave populacije medveda v Sloveniji. I. Del. Varstvena genetika in ocena številčnosti medveda 2007. [Analysis of removed brown bears and genetic-molecular studies on brown bear population in Slovenia. Part I. Conservation genetics and bear population size estimate for 2007.]. Final report. Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia. [In Slovenian].
- Smith, J. L. D. 1993. The role of dispersal in structuring the Chitwan tiger population. *Behaviour* 124:165-195.
- Stelmock, J. J., and F. C. Dean. 1986. Brown bear activity and habitat use, Denali National Park: 1980. *Ursus* 6:155-167.
- Steyaert, S. M. J. G., F. J. Hütter, M. Elfström, A. Zedrosser, K. Hackländer, M. H. Lê, W. Windisch, J. Swenson, and T. Isaksson. 2012. Fecal spectroscopy: a practical tool to assess diet quality in an opportunistic omnivore. *Wildlife Biology* 18:431-438.

- Steyaert, S. M. J. G., J. Kindberg, J. Swenson, and A. Zedrosser. 2013. Male reproductive strategy explains spatiotemporal segregation in brown bears. *Journal of Animal Ecology* 82:836-845.
- Storónov, D., and A. Stokes, W. 1972. Social behavior of the Alaska brown bear. *Ursus* 2:232-242.
- Støen, O.-G., E. Bellemain, S. Sæbø, and J. E. Swenson. 2005. Kin-related spatial structure in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 59:191-197.
- Støen, O.-G., A. Zedrosser, S. Sæbø, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* 148:356-364.
- Swenson, J. E., F. Sandegren, S. Brunberg, and P. Wabakken. 1997a. Winter den abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildlife Biology* 3:35-38.
- Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzen, and P. Wabakken. 1997b. Infanticide caused by hunting of male bears. *Nature* 386:450-451.
- Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 77:551-561.
- Swenson, J. E., B. Dahle, and F. Sandegren. 2001. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12:81-92.
- Taberlet, P., E. Coissac, F. Pompanon, C. Brochmann, and E. Willerslev. 2012. Towards next-generation biodiversity assessment using DNA metabarcoding. *Molecular Ecology* 21:2045-2050.
- Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17:1491-1499.

- White, P. J., K. M. Proffitt, and T. O. Lemke. 2012. Changes in Elk Distribution and Group Sizes after Wolf Restoration. *American Midland Naturalist* 167:174-187.
- Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to humans. *Wildlife Society Bulletin* 26:312-317.
- Wielgus, R. B., and F. L. Bunnell. 1994. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405-413.
- Wielgus, R. B., and F. L. Bunnell. 1995. Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59:552-560.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126-2128.
- Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3:165-173.
- Zedrosser, A., B. Dahle, J. E. Swenson, and N. Gerstl. 2001. Status and management of the brown bear in Europe. *Ursus* 12:9-20.
- Zedrosser, A., O. Støen, S. Sæbø, and J. Swenson. 2007. Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour* 74:369-376.

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PAPER I

REVIEW

Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications

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ABSTRACT

1. Large carnivores (LCs), such as bears (Ursidae), are commonly believed to occur near human settlements because they have a learned tolerance of humans (human habituation) and because they associate humans with accessible high-quality foods (food conditioning). Young bears and females with cubs are often overrepresented among 'problem' bears near settlements.

2. We review the mechanisms underlying the occurrence of brown and black bears (*Ursus arctos*, *Ursus americanus*, *Ursus thibetanus*) near settlements, and consider four hypotheses designed to separate ultimate and proximate mechanisms.

3. Increased occurrence of bears near people or settlements can be explained by (i) the human habituation hypothesis; increased use of human-derived foods can be explained by (ii) the food-conditioning hypothesis. However, both mechanisms are proximate, because they can only apply if bears have earlier experience of people and/or human-derived food.

4. A lack of human experience can explain the increased occurrence of younger bears near people or settlements: (iii) the naivety hypothesis. This is a proximate mechanism, because movements of naive bears are typically triggered by aggression and/or competition among conspecifics.

5. We conclude that the disproportionate occurrence of bears in certain sex, age and reproductive classes near people or settlements can only be explained by predation avoidance and/or interference competition, i.e. by (iv) the despotic distribution hypothesis. Therefore, a despotic distribution must be an ultimate mechanism causing the proximate mechanisms of habituation or conditioning. Thus, bears using settlements as predation refuges should not be considered 'unnatural', but rather as exhibiting an adaptive behaviour, because of the despotic distribution among conspecifics.

6. Management of LCs includes attractant management, to counteract food conditioning, but failure to consider despotic behaviour among conspecifics may

lead to treating only the symptom, e.g. habituation or conditioning. The ultimate cause of attraction to specific settlements may be identified by considering the type of bear involved; the occurrence of large solitary bears near settlements suggests attractive habitat or food shortage in remote areas, whereas subadults and females with cubs suggest lower-quality habitat.

INTRODUCTION

People have considered large carnivores (LCs) to be a problem or threat throughout their common history, because LCs can kill other wildlife, livestock or even humans (Woodroffe 2000, Linnell et al. 2001). Today conflicts among people regarding LCs are most common where humans encroach into LC habitat or where LC populations expand into human-dominated landscapes (Mattson 1990). Despite generally positive attitudes towards LCs in the western world, many people are afraid of LCs (Johansson & Karlsson 2011) and expect them to avoid settlements (defined as inhabited single houses, villages or towns). LCs near settlements and sometimes using human-derived foods (i.e. livestock, garbage) are often considered 'unnatural' and their existence forms a major obstacle for conserving LC populations (Swenson et al. 2000).

Common management responses to problems involving bears include securing the anthropogenic food source, driving the bears away or removing them by translocation or destruction. Human activity disturbs bears (Chruszcz et al. 2003, Ordiz et al. 2011), and may cause stress, habitat avoidance, failure to find food and lowered reproduction (Rode et al. 2007, Barber et al. 2009), and trigger antipredator responses (Ordiz et al. 2011). However, individual bears may develop tolerance towards humans, and may associate humans with easily accessible food.

Here, we review the mechanisms underlying the occurrence of LCs near settlements, a topic with a vast scientific literature. An extended literature list can be provided on request. We have chosen bears (Ursidae) as model species; we focus on the brown bear *Ursus arctos*, but also consider American black bears *Ursus americanus* and Asiatic black bears *Ursus thibetanus*. Bears exhibit characteristics that make them common 'problem' LCs (Swenson et al. 2000): they may have close encounters with humans, cause property damage, injure humans or elicit responses from humans in other ways. Bears are individualistic, adaptable, good learners and disperse over large distances (Herrero 1985). They are opportunistic omnivores, utilizing all easily accessible foods, both natural and anthropogenic, including livestock (Gunther et al. 2004, Robbins et al. 2004). However, bears have also been observed near settlements without accessible human-related foods, or without utilizing available human-related foods (McCullough 1982), and

public complaints are often based on fear rather than actual damages (Garshelis 1989).

The bears most often involved in bear-human incidents are subadults (i.e. young, sexually immature individuals), especially males (Schwartz et al. 2006, Hristienko & McDonald 2007), and females with cubs (Kaczensky et al. 2006, Rode et al. 2006b). Only ultimate mechanisms, which do not require prior exposure or experience, can explain differences in the likelihood of occurrence of bears of different sex, age and reproductive classes near settlements.

This review is, to our knowledge, the first to distinguish between ultimate and proximate mechanisms underlying the occurrence of bears near people and settlements. Published research was gathered by searching topics (e.g. conditioning, conflict, despotic, habituation, ideal free, interference, nuisance, predation, problem, social dominance, *Ursus*) in scientific databases, research cited by others and scientific conference websites. For published research with similar methods and conclusions, we used the most recent publication(s) to test the predictions of the following four hypotheses to explain ultimate and proximate mechanisms, particularly regarding the behaviour of bears of various sex, age and reproductive categories: (i) human habituation: predicts increasing human tolerance with increasing frequency of benign human encounters; (ii) food conditioning: predicts attraction to people or settlements due to an association between humans and food; (iii) naivety: predicts that subadult bears occur near people or settlements due to their lack of experience with them; (iv) despotic distribution: predicts that large, dominant bears (especially adult males) exploit the habitats with the highest food quality, and occur mainly in remote areas to avoid humans, whereas bears vulnerable to intraspecific predation (i.e. subadults, females with dependent offspring) avoid adult males by occupying areas closer to people or settlements.

HYPOTHESIS 1: HUMAN HABITUATION

Animals near settlements are expected to have lost their normal wariness and to tolerate humans. Can the process of losing fear of people, as proposed in the human habituation hypothesis, explain why bears of some sex, age or reproductive classes are more often found near settlements than others?

We use Immelmann and Beer's (1989) definition of habituation: a 'stimulus-specific waning of response; learning not to respond to something on finding that nothing significant is contingent upon its occurrence'. An individual's tolerance levels increase during a habituation process (Bejder et al. 2009). Habituation processes are common and probably occur when the benefits of not responding to a stimulus outweigh the perceived risks or costs involved in responding to it (Alcock 1988, Albert & Bowyer 1991, Rodríguez-Prieto et al. 2010). When repeatedly exposed to a neutral situation, an animal can conserve energy by muting its reaction (Herrero et al. 2005, Rodríguez-Prieto et al. 2010). Human habituation might occur wherever bears and people meet frequently without negative reinforcement, even without the involvement of food (McCullough 1982, Mattson et al. 1992), although other factors, e.g. individual temperament and innate sexual differences, may also be involved (Martin & Reale 2008, Ellenberg et al. 2009). The sexual selection theory predicts that males take greater risks than females in polygynous, dimorphic species because males have greater variance in reproductive success (Andersson 1994). Thus, males may be involved in more stress-inducing incidents with people than females because of their 'high risk-high gain' strategy promoting reproductive success (Sukumar 1991, Ahlering et al. 2011). Avoidance of people and settlements by brown bears suggests that human presence causes stress (Nellemann et al. 2007). However, there is no clear pattern in either short-term or long-term stress responses among brown bears of different sexes or ages in relation to human activities (von der Ohe et al. 2004, Macbeth et al. 2010).

European brown bears show predominantly nocturnal or crepuscular activity peaks, suggesting more wary behaviour than North American bears, which are more active during daytime (Klinka & Reimchen 2002, Kaczensky et al. 2006). Brown bears and black bears in areas used little by humans show diurnal activity, but they may become crepuscular or nocturnal and avoid open areas when resting in response to human presence (MacHutchon et al. 1998, Schwartz et al. 2010). Hunting may increase bears' wariness towards humans, as bears seem to avoid people during the hunting season (Treves 2009, Ordiz et al. 2011), probably due to learning, rather than selective removal of genetically inherited aggressiveness (McCullough 1982, Swenson 1999, Kaczensky et al. 2006).

Bears' tolerance of conspecifics and people also may be positively related to bear density, explaining why aggressiveness of bears towards humans varies regionally (Smith et al. 2005). Responses to people may be similar if bears are inherently tolerant of people or become habituated through learning (Smith et al. 2005). An innate high tolerance or bear-to-bear habituation, due to high bear density, may explain high human tolerance in remote areas, e.g. at fishing

rivers used by bears, whereas human habituation may occur in areas with high human activity (Smith et al. 2005). However, an innate tolerance of people does not allow the prediction of which bears occur near settlements, but rather explains differences among areas or bear populations as a function of bear density, aggregated food sources or prior exposure to hunting.

Consistency and predictability may be important in the process of habituation (Nisbet 2000, Nevin & Gilbert 2005b) and may help explain why bears tolerate people better on trails than off-road (Jope 1985). Most importantly, the learning process of human habituation may be related to the frequency of (benign) human encounters, thus requiring previous human experience (McCullough 1982, McArthur Jope 1983, Jope 1985, Gilbert 1989, Mueller et al. 2004, Herrero et al. 2005, Rogers 2011). Human habituation therefore does not explain any variation in exposure to people among sex, age or reproductive classes of bears, because this would imply behavioural responses to people before encountering them. Therefore, the human habituation hypothesis seems only to explain the occurrence of bears near people or settlements as a response to earlier experience. It is therefore not an ultimate mechanism.

HYPOTHESIS 2: FOOD CONDITIONING

Animals occurring near settlements may gain access to human-derived foods. Can the process of learning to use human-derived foods and frequenting settlements, as predicted by the food-conditioning hypothesis, explain why bears of certain sex, age or reproductive classes more often exploit these food sources?

There are numerous reports of brown and black bears utilizing garbage and other human-related foods near settlements (Swenson et al. 2000, Gunther et al. 2004, Sato et al. 2005, Greenleaf et al. 2009). The use of anthropogenic foods by bears may be the result of (i) associating people or settlements with foods, hereafter called food conditioning, (ii) an omnivorous and opportunistic feeding behaviour, or (iii) a combination of these. Food conditioning is, alone or in combination with human habituation, the most widely accepted mechanism to explain the occurrence of bears near settlements (McCullough 1982, Herrero et al. 2005).

Reducing the accessibility of food attractants near people has reportedly reduced brown and black bear occurrence near settlements (Gniadek & Kendall 1998, Schwartz et al. 2006, Madison 2008, Greenleaf et al. 2009). However, other researchers found that reducing food attractants had no such effect (Mattson et al. 1992, Pease & Mattson 1999). Peaks in damage to property by brown bears and in their use of human-derived foods differ among studies, coinciding with the period of hyperphagia (Gunther et al. 2004),

the spring, or from midsummer, and then decreasing through autumn (McArthur Jope 1983, Albert & Bowyer 1991).

Gilbert (1989) and Aumiller and Matt (1994) argued that brown bears can transmit human tolerance by observational learning from mother to offspring, i.e. by social or cultural transmission. Similarly, young bears may become food conditioned through their mother's behaviour (Madison 2008). However, Breck et al. (2008) found no evidence of transmission of food-conditioning behaviour in related lineages of black bears.

Regardless of the influence of cultural transmission, the development of positive associations between bears and human-derived foods requires some earlier experience with, or cues from, people, human activity or settlements, similar to human habituation (McArthur Jope 1983, Herrero et al. 2005, Rogers 2011). Therefore, the food-conditioning hypothesis seems valid to explain the occurrence of bears near people or settlements only as a response to earlier experience, similar to the human habituation hypothesis. Thus, food conditioning does not explain any variation among sex, age or reproductive classes in bears' exposure to people and their foods or other stimuli, because this would imply behavioural responses before encountering them.

HYPOTHESIS 3: NAIVETY

Animals can occur near settlements without prior experience with people or food attractants. Can the lack of experience with people, as proposed in the naivety hypothesis, explain why bears of certain sex, age or reproductive classes occur more often near settlements?

Occurrence of younger bears near settlements, in combination with their diurnal activity peaks, has been suggested to be due to naive behaviour (reflecting lack of experience) in brown bears (Blanchard & Knight 1991, McLellan et al. 1999, Kaczensky et al. 2006) and black bears (Madison 2008, Rogers 2011). Yearlings are more diurnal than adult brown bears, whereas subadults are intermediate between adults and yearlings in their temporal activity pattern (Kaczensky et al. 2006). Kaczensky et al. (2006) suggested that younger bears initially consider other bears to be more dangerous than people, but that this may change with increasing size and age, increasing human exposure and higher intraspecific competitive capability. Rogers (2011) argued that diurnal activity near people has often been misinterpreted as bold behaviour; it rather reflects the normal circadian activity pattern and a naive response to human activity. In contrast, subadult bears may occur near people or settlements because they are innately bolder and more curious than adults (Gilbert 1989, Clark et al. 2002b). However, aggression by older bears towards cubs and young (McLellan et al. 1999, Swenson et al. 2001) suggests selection for

wary behaviour towards conspecifics, and potentially also towards other threats, among younger individuals, rather than bold behaviour.

Subadults may approach people or settlements due to their naivety, but avoiding resident conspecifics affects their habitat use. Dispersal in bears probably occurs to avoid competition and aggression from dominant conspecifics, which explains why subadults often appear in developed areas unoccupied by other bears (Rogers 1987, Schwartz & Franzmann 1992). Dispersal probability is inversely density dependent, probably due to elevated encounter risks with conspecifics (Støen et al. 2006), and in females due to the occurrence of matrilineal (Støen et al. 2005). However, male dispersal may also be a result of inbreeding avoidance (Zedrosser et al. 2007). Dispersal by bears is sex-biased: more males disperse than females (Blanchard & Knight 1991, Zedrosser et al. 2007). Dispersal takes place during the mating season, when most females separate from their offspring (Schwartz & Franzmann 1992, Dahle & Swenson 2003a) and adults are aggressive towards cubs and subadults (Swenson et al. 2001). However, some dispersal by subadult males occurs in late autumn, when aggression and testosterone levels seem to be lower (McMillin et al. 1976, Rogers 1987). Thus, family break-up and intraspecific aggression during the mating season may explain dispersal from natal areas early in the season, but movements by young and subordinate bears might also be inhibited during this period of high aggression.

Young males dominate at the extremities of geographical ranges, when bear populations are expanding (Swenson et al. 1998). Hence, naive subadults may be overrepresented in bear populations expanding towards concentrated settlements. When subadults disperse, they often move far, which, in combination with diurnal activity peaks, increases their risk of encountering humans and, therefore, of becoming habituated to humans (Craighead et al. 1995, MacHutchon et al. 1998, Mueller et al. 2004). However, movements do not explain the occurrence of females with cubs near settlements, because they have smaller ranges than roaming males and oestrous females (Blanchard & Knight 1991, Dahle & Swenson 2003c). Nevertheless, the naivety hypothesis may help explain the occurrence of young and inexperienced animals near settlements because of exploratory movements and avoidance of resident conspecifics.

HYPOTHESIS 4: DESPOTIC DISTRIBUTION

The hypothesis

Different sex, age or reproductive classes of animals often show disproportionate use of habitats near settlements or areas of higher food quality and availability. This pattern

may be explained by predation avoidance and/or interference competition, i.e. by the despotic distribution hypothesis, rather than by learning processes (food conditioning and human habituation) or by a lack of learning (naivety). Fretwell and Lucas (1970) described animals forcing some conspecifics into less preferred habitats, resulting in different averaged reproductive success among habitats, as an ideal despotic distribution. Based on this despotic distribution, dominant individuals are predicted to exploit habitats of high quality (in terms of food and/or security) more often than subordinate conspecifics. This spatiotemporal segregation may be explained by (i) dominant individuals actively guarding these habitats by interference competition, thereby excluding subordinate competitors, and/or (ii) smaller conspecifics actively avoiding these habitats due to increased risk of intraspecific aggression or predation. Contrary to a despotic distribution, if animals are distributed according to an ideal-free distribution, no aggression or interference among conspecifics is predicted, but rather a scramble competition among equal competitors, and similar reproductive rates among patches or habitats (Fretwell & Lucas 1970). However, an ideal-free distribution may not be violated if smaller animals distribute themselves around larger ones, so that numbers of animals are balanced according to habitat quality and body size, thus creating averaged equal food intake and reproduction among habitats (Parker & Sutherland 1986, Sutherland & Parker 1992).

Aggression and dominance among bears

Intraspecific mortality dominates natural mortality among cubs and subadult brown bears (Swenson et al. 2001, McLellan 2005) and American black bears (Rogers 1987, Schwartz & Franzmann 1992). Most intraspecific killing is directed towards cubs, i.e. it is infanticide, but intraspecific predation also occurs on independent 1–3-year-old bears, and perpetrators are most often adult (e.g. dominant) males, but may also be adult females (McLellan 1994, Swenson et al. 2001). Most infanticide and intraspecific predations occur during the mating season (May–July) in brown and black bears (Lecount 1987, Schwartz et al. 2006), and evidence suggests that infanticidal males might also kill subadults (Swenson et al. 1997, 2001).

Social behaviour is affected by food abundance at food aggregation sites, such as salmon *Oncorhynchus* spp. runs and garbage dumps, where resources are defendable and predictable. Reduced food abundance at aggregation sites leads to higher aggression levels and therefore pronounced social hierarchies among brown and black bears (Herrero 1983, Rogers 1987, Blanchard & Knight 1991, Craighead et al. 1995). Social dominance has even been reported to be more important than food abundance in determining foraging efficiency at a salmon river (Gende & Quinn 2004).

Typically, larger males have the highest social rank, followed in decreasing rank order by females with dependent young, solitary females and subadults (Egbert & Stokes 1976, Rogers 1987). Although females with dependent young may show high social intolerance, the vulnerability of their young may mean that their security requirements are higher than those of solitary females (Mattson 1990). Subadult black and brown bears at aggregated food sites are more vulnerable to intraspecific predation (Stringham 1989, Mattson & Reinhart 1995). Brown and black bears exploiting aggregated food sites tend to be larger and have higher reproduction rates (Rogers 1987, Robbins et al. 2004, Peirce & Van Daele 2006), although lower reproduction nearer food aggregation sites has also been reported (Mattson & Reinhart 1995). These patterns indicate violations of an ideal-free distribution, regarding equal competitors, mortality and reproduction among patches.

Bears near settlements in relation to natural food availability

Several studies of brown bears and American and Asiatic black bears show that a negative correlation exists between the abundance of naturally occurring bear foods and the occurrence of bears damaging human property and obtaining anthropogenic foods (Rogers 1987, Mattson et al. 1992, Schwartz et al. 2006, Oka et al. 2004). This may be explained partially by a reduced occurrence of major food sources in remote areas, where older bears dominate (Blanchard & Knight 1991, 1995, Mattson et al. 1992, Schwartz et al. 2006, Kozakai et al. 2011). Smaller bears, especially females, are more likely to make late-season migrations outside their normal ranges when food availability is high outside their home ranges and lower within them, because migration behaviour is costly (Noyce & Garshelis 2011). This suggests that some bears may be forced to approach settlements in search of food. However, Yamanaka et al. (2009) and Oi et al. (2009) found no correlation between body condition and numbers of 'problem' bears killed annually. Herrero (1985) argued that bears approach settlements in years of poor natural food availability because they become bolder, whereas Rogers (2011) argued that hunger was the driving force.

The spatiotemporal distribution of important natural bear food resources in relation to settlements is likely to differ significantly among areas, making it difficult to generalize about correlations between bear problems and food productivity. Food availability may have a larger effect on bears at the home-range scale, whereas avoidance of intraspecific predation may have stronger effects at finer scales (McLoughlin et al. 2002, Ciarniello et al. 2007). However, spatial or temporal segregation among sex, age or reproductive classes of bears near people suggests that mechanisms other than food searching or boldness explain this pattern.

Spatiotemporal segregation in relation to food quality

Adult male brown bears occur preferentially in habitats with higher food quality than do subadults and females with cubs (Stelmock & Dean 1986, Mattson et al. 1987, 1992, Blanchard & Knight 1991, Wielgus & Bunnell 1994, 1995, Ben-David et al. 2004). Blanchard and Knight (1991) reported that only adult males occupied the highest-quality habitat in years with poorer food availability, and that subadult males and females with dependent offspring avoided both lone females and adult males by choosing more secure over more productive habitats. Temporal segregation is also common at food aggregation sites, where adult male brown bears occur more often, and displace females with dependent offspring and subadults (Storonov & Stokes 1972, Craighead et al. 1995, Olson et al. 1997, Nevin & Gilbert 2005a, b, Peirce & Van Daele 2006, Rode et al. 2006b). Subadults and females with cubs may be risk-averse because they exploit salmon streams less when large males are present and when foraging efficiency is high (i.e. at night; Klinka & Reimchen 2002). Ben-David et al. (2004), Rode et al. (2006b) and Nevin and Gilbert (2005a) also reported that females with cubs utilized high-nutritive food sites (i.e. salmon streams) less than solitary females, indicating a trade-off between nutritional requirements and risk of infanticide.

Spatiotemporal segregation in relation to settlements and human activity

Subadult bears, especially males, are more often involved in incidents with people, and are therefore more often considered problem bears by managers, than adults, in brown bears throughout North America (Dau 1989, Mattson et al. 1992, McLellan et al. 1999, Pease & Mattson 1999, Schwartz et al. 2006) and Europe (Elfström et al. unpublished data), and in black bears throughout North America (Garshelis 1989, McLean & Pelton 1990, Clark et al. 2002b, Hristienko & McDonald 2007) and in Japan (Izumiyama et al. 2008, Kishimoto 2009). Hristienko and McDonald (2007) reported that younger bears are involved in >70% of complaints of nuisance North American black bears. Adult males have more often been labelled problem bears in remote areas (Beeman & Pelton 1976, Singer & Bratton 1980), where they may prefer larger garbage dumps (Tietje & Ruff 1983).

Older brown bears stay farther away from heavily used roads than younger bears and females with cubs (McLellan & Shackleton 1988, Mueller et al. 2004), although female American black bears have been found to stay farther away from roads than males (Young & Beecham 1986). However, adult male brown bears have also been found near roads with high-quality food (Gibeau et al. 2002, Roever et al.

2008a, b), and may occupy these habitats more than females and subadults (Mattson et al. 1987, Chruszcz et al. 2003). Males occur closer to low-traffic roads, but avoid high-traffic roads more than females (Wielgus et al. 2002, Chruszcz et al. 2003). Bears may respond differently to roads and settlements: females and subadults may occur farther from roads but closer to settlements than males (Gibeau et al. 2002).

Bears may be more wary of conspecifics than of people, due to intraspecific predation and antagonistic behaviours among them (Swenson et al. 2001, Nevin & Gilbert 2005a, b, Rode et al. 2006b, Schwartz et al. 2010). They consistently show wariness when approaching conspecifics, e.g. at salmon rivers; bears habituated to people are not wary of them (Smith et al. 2005). Several researchers suggest that adult males decrease their activity with increasing human activity, whereas increased human activity creates refuge and feeding opportunities for subadults and females with cubs at brown bear viewing sites at salmon rivers (Smith 2002, Nevin & Gilbert 2005a, b, Rode et al. 2006b) and meadows (Gunther 1990). More female brown bears than males, and more subadults than adults, occur with increasing numbers of humans at salmon streams (Warner 1987, Olson et al. 1997). Male polar bears *Ursus maritimus* also show increased vigilance towards viewing tourists, whereas females respond in the opposite manner, by increasing vigilance when people are not present (Dyck & Baydack 2004). Similarly, adult male brown bears are more nocturnal than lone females (Schwartz et al. 2010), females with cubs and subadults (Kaczensky et al. 2006), whereas subadults are more diurnal and occur more frequently in areas with higher human activity (MacHutchon et al. 1998). Adult males are more often found in remote areas, whereas females and subadults more often occur near people and settlements throughout North America (Mattson et al. 1987, 1992, Gibeau et al. 2002, Rode et al. 2006a). In Scandinavia, Nellemann et al. (2007) reported that both adult males and females occurred farther from settlements than subadult brown bears.

Despotic distribution when exploiting food resources

Can sex or age class segregation in bears be explained only by resource competition without considering predation avoidance? Animals should monopolize resources (i.e. food) only when resources are clumped and predictable, or not widely dispersed and abundant (Clutton-Brock & Harvey 1978). Generally in carnivores, the most important factors determining the size and spacing of home ranges are probably body mass and spatiotemporal availability of food (Clutton-Brock & Harvey 1978). McLoughlin et al. (2000) reported that home-range sizes of North American brown

bears were negatively related to habitat quality. The lowest degree of home-range overlap occurs where habitat quality is moderate; perhaps, territorial behaviour is reduced in high-quality habitat, and there is little benefit in defending scarcely distributed food resources in low-quality habitat (McLoughlin et al. 2000). Thus, large home ranges with dispersed food and considerable home-range overlap suggest an inability to monopolize food resources and a random (ideal-free) distribution, with scramble competition for food resources (Fretwell & Lucas 1970, Parker & Sutherland 1986). However, scramble competition for food does not explain habitat segregation by sex or age classes in low-density populations of LCs, e.g. most bear populations, as Miquelle et al. (1992) concluded for ungulates. Female brown bear body size increases with better food conditions and lower bear densities (Zedrosser et al. 2006), and home-range size decreases with increasing bear densities (Dahle & Swenson 2003b, Dahle et al. 2006). This suggests food competition for evenly distributed food resources, i.e. when foraging on berries (Zedrosser et al. 2006). Meanwhile, reproductive strategy (i.e. reducing infanticide risk), rather than food availability, probably explains the restricted home-range sizes of female brown bears with cubs during the mating season (Dahle & Swenson 2003c). Similarly, spatial segregation between adult males and females when food resources are evenly distributed and abundant suggests avoidance of intraspecific predation, rather than competition for food resources (Mattson et al. 1987, Wielgus & Bunnell 1994).

Sexual dimorphism may cause sexual differences in ingestion capacity or nutrient demands, causing sexual segregation, as described by the sexual dimorphism-body size hypothesis (Main et al. 1996). However, Main et al. (1996) found little support for this hypothesis in ungulates; most evidence supported a reproductive-strategy hypothesis to explain sexual segregation. Bears are sexually dimorphic (Rode et al. 2006b) but, unlike ungulates, larger bears seem to have higher nutrient requirements than smaller bears, due to their larger absolute energetic requirements and relatively small intake capability (Welch et al. 1997, Rode et al. 2001). Thus, adult males may require access to habitats with higher food quality than other sex or age classes of bears, considering their larger size (Robbins et al. 2004). Rode et al. (2006b) concluded that, in bears, both sexual dimorphism and reproductive strategies seem to lead to sexual segregation. To maximize fitness, males must maximize growth by exploiting areas with abundant high-quality food, whereas females must prioritize offspring security (Andersson 1994, Main et al. 1996). Thus, a spatial or temporal habitat segregation among specific sex or age classes of bears would resemble an ideal despotic distribution due ultimately to reproductive strategies, and manifested by interference competition due to aggression and social dominance (Parker & Sutherland 1986,

Kennedy et al. 1994). This reproductive strategy may thereby indirectly reduce food competition, as suggested in ungulates (Ciuti & Apollonio 2008).

Social organization creating despotic distribution

The occurrence of reproductive suppression, kin-related social organization, inversely density-dependent home-range sizes and natal dispersal (Rogers 1987, Blanchard & Knight 1991, Mattson et al. 1992, Støen et al. 2005, 2006, Dahle et al. 2006, Ordiz et al. 2008) further supports a despotic rather than an ideal-free distribution in bears. Bears interact at an individual level, but interactions can cause population-level responses by spatial avoidance (Belant et al. 2010), where settlements might redistribute bears at a landscape scale (Beckmann & Berger 2003). Beckmann and Berger (2003) described a despotic distribution in black bears: bears near settlements occurred at higher densities, had larger body mass, smaller home ranges, higher fecundity and shorter denning periods than bears in more remote areas. During the winter denning period, brown bears avoid areas where humans are active, and adult males choose den sites in more remote areas than other bears (Elfström et al. 2008, Elfström & Swenson 2009), whereas females with cubs avoid den sites near adult males, which Libal et al. (2011) interpreted as despotic distribution.

DISCUSSION

Proximate and ultimate mechanisms

In Table 1, we summarize results of the tests of our four hypotheses to separate proximate and ultimate mechanisms underlying occurrences of bears near settlements, considering: availability of food attractants near settlements, increased annual food availability in remote areas, timing of bear occurrence, types of bears near settlements, effects of increased bear density and presence of aggression or social dominance among bears. Habituation to humans and food conditioning require earlier experience with humans (McArthur Jope 1983, Herrero et al. 2005, Rogers 2011). Therefore, we argue that the human habituation and food-conditioning hypotheses are not ultimate mechanisms explaining the disproportionate occurrence of different sex, age and reproductive classes of bears near settlements, because this would imply responses to people before gaining experience with them. The disproportionate use of habitats with high food quality by different sex, age and reproductive classes of bears also cannot be explained by the human habituation and the food-conditioning hypotheses because these habitats are not necessarily correlated with human occurrence. We suggest that human habituation and food

Table 1. Variables used to evaluate predictions from ultimate and proximate mechanisms underlying the occurrence of bears near human settlements, based on an extensive literature review

Variables (presence of or increased amount)	Proximate mechanisms			Ultimate mechanisms	
	Human habituation	Food conditioning	Naivety	Despotic distribution	
				Interference competition	Predation refuge
Food attractants	0	+	0	0 or +	0
Food availability away from settlements	0	0 or –	0	–	0 or –
Seasonal timing of bear occurrence near settlements	0	With limited food availability: before hypophagia and during hyperphagia	Dispersal during mating or post-mating seasons	With limited food availability: before hypophagia and during hyperphagia	During mating season
Age, sex or reproductive classes of problem bears	All	All	Subadults, mostly males	Small-sized or subadults*	Mostly subadults and females with offspring*
Bear density	0	0	– or +	+	+
Aggression or dominance	0	0	0 or +	+	+

In order to show relationships between variables and mechanisms conceptually, variables are presented separately for each mechanism, although interactions also occur among mechanisms.

0 = no evident relationship, – = negative relationship, + = positive relationship.

*Assuming the particular area near human settlement(s) is considered unattractive by dominant bears.

conditioning explain movements and habitat use only after an animal has obtained experience with people, and therefore must be proximate mechanisms. Naive behaviour involving approaching threats should be maladaptive, especially for younger and vulnerable animals, and does not explain a disproportionate number of females with cubs near people or settlements, whereas dispersal seems to be triggered by despotic behaviour among conspecifics. Therefore, bears' naivety towards people must also be a proximate mechanism underlying occurrence near settlements.

The despotic distribution, on the other hand, can explain the pattern seen in bears, in which predation-vulnerable or subordinate individuals seek predation refuges near people and settlements. As this is based on a reproductive strategy (or juvenile predation risk), it is an ultimate mechanism explaining this pattern. A despotic distribution also explains why predominantly adult males, but also lone adult females, exploit habitats with the highest food quality. Hence, a despotic distribution may reinforce human habituation and/or food conditioning, because these processes are more advantageous for subordinate and predation-vulnerable animals (Albert & Bowyer 1991).

The human shield

Avoidance of humans by LCs creates predator-relaxed habitats, protected by so-called human shields, for several species (Berger 2007, Barber et al. 2009). Brown bears displace black bears (MacHutchon et al. 1998, Belant et al. 2006, 2010, Fortin et al. 2007, Garneau et al. 2008) through interference competition, especially at clumped or patchy

food sources (McLellan 1993, Belant et al. 2010). Black bears may reduce the levels of competition with and predation by brown bears they experience, by using areas near humans (MacHutchon et al. 1998, Schwartz et al. 2010). Settlements or areas in which humans are active have been suggested to form refuges for some brown bears against conspecifics (Mattson et al. 1987, Mattson 1990, Albert & Bowyer 1991, Wielgus & Bunnell 1994, Olson et al. 1997, Mueller et al. 2004, Nevin & Gilbert 2005a, Rode et al. 2006a, b, Schwartz et al. 2010).

Increased human-induced mortality of bears near settlements might explain why adult males typically avoid settlements, if young bears have lower survival near people (Beeman & Pelton 1976, Rogers et al. 1976, Bunnell & Tait 1985, Mattson et al. 1992, Mueller et al. 2004). However, Nielsen et al. (2004) reported that the mortality risk tended to be greater farther from human access features (e.g. roads) for subadult male bears than for adults and subadult females. Mortality rates should be documented in relation to settlements, to separate the effects of human-induced mortality and adult avoidance of people on the observed segregation pattern.

MANAGEMENT IMPLICATIONS

Human injuries and damage to property

Human-habituated or food-conditioned bears pose a potentially increased risk to humans (McCullough 1982). However, aggression towards humans may decrease when bears become familiarized or habituated to humans (Jope

1985, Aumiller & Matt 1994), because sudden, unexpected encounters between bears and humans are the most likely to result in bear-induced human injuries (Herrero & Fleck 1990). Human habituation also might increase the risk of human injury, although the risk of injury in an individual encounter is low, by increasing the total number of aggressive interactions due to an increased encounter rate (Herrero et al. 2005). The potential for a reward (i.e. food) may affect search behaviour, and bears may revisit feeding sites even when not receiving food (Rogers 1987). We acknowledge that measures, such as securing anthropogenic foods to avoid food conditioning, must continue, in order to reduce risks of injuries, property damage and public anxiety. Such management techniques are independent of ultimate and proximate mechanisms. However, failure to consider despotic behaviour as an ultimate mechanism may lead to treating only the symptoms. Bears using settlements as predation refuges should not be considered 'unnatural', but rather as exhibiting an adaptive behaviour, because of the despotic distribution among conspecifics.

Types of problem animal can serve to identify ultimate mechanisms

Based on our conclusion that the despotic distribution is a key mechanism underlying the occurrence of bears near settlements, attraction to settlements may be evaluated on the basis of the types of bear involved. We suggest that the occurrence of mostly large and solitary animals near settlements indicates that these areas represent an attractive habitat (with e.g. food attractants and little disturbance), and that there may be a lack of available foods in remote areas. Considering bears' reluctance to use open areas while near settlements (Ordiz et al. 2011), we recommend attractant management, such as removing dense vegetation near settlements, to reduce habitat suitability and prevent future problems, besides removing problem animals (Herrero 1985). In contrast, the occurrence of predominantly females with cubs and independent subadults near a settlement indicates that the area represents lower-quality habitat, because adult males would dominate high-quality habitats. Attractant management is unlikely to be successful in reducing the occurrence of these potentially displaced bears. Applying aversive conditioning to a displaced bear to scare it away might not be very effective either, because dominant individuals function as continuous negative stimuli in more remote areas.

Translocation of problem animals

Although translocations are popular with the public, because they are non-lethal, many North American agencies have stopped translocating bears because it is ineffective.

Most relocated animals leave the release area and return to their capture area (Blanchard & Knight 1995, Linnell et al. 1997), although there are examples of successful relocations (Armistead et al. 1994, Shivik et al. 2011). High food availability in areas where bears are common may increase return rates (Clark et al. 2002b). Good homing ability also may explain high return rates after translocations, as suggested by an inverse relationship between distance moved and return probability (Singer & Bratton 1980, Landriault et al. 2009), although subadults may have less homing ability and be less philopatric than adults (Clark et al. 2002a, Landriault et al. 2009). Translocating LCs into remote areas occupied by dominant conspecifics can disrupt their social organization and cause increased intraspecific aggression and predation (Treves & Karanth 2003, Robbins et al. 2004). Stokes (1970) concluded that immigrants are usually at a disadvantage compared to established residents, suggesting elevated mortality in translocated bears. Thus, especially subadults tend to leave release areas and return to settlements to avoid established conspecifics, as well as to exploit high food availability at settlements.

Supplementary feeding

Instead of translocation, Robbins et al. (2004) and Rogers (2011) recommend temporally restricted supplemental feeding within established home ranges, with the aim to reduce nutritional stress when natural food abundance is low (e.g. shortly after den emergence and autumn mast failures). This method may reduce problems rather than cause them, provided that bears do not become food conditioned. Supplemental feeding in Central Europe is not allowed near settlements, in order to avoid food conditioning (Huber et al. 2008). Rogers (1989, 2011) argued that diversionary feeding is the only effective action when natural foods are scarce, and that aversive conditioning and attractant reduction may only be effective when natural foods are at least moderately abundant. It is unclear whether dominant bears at feeding sites limit access for subdominant conspecifics (Witmer & Whittaker 2001). Diversionary and supplemental feeding might amplify a despotic distribution by allowing larger bears to dominate feeding sites and, therefore, may increase, rather than reduce, the occurrence of bears near settlements.

CONCLUSION

People fear bears near settlements, whereas predation-vulnerable bears seem to fear dominant conspecifics more than they fear people. Behavioural strategies including avoidance of intraspecific aggression explain the type of bears occurring near settlements better than naivety, human

habituation or food conditioning. Bears approaching settlements should not be considered 'unnatural', but rather individuals showing an adaptive behaviour, and using predation refuges as an ultimate mechanism of bears' despotic distribution.

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REFERENCES

- Ahlering MA, Millspaugh JJ, Woods RJ, Western D, Eggert LS (2011) Elevated levels of stress hormones in crop-raiding male elephants. *Animal Conservation* 14: 124–130.
- Albert DM, Bowyer RT (1991) Factors related to grizzly bear-human interactions in Denali National Park. *Wildlife Society Bulletin* 19: 339–349.
- Alcock J (1988) *Animal Behavior: an Evolutionary Approach*, 4th ed. Sinauer Associates, Massachusetts, USA.
- Andersson M (1994) *Sexual Selection*. Princeton University Press, Princeton, New Jersey, USA.
- Armistead AR, Mitchell K, Connolly GE (1994) Bear relocations to avoid bear/sheep conflicts. *Proceedings of the 16th Vertebrate Pest Conference*, 31–35.
- Aumiller LD, Matt CA (1994) Management of McNeil River state game sanctuary for viewing of brown bears. *Ursus* 9: 51–61.
- Barber JR, Crooks KR, Fristrup KM (2009) The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25: 180–189.
- Beckmann JP, Berger J (2003) Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy* 84: 594–606.
- Beeman LE, Pelton MR (1976) Homing of black bears in the Great Smoky Mountains National Park. *Ursus* 3: 87–95.
- Bejder L, Samuels A, Whitehead H, Finn H, Allen S (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series* 395: 177–185.
- Belant JL, Kielland K, Follmann EH, Adam LG (2006) Interspecific resource partitioning in sympatric ursids. *Ecological Applications* 16: 2333–2343.
- Belant JL, Griffith B, Zhang Y, Follmann EH, Adams LG (2010) Population-level resource selection by sympatric brown and American black bears in Alaska. *Polar Biology* 33: 31–40.
- Ben-David M, Titus K, Beier LR (2004) Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138: 465–474.
- Berger J (2007) Fear, human shields and redistribution of prey and predators in protected areas. *Biology Letters* 3: 620–623.
- Blanchard BM, Knight RR (1991) Movements of Yellowstone grizzly bears. *Biological Conservation* 58: 41–67.
- Blanchard BM, Knight RR (1995) Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. *Journal of Wildlife Management* 59: 560–565.
- Breck SW, Williams CL, Beckmann JP, Matthews SA, Lackey CW, Beecham JJ (2008) Using genetic relatedness to investigate the development of conflict behavior in black bears. *Journal of Mammalogy* 89: 428–434.
- Bunnell FL, Tait DEN (1985) Mortality rates of North-American bears. *Arctic* 38: 316–323.
- Chruszcz B, Clevenger AP, Gunson KE, Gibeau ML (2003) Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81: 1378–1391.
- Ciarniello LM, Boyce MS, Seip DR, Heard DC (2007) Grizzly bear habitat selection is scale dependent. *Ecological Applications* 17: 1424–1440.
- Ciuti S, Apollonio M (2008) Ecological sexual segregation in fallow deer (*Dama dama*): a multispatial and multitemporal approach. *Behavioral Ecology and Sociobiology* 62: 1747–1759.
- Clark JD, Huber D, Servheen C (2002a) Bear reintroductions: lessons and challenges. *Ursus* 13: 335–345.
- Clark JE, van Manen FT, Pelton MR (2002b) Correlates of success for on-site releases of nuisance black bears in Great Smoky Mountains National Park. *Wildlife Society Bulletin* 30: 104–111.
- Clutton-Brock TH, Harvey PH (1978) Mammals, resources and reproductive strategies. *Nature* 273: 191–195.
- Craighead JJ, Sumner JS, Mitchell JA (1995) *The Grizzly Bears of Yellowstone: Their Ecology in the Yellowstone Ecosystem, 1959–1992*. Island Press, Washington DC, USA.
- Dahle B, Swenson JE (2003a) Family break-up in brown bears: are young forced to leave? *Journal of Mammalogy* 84: 536–540.
- Dahle B, Swenson JE (2003b) Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* 260: 329–335.
- Dahle B, Swenson JE (2003c) Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology* 72: 660–667.
- Dahle B, Støen OG, Swenson JE (2006) Factors influencing home-range size in subadult brown bears. *Journal of Mammalogy* 87: 859–865.
- Dau CP (1989) Management and biology of brown bears at Cold Bay, Alaska. In: Bromley M (ed.) *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*, 19–26. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Dyck MG, Baydack RK (2004) Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biological Conservation* 116: 343–350.

- Egbert AL, Stokes AW (1976) The social behaviour of brown bears on an Alaskan salmon stream. *Ursus* 3: 41–56.
- Elfström M, Swenson JE (2009) Effects of sex and age on den site use by Scandinavian brown bears. *Ursus* 20: 85–93.
- Elfström M, Swenson JE, Ball JP (2008) Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* 14: 176–187.
- Ellenberg U, Mattern T, Seddon P (2009) Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Animal Behaviour* 77: 289–296.
- Fortin JK, Farley SD, Rode KD, Robbins CT (2007) Dietary and spatial overlap between sympatric ursids relative to salmon use. *Ursus* 18: 19–29.
- Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16–36.
- Garneau DE, Boudreau T, Keech M, Post E (2008) Habitat use by black bears in relation to conspecifics and competitors. *Mammalian Biology* 73: 48–57.
- Garshelis DL (1989) Nuisance bear activity and management in Minnesota. In: Bromley M (ed.) *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*, 169–180. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Gende SM, Quinn TP (2004) The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology* 82: 75–85.
- Gibeau ML, Clevenger AP, Herrero S, Wierzbowski J (2002) Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation* 103: 227–236.
- Gilbert B (1989) Behavioural plasticity and bear-human conflicts. In: Bromley M (ed.) *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*, 1–8. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Gniadek SJ, Kendall KC (1998) A summary of bear management in Glacier National Park, Montana, 1960–1994. *Ursus* 10: 155–159.
- Greenleaf SS, Matthews SM, Wright RG, Beecham JJ, Leithead HM (2009) Food habits of American black bears as a metric for direct management of human–bear conflict in Yosemite Valley, Yosemite National Park, California. *Ursus* 20: 94–101.
- Gunther KA (1990) Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. *Ursus* 8: 73–78.
- Gunther KA, Haroldson MA, Frey K, Cain SL, Copeland J, Schwartz CC (2004) Grizzly bear-human conflicts in the Greater Yellowstone Ecosystem, 1992–2000. *Ursus* 15: 10–22.
- Herrero S (1983) Social behaviour of black bears at a garbage dump in Jasper National Park. *Ursus* 5: 54–70.
- Herrero S (1985) *Bear Attacks: Their Causes and Avoidance*. Lyons and Burford, New York, USA.
- Herrero S, Fleck S (1990) Injury to people inflicted by black, grizzly or polar bears: recent trends and new insights. *Ursus* 8: 25–32.
- Herrero S, Smith T, DeBruyn TD, Gunther K, Matt CA (2005) From the field: brown bear habituation to people – safety, risks, and benefits. *Wildlife Society Bulletin* 33: 362–373.
- Hristienko H, McDonald JE (2007) Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* 18: 72–88.
- Huber D, Kusak J, Majic'-Skrbinsek A, Majnaric' D, Sindicic' M (2008) A multidimensional approach to managing the European brown bear in Croatia. *Ursus* 19: 22–32.
- Immelmann K, Beer C (1989) *A Dictionary of Ethology*. Harvard University Press, Cambridge, Massachusetts, USA.
- Izumiyama S, Mochizuki T, Kishimoto R, Gotoh M, Hayashi H (2008) Elucidation of massive haunt factor to Asiatic black bear depend to rural area capture time and age assessment in the Nagano Prefecture. *Bulletin of the Shinshu University Alpine Field Center* 6: 19–24. [In Japanese.]
- Johansson M, Karlsson J (2011) Subjective experience of fear and the cognitive interpretation of large carnivores. *Human Dimensions of Wildlife* 16: 15–29.
- Jope KL (1985) Implications of grizzly bear habituation to hikers. *Wildlife Society Bulletin* 13: 32–37.
- Kaczensky P, Huber D, Knauer F, Roth H, Wagner A, Kusak J (2006) Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *Journal of Zoology* 269: 474–485.
- Kennedy M, Shave CR, Spencer HG, Gray RD (1994) Quantifying the effect of predation risk on foraging bullies – no need to assume an IFD. *Ecology* 75: 2220–2226.
- Kishimoto R (2009) Status of the 2006 drastic rise of Asiatic black bear (*Ursus thibetanus*) intrusions into residential areas in Nagano Prefecture. In: Toru Oi, Naoki Ohnishi, Toru Koizumi, Isamu Okochi (eds) *FFPRI Scientific Meeting Report 4 'Biology of Bear Intrusions'*, 35–39. Forestry and Forest Products Research Institute, Ibaraki, Japan.
- Klinka DR, Reimchen TE (2002) Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. *Canadian Journal of Zoology* 80: 1317–1322.
- Kozakai C, Yamazaki K, Nemoto Y, Nakajima A, Koike S, Abe S, Masaki T, Kaji K (2011) Effect of mast production on home range use of Japanese black bear. *Journal of Wildlife Management* 75: 867–875.
- Landriault LJ, Brown GS, Hamr J, Mallory FF (2009) Age, sex and relocation distance as predictors of return for relocated nuisance black bears *Ursus americanus* in Ontario, Canada. *Wildlife Biology* 15: 155–164.
- Lecount AL (1987) Causes of black bear cub mortality. *Ursus* 7: 75–82.
- Libal N, Belant J, Leopold B, Wang G, Owen P (2011) Despotism and risk of infanticide influence grizzly bear den-site selection. *PLoS ONE* 6: 1–10.
- Linnell JDC, Aanes R, Swenson JE, Odden J, Smith ME (1997) Translocation of carnivores as a method for managing

- problem animals: a review. *Biodiversity and Conservation* 6: 1245–1257.
- Linnell JDC, Swenson JE, Andersen R (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4: 345–349.
- Macbeth BJ, Cattet MRL, Stenhouse GB, Gibeau ML, Janz DM (2010) Hair cortisol concentration as a noninvasive measure of long-term stress in free-ranging grizzly bears (*Ursus arctos*): considerations with implications for other wildlife. *Canadian Journal of Zoology* 88: 935–949.
- MacHutchon G, Himmer S, Davis H, Gallagher M (1998) Temporal and spatial activity patterns among coastal bear populations. *Ursus* 10: 539–546.
- Madison JS (2008) Yosemite National Park: the continuous evolution of human-black bear conflict management. *Human-Wildlife Conflicts* 2: 160–167.
- Main MB, Weckerly FW, Bleich VC (1996) Sexual segregation in ungulates: new directions for research. *Journal of Mammalogy* 77: 449–461.
- Martin JGA, Reale D (2008) Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behavioural Processes* 77: 66–72.
- Mattson D (1990) Human impacts on bear habitat use. *Ursus* 8: 33–56.
- Mattson D, Reinhart DP (1995) Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. *Canadian Journal of Zoology* 73: 2072–2079.
- Mattson DJ, Knight RR, Blanchard BM (1987) The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Ursus* 7: 259–273.
- Mattson DJ, Blanchard BM, Knight RR (1992) Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* 56: 432–442.
- McArthur Jope KJ (1983) Habituation of grizzly bears to people: a hypothesis. *Ursus* 5: 322–327.
- McCullough DR (1982) Behavior, bears, and humans. *Wildlife Society Bulletin* 10: 27–33.
- McLean PK, Pelton MR (1990) Some demographic comparisons of wild and panhandler bears in the Smoky Mountains. *Ursus* 8: 105–112.
- McLellan B (1994) Density-dependent population regulation of brown bears. In: Taylor M (ed.) *Density-dependent Population Regulation of Black, Brown, and Polar Bears*, 15–24. *Ursus*, Monograph series 3.
- McLellan BN (1993) Competition between black and grizzly bears as a natural population regulating factor. *Proceedings from Western Black Bear Workshop* 4: 111–116.
- McLellan BN (2005) Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16: 141–156.
- McLellan BN, Shackleton DM (1988) Grizzly bears and resource-extraction industries – effects of roads on behavior, habitat use and demography. *Journal of Applied Ecology* 25: 451–460.
- McLellan BN, Hovey FW, Mace RD, Woods JG, Carney DW, Gibeau ML, Wakkinen WL, Kasworm WF (1999) Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management* 63: 911–920.
- McLoughlin PD, Ferguson SH, Messier F (2000) Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology* 14: 39–60.
- McLoughlin PD, Case RL, Gau RJ, Cluff HD, Mulders R, Messier F (2002) Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132: 102–108.
- McMillin JM, Seal US, Rogers L, Erickson AW (1976) Annual testosterone rhythm in black bear (*Ursus americanus*). *Biology of Reproduction* 15: 163–167.
- Miquelle DG, Peek JM, Vanballenberghe V (1992) Sexual segregation in Alaskan moose. *Wildlife Monographs* 122: 1–57.
- Mueller C, Herrero S, Gibeau ML (2004) Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15: 35–47.
- Nellemann C, Støen O, Kindberg J, Swenson J, Vistnes I, Ericsson G, Katajisto J, Kaltenborn B, Martin J, Ordiz A (2007) Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138: 157–165.
- Nevin OT, Gilbert BK (2005a) Measuring the cost of risk avoidance in brown bears: further evidence of positive impacts of ecotourism. *Biological Conservation* 123: 453–460.
- Nevin OT, Gilbert BK (2005b) Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? *Biological Conservation* 121: 611–622.
- Nielsen S, Herrero S, Boyce MS, Mace RD, Benn B, Gibeau ML, Jevons S (2004) Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation* 120: 101–113.
- Nisbet ICT (2000) Disturbance, habituation, and management of waterbird colonies – commentary. *Waterbirds* 23: 312–332.
- Noyce KV, Garshelis DL (2011) Seasonal migrations of black bears (*Ursus americanus*): causes and consequences. *Behavioral Ecology and Sociobiology* 65: 823–835.
- von der Ohe CG, Wasser SK, Hunt KE, Servheen C (2004) Factors associated with fecal glucocorticoids in Alaskan brown bears (*Ursus arctos horribilis*). *Physiological and Biochemical Zoology* 77: 313–320.
- Oi T, Ohnishi N, Furusawa H, Fujii T (2009) Nutritional condition and dietary profile of invasive bears in Hiroshima Prefecture, western Japan. In: Toru Oi, Naoki Ohnishi, Toru Koizumi, Isamu Okochi (eds) *FFPRI Scientific Meeting Report*

- 4 'Biology of Bear Intrusions', 44–47. Forestry and Forest Products Research Institute, Ibaraki, Japan.
- Oka T, Miura S, Masaki T, Suzuki W, Osumi K, Saitoh S (2004) Relationship between changes in beechnut production and Asiatic black bears in northern Japan. *Journal of Wildlife Management* 68: 979–986.
- Olson TL, Gilbert BK, Squibb RC (1997) The effects of increasing human activity on brown bear use of an Alaskan river. *Biological Conservation* 82: 95–99.
- Ordiz A, Støen OG, Swenson JE, Kojola I, Bischof R (2008) Distance-dependent effect of the nearest neighbor: spatiotemporal patterns in brown bear reproduction. *Ecology* 89: 3327–3335.
- Ordiz A, Støen O-G, Delibes M, Swenson JE (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166: 59–67.
- Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* 34: 1222–1242.
- Pease CM, Mattson DJ (1999) Demography of the Yellowstone grizzly bears. *Ecology* 80: 957–975.
- Peirce KN, Van Daele LJ (2006) Use of a garbage dump by brown bears in Dillingham, Alaska. *Ursus* 17: 165–177.
- Robbins CT, Schwartz CC, Felicetti LA (2004) Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15: 161–171.
- Rode KD, Robbins CT, Shipley LA (2001) Constraints on herbivory by grizzly bears. *Oecologia* 128: 62–71.
- Rode KD, Farley SD, Robbins CT (2006a) Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* 133: 70–80.
- Rode KD, Farley SD, Robbins CT (2006b) Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87: 2636–2646.
- Rode KD, Farley SD, Fortin J, Robbins CT (2007) Nutritional consequences of experimentally introduced tourism in brown bears. *Journal of Wildlife Management* 71: 929–939.
- Rodríguez-Prieto I, Martín J, Fernández-Juricic E (2010) Habituation to low-risk predators improves body condition in lizards. *Behavioral Ecology and Sociobiology* 64: 1937–1945.
- Roever CL, Boyce MS, Stenhouse GB (2008a) Grizzly bears and forestry – II: grizzly bear habitat selection and conflicts with road placement. *Forest Ecology and Management* 256: 1262–1269.
- Roever CL, Boyce MS, Stenhouse GB (2008b) Grizzly bears and forestry I: road vegetation and placement as an attractant to grizzly bears. *Forest Ecology and Management* 256: 1253–1261.
- Rogers LL (1987) Effects of food supply and kinship on social behavior, movements, and population dynamics of black bears in northeastern Minnesota. *Wildlife Monographs* 97: 1–72.
- Rogers LL (1989) Black bears, people, and garbage dumps in Minnesota. In: Bromley M (ed.) *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*, 48–51. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Rogers LL (2011) Does diversionary feeding create nuisance bears and jeopardize public safety? *Human-Wildlife Interactions* 5: 287–295.
- Rogers LL, Stowe CM, Erickson EM, Verme LJ, Ozoga JJ (1976) Characteristics and management of black bears that feed in garbage dumps, campgrounds, or residential areas. *Ursus* 3: 169–175.
- Sato Y, Mano T, Takatsuki S (2005) Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan. *Wildlife Biology* 11: 133–144.
- Schwartz CC, Franzmann AW (1992) Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 56: 426–431.
- Schwartz CC, Haroldson MA, White GC, Harris RB, Cherry S, Keating KA, Moody D, Servheen C (2006) Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161: 1–68.
- Schwartz CC, Cain SL, Podrutzny S, Cherry S, Frattaroli L (2010) Contrasting activity patterns of sympatric and allopatric black and grizzly bears. *Journal of Wildlife Management* 74: 1628–1638.
- Shivik JA, Ruid D, Willging RC, Mock KE (2011) Are the same bears repeatedly translocated from corn crops in Wisconsin? *Ursus* 20: 114–119.
- Singer FJ, Bratton SP (1980) Black bear/human conflicts in the Great Smoky Mountains National Park. *Ursus* 4: 137–139.
- Smith TS (2002) Effects of human activity on brown bear use of the Kulik River, Alaska. *Ursus* 13: 257–267.
- Smith TS, Herrero S, DeBruyn TD (2005) Alaskan brown bears, humans, and habituation. *Ursus* 16: 1–10.
- Stelmock JJ, Dean FC (1986) Brown bear activity and habitat use, Denali National Park: 1980. *Ursus* 6: 155–167.
- Stokes AW (1970) An ethologist's views on managing grizzly bears. *BioScience* 20: 1154–1157.
- Storonov D, Stokes AW (1972) Social behavior of the Alaska brown bear. *Ursus* 2: 232–242.
- Støen O-G, Bellemain E, Sæbø S, Swenson JE (2005) Kin-related spatial structure in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 59: 191–197.
- Støen O-G, Zedrosser A, Sæbø S, Swenson JE (2006) Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* 148: 356–364.
- Stringham SF (1989) Demographic consequences of bears eating garbage at dumps: an overview. In: Bromley M (ed.) *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*, 35–42. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Sukumar R (1991) The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation* 55: 93–102.

- Sutherland WJ, Parker GA (1992) The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Animal Behaviour* 44: 345–355.
- Swenson JE (1999) Does hunting affect the behavior of brown bears in Eurasia? *Ursus* 11: 157–162.
- Swenson JE, Sandegren F, Söderberg A, Bjärvall A, Franzen R, Wabakken P (1997) Infanticide caused by hunting of male bears. *Nature* 386: 450–451.
- Swenson JE, Sandegren F, Bjärvall A, Wabakken P (1998) Living with success: research needs for an expanding brown bear population. *Ursus* 10: 17–23.
- Swenson JE, Gerstl N, Dahle B, Zedrosser A (2000) Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe. *Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention)*. Nature and environment, No. 114. Council of Europe, Strasbourg, France.
- Swenson JE, Dahle B, Sandegren F (2001) Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12: 81–92.
- Tietje WD, Ruff RL (1983) Responses of black bears to oil development in Alaska. *Wildlife Society Bulletin* 11: 99–112.
- Treves A (2009) Hunting for large carnivore conservation. *Journal of Applied Ecology* 46: 1350–1356.
- Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* 17: 1491–1499.
- Warner SH (1987) Visitor impact on brown bears, Admiralty Island, Alaska. *Ursus* 7: 377–382.
- Welch CA, Keay J, Kendall KC, Robbins CT (1997) Constraints on frugivory by bears. *Ecology* 78: 1105–1119.
- Wielgus RB, Bunnell FL (1994) Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58: 405–413.
- Wielgus RB, Bunnell FL (1995) Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59: 552–560.
- Wielgus RB, Vernier PR, Schivatcheva T (2002) Grizzly bear use of open, closed, and restricted forestry roads. *Canadian Journal of Forest Research* 32: 1597–1606.
- Witmer GW, Whittaker DG (2001) Dealing with nuisance and depredating black bears. *Wildlife Damage Management, Internet Center for USDA National Wildlife Research Center. Western black bear workshop*, 7: 73–81.
- Woodroffe R (2000) Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* 3: 165–173.
- Yamanaka A, Asano M, Suzuki M, Mizoguchi T, Shimozuru M, Tsubota T (2009) Is there any relationship between the number of nuisance-killed Japanese black bears (*Ursus thibetanus japonicus*) and their nutritional condition? In: Toru Oi, Naoki Ohnishi, Toru Koizumi, Isamu Okochi (eds) *FFPRI Scientific Meeting Report 4 'Biology of Bear Intrusions'*, 48–51. Forestry and Forest Products Research Institute, Ibaraki, Japan.
- Young DD, Beecham JJ (1986) Black bear habitat use at Priest Lake, Idaho. *Ursus* 6: 73–80.
- Zedrosser A, Dahle B, Swenson JE (2006) Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87: 510–518.
- Zedrosser A, Støen O, Sæbø S, Swenson J (2007) Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour* 74: 369–376.

PAPER II

Effects of sex and age on den site use by Scandinavian brown bears

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Abstract: We asked whether den site characteristics of Scandinavian brown bears (*Ursus arctos*) were related to bear sex or age by analyzing the nearest distances to human structures within 10 km, the forest composition within 50 m, and topography within 5 m of 391 winter dens used by 114 individuals during 1986–2003 in south-central Sweden. Subadult males and subadult females used more pine (*Pinus sylvestris*) than spruce (*Picea abies*) denning habitats than did adult males. Adult males selected nest dens over rock dens more strongly than did subadult males, and they selected nest dens over anthill, soil, and rock dens more strongly than did subadult females, pregnant females, or females with cubs. Topography differed among den types but showed a poor relationship with different age–sex classes of bears. Abandoned dens were located closer to plowed roads than dens used successfully all winter. Adult males denned farther from permanently occupied houses and plowed roads than did other categories of bears, perhaps because they were least tolerant of human disturbance. In general, den sites of adult males differed the most from other age–sex classes of bears.

Key words: abandonment, brown bear, den site characteristics, denning habitat, Scandinavia, Sweden, *Ursus arctos*

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Brown bears (*Ursus arctos*) spend up to half their life hibernating in winter dens, and females give birth there. Because winter dormancy typically results in a 20–40% weight loss (Kingsley et al. 1983), bears benefit by choosing den sites that conserve energy and reduce disturbance by people or detection by predators.

Friebe et al. (2001) reported that among brown bears in Scandinavia, females with cubs have the longest and males the shortest denning periods, similar to reports for North American black bears (*U. americanus*) and brown bears (LeCount 1983, O’Pezio 1983, Schoen et al. 1987, Schwartz et al. 1987, Miller 1990, Van Daele et al. 1990, Ciarniello et al. 2005). Studies from Scandinavia suggest that human disturbance influences abandonment of winter dens and choice of den location (Swenson et al. 1996, Swenson et al. 1997, Elfström et al. 2008), and that abandonment of winter dens by pregnant females reduces reproductive success (Swenson et al.

1997). After females give birth, the cost of den relocation rises dramatically, because young cubs are exposed to thermal stress and perhaps predation before they are fully mobile. Therefore, females with cubs should tolerate greater levels of disturbance without abandoning dens (Linnell et al. 2000).

Linnell et al. (2000) concluded that brown bears tolerate industrial activity as long as the source of the noise is some kilometers from the den. Nevertheless, dens visited directly by people were often abandoned. Because males may show infanticidal behavior (Swenson 2003, Bellemain et al. 2006), females that avoid adult males in the spring breeding season may have a greater probability of successfully raising their young. Hence, for both energetic reasons and perhaps to avoid human disturbance or potentially predaceous male brown bears, different age–sex classes of bears may select different denning habitat.

Manchi and Swenson (2005) reported that mean distances between dens used in successive years by Scandinavian brown bears varied with age and sex due to dispersal behavior, and that duration of denning decreased with increasing age and body

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mass. Elfström et al. (2008) found that bears in this same area showed distinct preferences in selection of denning habitats at a landscape scale, but found no major differences related to age and sex at this large scale. However, habitat use may be scale dependent (Aebischer et al. 1993), and therefore it is still unclear whether there are differences in use of denning habitat among age–sex classes of Scandinavian brown bears at other scales. In American black bears, Klenzendorf et al. (2002) reported that different age and sex classes used different den types, and Pelton et al. (1980) and Manville (1987) reported that females were more selective than males.

Here, we describe denning habitat of Scandinavian brown bears and evaluate differences related to age and sex. We analyzed the nearest distances to human structures within 10 km, the forest composition within 50 m, and topography within 5 m of 391 dens. We also compared the habitats at dens used during the entire winter with habitats where dens were abandoned during the winter.

Study area

The study area encompassed about 21,000 km² in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (67°N, 13°E), covering the southern part of brown bear distribution in Scandinavia (Fig. 1). The area was dominated by coniferous forest (60%) of mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Deciduous forest, composed mainly of birches (*Betula pubescens*, *B. pendula*), alder (*Alnus incana*), and mountain ash (*Sorbus aucuparia*) covered 8% of the area. The ground vegetation was mainly ericaceous shrubs (*Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum*) and mosses. Bogs covered 15% of the landscape. Other features were open habitat (mainly grassland, 7%), open water (7%), and mountain forest (alpine birch, *B. pubescens* ssp. *czerepanovii*, and open canopy coniferous; 4%) (Elfström et al. 2008). Precipitation was 350–450 mm during the vegetation period (mean temperature $\geq 5^{\circ}\text{C}$) with 800–1100 degree-days (Swenson et al. 1996). Snow cover normally lasted from about November to April or early May (Swenson et al. 1996). Elevations ranged from 140 m in the east to 1,045 m in the west toward the Norwegian border. About 11% of the study area was below 160 m, 31% between 160 and 320 m, 50% between 320 and 650 m, and 8% above

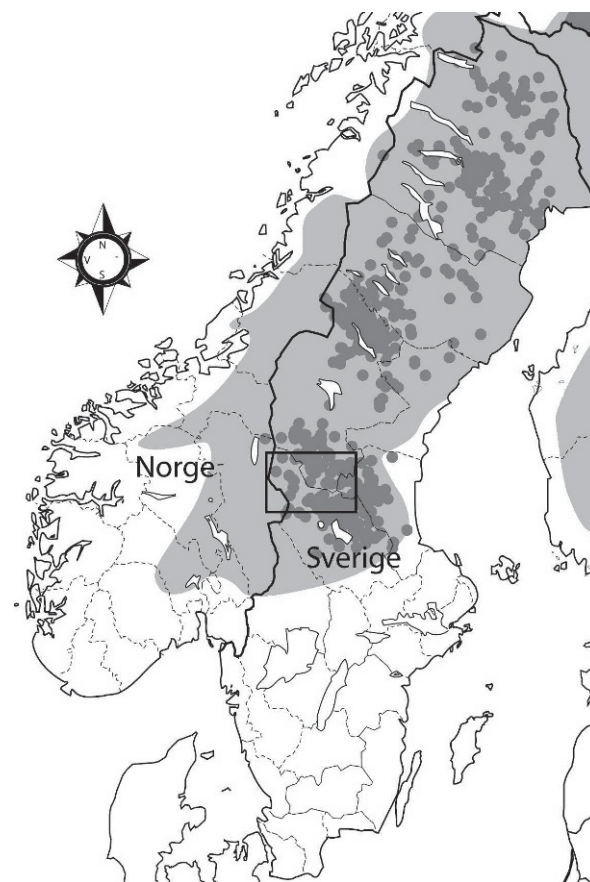


Fig. 1. Rectangle represents study area in south-central Sweden. The shaded area is the distribution of brown bears, with dark plots indicating areas of higher bear densities where female bears were shot in Sweden.

650 m. The terrain in the southeastern part was relatively flat, with more topographically diverse and elevated terrain in the west. The slopes were less than 8° in over 90% of the study area (Elfström et al. 2008).

Methods

Bears were immobilized and fitted with radio-transmitters (Arnemo et al. 2006, Arnemo and Fahlman 2007) after being darted from a helicopter with DAN-INJECT® equipment (DAN-INJECT AdS, Børkop, Denmark). We determined the locations of denned bears during 1985–2003 by triangulation from the ground and by aerial telemetry. Coordinates of the dens were obtained with global positioning system (GPS) units when the dens were

visited on the ground. Some bears were tracked with radiotransmitters from their year of birth. For bears that were not marked during their first year, age was estimated using cementum annuli of an upper premolar (Matson et al. 1993).

We separated radiocollared brown bears into 5 age–sex classes: adult males ≥ 5 years old, subadult males < 5 years old (Dahle and Swenson 2003), subadult females in prereproductive status, pregnant adult females that gave birth during denning, and adult females with cubs (i.e., females that denned with cubs, which became yearlings in the den). Very few females in this area entered the den with yearlings (we detected only 1). Eight adult females entered the den alone and did not have young when they left the den; they were excluded from the analysis due to small sample size. We considered age as a continuous factor explaining variation in den site characteristics.

We placed dens into 4 categories: anthill den, soil den, rock den (under a large rock or glacial boulder), and nest den (a nest of sticks on the ground; Sandegren and Swenson 1997). We described the habitat within 50 m around the den, referred to as the den site. The forest composition within the den site was placed into 1 of 3 habitat categories: dominated by birch, Norway spruce, or Scots pine. We obtained distances to human structures within 10 km of dens from a 1:50,000 Geographical Sweden Data (GSD) map, but these data were corrected during field work when necessary. We obtained elevation to the nearest 5 m from the GSD map. Degree of slope was estimated visually within 5 m of the den by comparing the vertical length from the uppermost point to the lowermost point with the length of its horizontal axis. Not all parameters were measured for every den.

We analyzed dens that were abandoned during the winter separately from successful dens. Bears in our study area apparently select their den site during the nondenning season, so factors affecting selection of the first and subsequent den sites during a winter may differ (Kolenosky and Strathearn 1987, Friebe et al. 2001). These subsequent dens (20 second dens and 3 third dens used the same winter) were excluded from all analyses. We found only 1 case of a bear reusing a den in successive years, and only 1 case of a den being reused by another bear. Therefore, we took a conservative approach and analyzed these dens only the first time they were used. Because a bear must select a den each year, each den was

considered to be independent, as in similar studies (Schwartz et al. 1987, Hayes and Pelton 1994, Clark et al. 1998, Hightower et al. 2002). However, to test whether pooling data across individuals was justified, we extracted the residuals for each parameter for each bear. We then plotted the residuals for individual bears and evaluated potential effects of repeated measures of individuals.

All statistical analyses were performed using SPSS for Windows® version 12.0 (SPSS Inc. 2003). We used Pearson χ^2 statistics to evaluate differences among age–sex classes, den type, and denning habitat, and to test differences between dens that were abandoned and not abandoned during the winter. We used 2×2 Pearson χ^2 comparisons with continuity correction if our global test was significant. A significance level of $\alpha = 0.05$ was assumed in our global tests. We considered repeated measures in our 2×2 comparisons by restricting the significance level according to Bonferroni [$\alpha = 0.05/(k - 1)$, where k represents number of tests].

To evaluate elevation and slope at den sites according to age–sex classes of bears and den types, in addition to covariate interactions, we used a general linear model one-way analysis of variance. We used Levene's test of homogeneity of variance for each dependent variable across all level combinations of the between-subject factors. We replaced missing values with the corresponding mean value for all parameters in the analysis. If statistical significance was found in the global test, we used η^2 (eta-squared) statistics to describe the proportion of total variability attributable to a factor. The estimates of effect size gave a partial η^2 value for each effect and each parameter estimate. We used post hoc multiple comparisons tests to determine which means differed within age–sex classes, den types, or both. We used the conservative Scheffé test if equal variance could be assumed for the dependent variable, and Tamhane's T2 conservative pairwise comparisons test if we could not assume equal variance.

We investigated whether elevation, slope, or distance to the nearest permanently occupied house, vacation house, plowed road, or unplowed road influenced whether a bear abandoned its den during the winter, using a backward Wald stepwise logistic regression and $\alpha = 0.10$ as the cutoff value for removal. The distances were log-transformed to obtain normal distributions. We replaced missing values with the corresponding mean value for all parameters in the analysis.

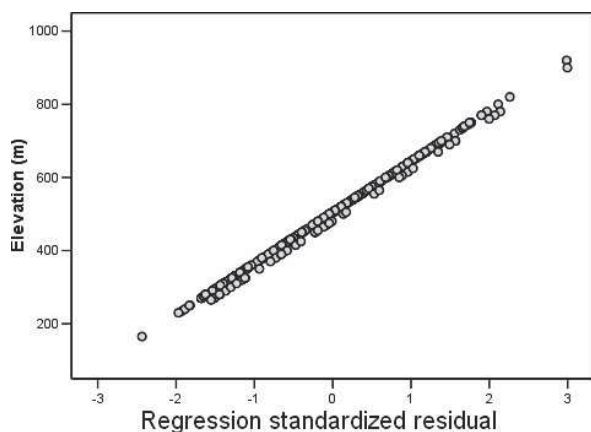


Fig. 2. Scatterplot of residuals for elevation at den sites of each Scandinavian brown bear in the 1986–2003 study.

We examined the distance of dens from human structures to determine whether this affected den site selection by age–sex classes of bears. Distances were log-transformed to obtain normal distributions. We tested 2 types of structures: houses and roads. For each type, we considered 2 levels of activity: plowed and unplowed roads, and permanently occupied and vacation houses. We expected that if these structures affected den site selection among age–sex classes, the effect would be greater at the higher level of activity. We used one-way analysis of variance for the global test, and the post hoc Tukey honest significant difference test with $\alpha = 0.05$ to identify differences among categories if the global test was significant.

Results

We documented 417 winter dens used by 114 individuals during 1986–2003. When additional dens (from the same winter) and reused dens were excluded, 391 dens were left for analysis (but type of den was missing for 3 dens). The mean age of bears when entering dens was 7.7 years (SD = 5.4, range 2–30).

The plotted scatter of residuals across individual bears showed no pattern that suggested an effect of individual for any den site parameter (Fig. 2 and 3). This suggests that pooling data across individuals did not affect our analyses.

Types of den used by categories of bears

The type of den used by bears was not independent of age–sex class ($\chi^2 = 59.41$, 12 df, $P < 0.001$,

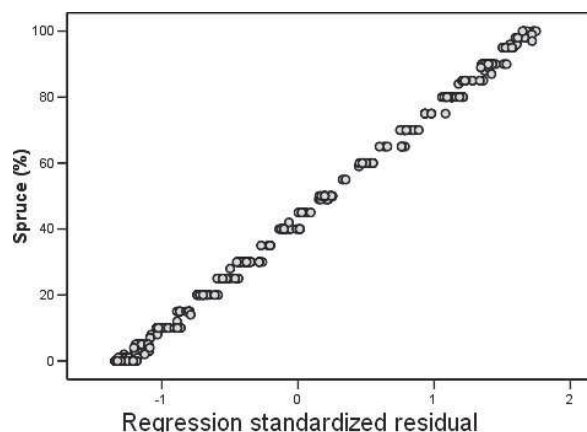


Fig. 3. Scatterplot of residuals for proportion of spruce at den sites of each Scandinavian brown bear in the 1986–2003 study.

Table 1). Adult males selected nest dens over rock dens more strongly than did subadult males ($\chi^2 = 10.26$, 1 df, $P = 0.001$, Table 1,2). Adult males selected nest dens over anthill ($\chi^2 = 13.08$, 1 df, $P < 0.001$), soil ($\chi^2 = 19.96$, 1 df, $P < 0.001$), and rock dens ($\chi^2 = 14.56$, 1 df, $P < 0.001$) more strongly than did subadult females. Adult males selected nest dens over anthill ($\chi^2 = 16.63$, 1 df, $P < 0.001$), soil ($\chi^2 = 12.75$, 1 df, $P < 0.001$), and rock dens ($\chi^2 = 11.72$, 1 df, $P = 0.001$) more strongly than did pregnant females. Adult males selected nest dens over anthill ($\chi^2 = 14.38$, 1 df, $P < 0.001$), soil ($\chi^2 = 10.70$, 1 df, $P = 0.001$), and rock dens ($\chi^2 = 15.62$, 1 df, $P < 0.001$) more strongly than did females with cubs (Table 1, 2). No significant differences in type of dens used were found among subadult males, subadult females, pregnant females, or females with cubs.

Topography at den site used by different categories of bears

Variation in den elevation was most closely related to type of den (ANOVA: $F = 11.59$; 3, 296 df; $P < 0.001$). Our test of homogeneity of variance was significant, indicating that we could not assume equal variance (Levene's test of equality of error variances: $F = 1.43$; 49, 261 df; $P = 0.041$). Anthill dens were higher in elevation than rock and nest dens (anthill–rock: mean difference = 146.80 m, SE = 27.13, $P < 0.001$ and anthill–nest: mean difference = 112.54 m, SE = 23.64, $P < 0.001$, Table 3), and soil dens were higher than rock dens (soil–rock: mean difference = 89.27 m, SE = 27.16, $P = 0.016$, Table 3). Elevation showed no significant relation-

Table 1. Sex and age distribution of brown bear among types of dens in south-central Sweden, 1986–2003. Pearson $\chi^2 = 59.41$, 12 df, $P < 0.001$ for dens successfully used and dens abandoned during the winter combined.

Den type	Age–sex class ^a										
	MS		MA		FS		FP		FC		Total
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Anthill	22	9.4	40	17.0	54	23.0	73	31.1	46	19.6	235
Soil	5	8.5	6	10.2	23	39.0	17	28.8	8	13.6	59
Rock	6	25.0	0	0.0	7	29.2	6	25.0	5	20.8	24
Nest ^b	5	15.6	18	56.3	3	9.4	5	15.6	1	3.1	32
Non-abandoned dens	38		64		87		101		60		350
Abandoned dens	4		4		3		12		3		26
Individual bears	27		27		41		39		26		160

^aMS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

^bA nest of sticks on the ground.

ship with age–sex class (ANOVA: $F = 0.57$; 4, 296 df; $P = 0.68$).

Slope at den sites also was related to type of den (ANOVA: $F = 3.42$; 3, 296 df; $P = 0.018$). Our test of homogeneity of variance was not significant, indicating that we could assume equal variance (Levene's test of equality of error variances: $F = 0.97$; 49, 261 df; $P = 0.54$). Nest dens were on flatter slopes than soil dens (soil–nest: mean difference = 8.21° , SE = 2.57, $P = 0.038$, Table 3). Slope was not significantly related to age–sex class (ANOVA: $F = 1.60$; 4, 296 df; $P = 0.17$).

Denning habitat by category of bears

We found a significant relationship between denning habitat and age–sex class ($\chi^2 = 20.67$, 8 df, $P = 0.008$, Table 4). Subadult males and subadult females selected pine-dominated over spruce-dominated denning habitats more than did adult males ($\chi^2 = 11.26$, 1 df, $P = 0.001$ and $\chi^2 = 14.56$, 1 df, $P < 0.001$, respectively, Table 4). No significant differences in denning habitat were found among subadult males, subadult females, pregnant females, or females with cubs.

Factors associated with den abandonment

A stepwise logistic regression model showed that only distance to the nearest plowed road was associated with whether a bear used the den the entire winter; abandoned dens were closer to plowed roads ($\beta = -0.517$, 1 df, $P = 0.005$). Altitude, slope, and distance to the nearest permanently occupied house, vacation house, and unplowed road showed no significant effect. We found no relationships between types of den or denning habitat and whether

dens were used successfully or were abandoned during the winter ($\chi^2 = 1.14$, 3 df, $P = 0.77$ and $\chi^2 = 3.54$, 2 df, $P = 0.17$, respectively).

Influence of human structures on denning sites by bears category

Differences in den placement among bear categories relative to human structures were greater for structures with higher human activity. There was no significant difference among bear categories in distance from nearest vacation houses (ANOVA: $F = 1.12$; 4, 233 df; $P = 0.35$) or from nearest unplowed roads (ANOVA: $F = 0.96$; 4, 213 df; $P = 0.43$). However, there were significant differences for distance to nearest permanently occupied houses (ANOVA: $F = 3.00$; 4, 205 df; $P = 0.020$) and

Table 2. Comparison of types of dens used by different age–sex class of brown bears in south-central Sweden (dens used the entire winter combined with dens abandoned during the winter), 1986–2003. All other 2×2 χ^2 comparisons among age–sex class and type of dens showed $P > 0.002$, non-significant when using the Bonferroni correction.

Age–sex class ^a	Type of den	df	χ^2	<i>P</i>
MA–MS	rock nest	1	10.26	0.001
MA–FS	anthill nest	1	13.08	0.000
	soil nest	1	19.96	0.000
	rock nest	1	14.56	0.000
MA–FP	anthill nest	1	16.63	0.000
	soil nest	1	12.75	0.000
	rock nest	1	11.72	0.001
MA–FC	anthill nest	1	14.38	0.000
	soil nest	1	10.70	0.001
	rock nest	1	15.62	0.000

^aMA = adult males, MS = subadult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

Table 3. Topography of den sites among age–sex classes and den types used successfully the entire winter for brown bears in south-central Sweden, including topography of dens that were abandoned during the winter, 1986–2003.

	Elevation (m)			Slope (°)		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Age–sex class ^a						
MS	481.1	158.3	40	13.3	15.6	35
MA	530.2	160.3	63	6.3	10.3	55
FS	496.4	140.3	90	12.2	12.9	83
FP	500.9	128.3	100	9.5	12.1	99
FC	505.8	119.0	63	13.7	15.7	54
Total	503.6	139.4	356	10.7	13.3	326
Den type						
Anthill	532.2	126.4	231	9.6	12.5	205
Soil	472.6	152.9	56	14.0	13.3	55
Rock	385.8	99.1	24	14.3	10.6	23
Nest ^b	418.2	136.8	31	4.9	8.6	29
Total	503.7	139.3	354	10.7	13.3	324
Abandoned dens	478.7	140.9	26	8.0	10.1	23

^aMS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

^bA nest made of sticks on the ground.

nearest plowed roads (ANOVA: $F = 7.06$; 4, 290 df; $P = 0.000$). The post hoc Tukey test indicated that adult males denned on average 1.7 km (SE = 1.2) farther from permanently occupied houses than subadult males ($P = 0.017$) and 1.5 km (SE = 1.2) farther than subadult females ($P = 0.044$, Table 5). The post hoc Tukey test also indicated that adult males denned farther from plowed roads than all other categories of bears, but that there were no other differences among bear categories (Fig. 4, Table 5). Adult males denned on average 2.4 km (SE = 1.3) farther from plowed roads than subadult males ($P = 0.001$), 2.0 km (SE = 1.2) farther than subadult females ($P = 0.002$), 2.5 km (SE = 1.2) farther than pregnant females ($P < 0.001$), and 2.4 km (SE = 1.2) farther than females with cubs ($P < 0.001$; Fig. 4, Table 5).

Discussion

We found differences among Scandinavian brown bear age–sex classes in den types, denning habitat, and topography at den sites, with adult males differing the most from other categories. As expected, human structures with higher human activity affected den placement more than those with lower levels of activity. Adult males used denning habitats with less potential human influence than other categories of bears. Abandoned den sites were located significantly closer to plowed roads than dens used all winter.

The topography at den sites differed by den type. Anthill dens occurred at higher elevations than soil, rock, and nest dens; nest dens were on flatter slopes than soil dens (Table 3). Topography (elevation and slope) at den sites did not differ by age–sex classes, except for adult males that used nest dens. Bears in

Table 4. Distribution of den sites in habitat types by age–sex classes of brown bears in south-central Sweden, 1986–2003. Pearson $\chi^2 = 20.67$, 8 df, $P = 0.008$ for dens used and dens abandoned during the winter combined. Includes denning habitats for dens abandoned during winter.

Denning habitat	Age–sex class ^a									
	MS		MA		FS		FP		FC	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Pine	16	13.8	8	6.9	37	31.9	33	28.4	22	19.0
Spruce	11	7.5	34	23.3	28	19.2	46	31.5	27	18.5
Birch	4	10.3	8	20.5	10	25.6	13	33.3	4	10.3
Non-abandoned dens	31		50		75		92		53	
Abandoned dens	3		4		3		9		3	
Individual bears	25		27		40		39		26	

^aMS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

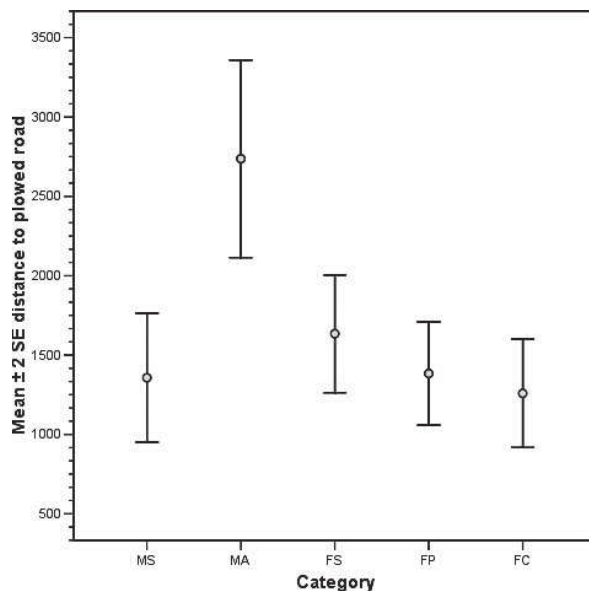


Fig. 4. Mean distance (m) from brown bear dens to the nearest plowed road by age–sex class of bears in south-central Sweden, 1986–2003. Adult males (MA) were significantly different from all other age–sex classes: subadult males (MS), subadult females (FS), pregnant females (FP), and females with cubs (FC), post hoc Tukey test: $P = 0.001$, $P = 0.002$, $P < 0.001$, and $P < 0.001$, respectively.

nest dens are most dependent on snow cover for insulation, due to lack of other elements that could provide insulation (Martorello and Pelton 2003). Although we found no difference in selection of topography at den sites among age–sex classes, adult males, subadult females, and lone females selected flatter slopes at the landscape scale in the same area (Elfström et al. 2008). Schoen et al. (1987) reported that female North American brown bears on Admiralty and Chichagof Islands, Alaska, denned on higher and steeper slopes than males.

Subadult males and subadult females used pine-dominated more than spruce-dominated denning habitats than did adult males. Different vegetation composition between adult males and all other age–sex classes at den sites has been reported in American brown bears (Darling 1987) and black bears (LeCount 1983); in the latter study, adult males denned in more open areas.

Dens of adult males differed the most from other age–sex classes of bears. This may be because of the different physiological demands of adult males (Schwartz et al. 1987, Hellgren 1995). Swenson et al. (2007) reported that adult male brown bears in

Scandinavia have larger body mass than adult females and that relative loss of body mass during denning is greater among females than males. Because adult males have greater fat stores than smaller bears and do not have to allocate resources for lactation, they may have different requirements for den sites.

Adult males denned farther from plowed roads than other categories of bears (Fig. 4, Table 5) and farther from permanently occupied houses than subadult males and subadult females (Table 5). Abandoned dens were closer to plowed roads than successfully used dens, suggesting that plowed roads are a source of disturbance, probably from increased human access to the forest for forestry, hunting, skiing, or snowmobiling. In the same study area, but at the landscape scale of analysis, Elfström et al. (2008) showed that brown bears selecting den locations avoided roads that had high traffic and easy access (such as plowed roads).

Linnell et al. (2000) suggested that females with cubs should tolerate greater levels of disturbance without abandoning dens than other categories, because Swenson et al. (1997) reported that abandoning a den was associated with lower reproductive success by female brown bears. The shorter distances to human structures shown by denned females and subadult males (Fig. 4, Table 5) may result from their greater tolerance of disturbance than that of adult males. Alternatively, because adult males occupy den sites farther from human activity and structures, females and subadult males may choose den sites closer to permanently occupied houses and plowed roads to avoid adult males. Manville (1987) reported that American black bear males also denned farther from human activity than females. During the nondenning period in our study area, Nellemann et al. (2007) found that bears avoid recreational resorts and settlements, and there is a higher proportion of subadults in areas within 10 km of recreational resorts and settlements, and a relatively higher proportion of old males (>7 years) ≥ 10 km from these areas. Rode et al. (2006) concluded that Alaskan female brown bears with young appear to prioritize avoidance of male bears over avoidance of humans when choosing habitats during the nondenning period.

Management implications

We found that female and subadult male brown bears denned closer to human activity and settlements than adult males. Other studies in this area

Table 5. Distance (m) to nearest human-related features of successfully used brown bear dens in south-central Sweden in relation to age–sex class, and den type, 1986–2003. Data includes distances to dens that were abandoned during winter.

Age–sex class ^a		Permanently occupied house	Vacation house	Plowed road	Unplowed road
MS	mean	3146.2	1618.3	1406.1	678.7
	SD	2051.0	1062.3	1286.4	840.1
	<i>n</i>	26	30	33	27
MA	mean	5187.8	2026.8	2778.1	919.1
	SD	2325.6	1213.4	2237.2	907.3
	<i>n</i>	37	41	48	47
FS	mean	3793.8	1865.6	1655.7	882.1
	SD	2170.4	1399.3	1685.7	1101.8
	<i>n</i>	55	52	77	56
FP	mean	3986.2	1821.4	1500.8	759.8
	SD	2065.5	1355.9	1517.0	569.3
	<i>n</i>	47	56	66	46
FC	mean	3754.8	1500.0	1260.3	626.7
	SD	1672.1	905.8	1232.2	391.4
	<i>n</i>	31	40	46	30
Total	mean	4011.0	1783.8	1719.5	799.4
	SD	2159.9	1233.1	1716.2	839.4
	<i>n</i>	196	219	270	206
Den type					
Anthill	mean	4161.5	1795.1	1819.3	823.7
	SD	2160.0	1227.4	1781.7	716.9
	<i>n</i>	123	150	180	139
Soil	mean	3474.3	1660.0	1612.4	935.0
	SD	2264.8	1346.2	1888.9	1358.8
	<i>n</i>	35	35	42	30
Rock	mean	4585.7	1471.4	992.7	334.1
	SD	2721.8	696.9	970.5	244.5
	<i>n</i>	7	7	15	11
Nest ^b	mean	3952.1	1919.0	1599.6	607.1
	SD	1803.6	985.1	1161.6	479.9
	<i>n</i>	24	21.0	24.0	21
Total	mean	4011.0	1783.8	1719.5	799.4
	SD	2159.9	1233.1	1716.2	839.4
	<i>n</i>	196	219	270	206
Abandoned dens	mean	4339.3	2328.9	991.4	725.0
	SD	2246.6	1698.1	782.0	693.0
	<i>n</i>	14	19	25	12

^aMS = subadult males, MA = adult males, FS = subadult females, FP = pregnant females, FC = females with cubs.

^bA nest made of sticks on the ground.

have shown that females with cubs have the longest and males the shortest denning periods. Taken together, this could suggest a higher probability of humans encountering and potentially disturbing females with cubs in dens close to settlements and plowed roads.

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Literature cited

- AEBISCHER, N.J., P.A. ROBERTSON, AND R.E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- ARNEMO, J.M., P. AHLQVIST, R. ANDERSEN, F. BERNTSEN, G. ERICSSON, J. ODDEN, S. BRUNBERG, P. SEGERSTRÖM, AND J.E. SWENSON. 2006. Risk of anaesthetic mortality in large free-ranging mammals: Experiences from Scandinavia. *Wildlife Biology* 12:109–113.
- , AND Å FAHLMAN, EDITORS. 2007. Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Norwegian School of Veterinary Science, Tromsø, Norway.
- BELLEMMAIN, E., J.E. SWENSON, AND P. TABERLET. 2006. Mating strategies in relation to sexually selected infanticide in a nonsocial carnivore: The brown bear. *Ethology* 112:1–9.
- CIARNIELLO, L.M., M.S. BOYCE, D.C. HEARD, AND D.R. SEIP. 2005. Denning behavior and den site selection of grizzly bears along the Parsnip River, British Columbia, Canada. *Ursus* 16:47–58.
- CLARK, J.D., S.R. HAYES, AND J.M. PLEDGER. 1998. A female black bear denning habitat model using a geographic information system. *Ursus* 10:181–185.
- DAHLE, B., AND J.E. SWENSON. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): Effect of population density, mass, sex, reproductive status and habitat type. *Journal of Zoology* 260:329–335.
- DARLING, L.M. 1987. Habitat use by grizzly bear family groups in interior Alaska. *International Conference on Bear Research and Management* 7:169–178.
- ELFSTRÖM, M., J.E. SWENSON, AND J.P. BALL. 2008. Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* 14:176–187.
- FRIEBE, A., J.E. SWENSON, AND F. SANDEGREN. 2001. Denning chronology of female brown bears in central Sweden. *Ursus* 12:37–46.
- HAYES, S.G., AND M.R. PELTON. 1994. Habitat characteristics of female black bear dens in northwestern Arkansas. *International Conference on Bear Research and Management* 9(1):411–418.
- HELLGREN, E.C. 1995. Physiology of hibernation in bears. *Ursus* 10:467–477.
- HIGHTOWER, D.A., R.O. WAGNER, AND R.M. PACE. 2002. Denning ecology of female American black bears in south-central Louisiana. *Ursus* 13:11–17.

- KINGSLEY, M.C.S., J.A. NAGY, AND R.H. RUSSEL. 1983. Patterns of weight gain and loss for grizzly bears in northern Canada. *International Conference on Bear Research and Management* 5:174–178.
- KLENZENDORF, S.A., M.R. VAUGHAN, AND D.D. MARTIN. 2002. Den-type use and fidelity of American black bears in Western Virginia. *Ursus* 13:39–44.
- KOLENOSKY, G.B., AND S.M. STRATHEARN. 1987. Winter denning of black bears in east-central Ontario. *International Conference on Bear Research and Management* 7:305–316.
- LECOUNT, A.L. 1983. Denning ecology of black bears in central Arizona. *International Conference on Bear Research and Management* 5:71–78.
- LINNELL, J.D.C., J.E. SWENSON, R. ANDERSEN, AND B. BARNES. 2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28:400–413.
- MANCHI, S., AND J.E. SWENSON. 2005. Denning behaviour of male Scandinavian brown bears (*Ursus arctos*). *Wildlife Biology* 11:207–213.
- MANVILLE, A.M. 1987. Den selection and use by black bears in Michigan's Northern Lower Peninsula. *International Conference on Bear Research and Management* 7:317–322.
- MARTORELLO, D.A., AND M.R. PELTON. 2003. Microhabitat characteristics of American black bear nest dens. *Ursus* 14:21–26.
- MATSON, G.M., L. VAN DAELE, E. GOODWIN, A. AUMILLER, H.V. REYNOLDS, AND H. HRISTENKO. 1993. A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth. Matson's Laboratory, Milltown, Montana, USA.
- MILLER, S.D. 1990. Denning ecology of brown bears in south-central Alaska and comparisons with a sympatric black bear population. *International Conference on Bear Research and Management* 8:279–287.
- NELLEMAN, C., O.G. STØEN, J. KINDBERG, J.E. SWENSON, I. VISTNES, E. ERICSSON, E. KATAJISTO, B.P. KALTENBORN, J. MARTIN, AND A. ORDIZ. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157–165.
- O'PEZIO, J.C., S.H. CLARKE, AND C. HACKFORD. 1983. Chronology of black bear denning in the Catskill Region of New York. *International Conference on Bear Research and Management* 5:87–94.
- PELTON, M.R., L.E. BEEMAN, AND D.C. EAGAR. 1980. Den selection by black bears in the Great Smoky Mountains National Park. *International Conference on Bear Research and Management* 4:149–151.
- RODE, K.D., S.D. FARLEY, AND C.T. ROBBINS. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636–2646.
- SANDEGREN, F., AND J. SWENSON. 1997. Björnen — viltet, ekologin och människan. Svenska Jägareförbundet, Örebro, Sweden. (In Swedish.)
- SCHOEN, J.W., L.R. BEIER, J.W. LENTFER, AND L.J. JOHNSON. 1987. Denning ecology of brown bears on Admiralty and Chichagof Islands. *International Conference on Bear Research and Management* 7:293–304.
- SCHWARTZ, C.C., S.D. MILLER, AND A. CHRISTENSEN. 1987. Denning ecology of three black bear populations in Alaska. *International Conference on Bear Research and Management* 7:281–291.
- SPSS INC. 2003. SPSS for Windows® version 12.0. SPSS Inc., Chicago, Illinois, USA.
- SWENSON, J.E., T.M. HEGGBERGET, P. SANDSTRÖM, F. SANDEGREN, P. WABAKKEN, A. BJÄRVALL, A. SÖDERBERG, R. FRANZÉN, J.D.C. LINNELL, AND R. ANDERSEN. 1996. Brunbjörnens arealbruk i forhold til menneskelig aktivitet. En utredning foretatt i forbindelse med Forsvarets planer for Regionfelt Østlandet. Del 5. (Use of area by brown bears in relation to human activity. A study undertaken in connection with the proposal by the Department of Defense to establish a shooting range in south-eastern Norway. Part 5.) Oppdragsmelding 416. Norwegian Institute for Nature Research, Trondheim, Norway. (In Norwegian with English summary.)
- , F. SANDEGREN, S. BRUNBERG, AND P. WABAKKEN. 1997. Winter den abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildlife Biology* 3:35–38.
- . 2003. Implications of sexually selected infanticide for hunting of large carnivores. Pages 171–189 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife management*. Island Press, Washington, DC, USA.
- , M. ADAMIĆ, AND D. HUBER. 2007. Brown bear body mass and growth in northern and southern Europe. *Oecologia* 153:37–47.
- VAN DAELE, L.J., V.G. BARNES, AND R.B. SMITH. 1990. Denning characteristics of brown bears on Kodiak Island, Alaska. *International Conference on Bear Research and Management* 8:257–267.

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PAPER III

Does Despotic Behavior or Food Search explain the Occurrence of Problem Brown Bears in Europe?

RH: Elfström et al. • Bears near Settlements: searching Food or Safety?

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KEY WORDS interference competition, naivety, predation, safety, supplemental feeding

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ABSTRACT Bears are usually considered to approach settlements in search of food, but this paradigm ignores interactions among bears. We analyzed the age distribution and body condition index (BCI) of shot brown bears in relation to densities of bears and people, and whether the shot bears were killed by managers ('problem' bears) ($n=149$), in self defense ($n=51$), or hunter-killed nonproblem bears ($n=1,896$), between 1990 and 2010. We compared patterns between Slovenia and Sweden, i.e. areas with and without supplemental feeding of bears, respectively, based on two hypotheses. The food-search/food-competition hypothesis (I) predicted that problem bears would have a higher BCI (e.g. exploiting easily accessible and/or nutritious human-derived foods) or lower BCI (e.g. because of food shortage) than nonproblem bears, a positive correlation between BCI and human density, and a negative correlation between problem bear occurrence and seasonal mean BCI (i.e. more problem bears during years of food failure). Food competition among bears predicts an inverse relationship between BCI and bear density. The safety-search /naivety hypothesis (II) (i.e. avoiding other bears or lack of human experience) predicted no difference between BCI for problem/nonproblem bears, no relation with human density, and no relation between problem bear occurrence and seasonal mean BCI. If food-competition or predation avoidance explained bear occurrence near settlements, we predicted younger problem than nonproblem bears, and a negative correlation between age and human density. However, if only food-search explained bear occurrence near settlements, we predicted no relation between age and problem/nonproblem bear status, or between age and human density. We found no difference in BCI or its variation between problem and nonproblem bears, no relation between BCI and human density, and no correlation between numbers of problem bears shot and seasonal mean BCI for either country. The peak of shot problem bears occurred from April to June in Slovenia and in June in Sweden, i.e. during the mating period when most intraspecific predation occurs and before hyperphagia during fall. Problem bears were younger than

nonproblem bears and both problem and nonproblem bears were younger in areas with higher human density. These age differences, in combination with similarities in BCI between problem and nonproblem bears and lack of correlation between BCI and human density, suggest safety-search and naïve dispersal to be the primary mechanisms behind bear occurrence near settlements. Younger bears are less competitive, more vulnerable to predation, and lack human experience, compared to adults. Other mechanisms may operate if extreme food shortages occur. BCI was inversely related to the bear density index in Sweden, whereas no correlation was found in Slovenia, suggesting that supplemental feeding may reduce food competition, in combination with high bear harvest rates. Bears shot in self defense were older and their BCI did not differ from that of nonproblem bears. Reasons other than food shortage apparently explain why most bears are involved in encounters with people or viewed as problematic near settlements.

KEY WORDS interference competition, naivety, predation, safety, supplemental feeding.

Populations of large carnivores have increased in numbers and geographical range in many areas around the world, because of conservation-based management (Linnell et al. 2001, Enserink and Vogel 2006). This increase has occurred even in areas with high human densities in Europe where effective management for conservation has been applied (Linnell et al. 2001). However, the occurrence of large carnivores near human settlements is often viewed as problematic, because they can cause damage to property and people fear them (Røskoft et al. 2003).

Bears (*Ursidae*) may approach human settlements in search of food, which can result in food-conditioning, i.e. learning to associate people or settlements with easily accessible and/or attractive foods (McCullough 1982, Gunther et al. 2004, Rogers 2011). In support of this, several studies report a negative correlation between occurrence of bears close to people or settlements and food availability in remote areas (Rogers 1987, Garshelis

1989, Mattson et al. 1992, Schwartz et al. 2006). This paradigm, that bears come close to settlements primarily to obtain food, is commonly accepted and thought to be the major reason why bears approach people (McCullough 1982, Herrero et al. 2005). To reduce the number of bears close to people and settlements, managers often secure anthropogenic foods, drive bears away, or remove them by translocation or ultimately by destruction (Beckmann et al. 2004, Spencer et al. 2007).

Although bears generally avoid human activity and settlements (Mace and Waller 1996, Nellemann et al. 2007), some animals do occur close to people or settlements, even when food sources are secured (McCullough 1982). Such individuals are often considered to exhibit an 'unnatural' behavior. Subadult bears are more often involved in bear-human incidents than adults (McLellan et al. 1999, Pease and Mattson 1999, Schwartz et al. 2006), and subadults and females with cubs generally occur near people more often than adult males and lone adult females (Nevin and Gilbert 2005, Rode et al. 2006, Steyaert et al. 2013).

Dominant bears may use more remote areas and, therefore, predation-vulnerable conspecifics may select habitats closer to people to avoid being killed by other bears, i.e. the habitat use among bears may be influenced by a despotic distribution (Elfström et al. 2013, Steyaert et al. 2013). Spatial or temporal segregation occurs among sex, age, and reproductive classes of bears (Mattson et al. 1987, Wielgus and Bunnell 1994, Ben-David et al. 2004, Steyaert et al. 2013) and social hierarchies occur at aggregation sites for feeding (Craighead et al. 1995). Because older bears kill younger conspecifics (McLellan 1994, Swenson et al. 2001a), subadults and females with dependent offspring are most vulnerable (Mattson 1990, Swenson et al. 2001a, McLellan 2005). Females with young of the year come closer to settlements than solitary adult females and adult males (Steyaert et al. 2013). Alternatively, dispersing subadult bears may approach people and settlements, because they are naïve, lacking experience with humans, compared to older conspecifics (McLellan et al.

1999, Kaczensky et al. 2006). Dispersal from natal areas probably occurs to avoid encounters with resident conspecifics (Støen et al. 2006) and inbreeding (Zedrosser et al. 2007).

The objective of this study was to test two hypotheses, food-search/food-competition and safety-search/naivety, to determine the mechanisms underlying the phenomenon of brown bear (*Ursus arctos*) occurrence near settlements, using data from Slovenia and Sweden. These two countries have different management regimes regarding supplemental feeding, bait hunting, and selectivity among harvested animals (Bischof et al. 2008, Krofel et al. 2012). We analyzed the abundance, location, age distribution, and body condition of removed “problem” bears and bears killed during regular hunting (referred to as nonproblem bears), in relation to densities of bears and people. Problem bears were killed by managers, because they were involved in incidents with people in or near settlements. We also analyzed the age class and body condition of Swedish bears shot in self defense during hunting.

The food-search/food-competition hypothesis predicts a different, either higher or lower, body condition in problem bears compared to nonproblem bears. A high body condition in problem bears near people may be caused by exploitation of easily accessible and highly nutritious foods, e.g. garbage (Hobson et al. 2000, Robbins et al. 2004), in combination with a reduced intraspecific food competition in areas with increased concentration of settlements. A low body condition in problem bears near people may be caused by failure to find food in remote areas in combination with high food competition among bears (Mattson et al. 1992, Schwartz et al. 2006). Predictability (i.e. reduced variation) of food availability may be higher among problem than nonproblem bears, if for instance problem bears exploit crops or other human-derived foods regularly supplied by people. Food competition among bears predicts an inverse relationship between body condition and bear density. If problem bears are primarily searching for food, more problem bears should be shot during years with lower remote food availability (Mattson et al. 1992,

Schwartz et al. 2006), and during times of the year with lower remote food availability (i.e. early spring after den emergence, or the hyperphagia period in fall if mast availability is poor) (Gunther et al. 2004). We expect the age distribution to be equal between problem and nonproblem bears if bears primarily search for food near settlements. However, if interference competition for food occurs among bears, food shortage may affect smaller, less competitive, bears more severely, because larger conspecifics dominate habitats with higher food quality (Craighead et al. 1995, Schwartz et al. 2006). Thus, intraspecific food competition predicts younger problem than nonproblem bears, and that nonproblem bears are younger in areas with a higher human density. Alternatively, due to decreasing foraging efficiency with increasing body size (Welch et al. 1997, Rode et al. 2001, Robbins et al. 2004), problem bears could be older than nonproblem bears, and nonproblem bears shot in areas with a higher human density would be older.

The safety-search/naivety hypothesis predicts no difference in body condition, nor its variation, between problem and nonproblem bears. We expect no correlation between problem bear occurrence and general food availability if avoidance of predation is more important than food competition. The occurrence of problem bears is expected to be higher during the breeding season, when more aggression is shown towards subadults (Swenson et al. 2001b), which also overlaps with the time of natal dispersal (Støen et al. 2006). The breeding season occurs from May to July in northern Europe (Dahle and Swenson 2003a), and from April to June in southern Europe (Krofel et al. 2010). A despotic distribution predicts that more young than adult bears would be shot as problem animals and that bears are younger in areas with higher human densities, because older bears avoid humans (Nellemann et al. 2007, Elfström et al. 2013).

Only if bears shot in self defense have experienced food shortage or nutritional disorders, would we expect them to have a lower body condition compared to nonproblem

bears. Younger bears are more likely than older individuals to leave their diurnal resting sites when approached by people (Moen et al. 2012). Therefore, we expect that, independently of body condition, bears shot in self defense would be older than nonproblem bears.

STUDY AREAS

Slovenian brown bears occurred mainly in and near the Dinaric Mountains, and represent the northwestern part of the Alpine-Dinaric-Pindos population (Zedrosser et al. 2001). The highest densities of Slovenian bears occurred inside a protected area within the Dinaric Range, established in 1966, and characterized by low human densities (Kryštufek and Griffiths 2003, Jerina et al. 2013). Skrbinšek et al. (2008) estimated a population size of 394-475 brown bears in Slovenia in 2007. The Swedish brown bear population size was estimated at 2970-3670 animals in 2008, distributed over the northern two-thirds of the country (Kindberg et al. 2009, Kindberg et al. 2011). Human density in the bear range was low, although more populated areas occurred at the edge of the bear distribution along the eastern coast (Kindberg et al. 2011). Body masses of bears were similar between Slovenia and Sweden, but they showed different patterns and trends between seasons (Swenson et al. 2007). Swedish bears were characterized by a greater body mass variation from fall to spring, probably because of a longer denning period of 6.9-7.5 months, compared to 2.9 months in southern Europe (Huber and Roth 1997, Manchi and Swenson 2005, Swenson et al. 2007). Slovenian bears loose body mass in spring, whereas Swedish bears gain in weight, perhaps because of higher use of protein-rich diet of meat and insects during spring in Sweden compared to Slovenia (Swenson et al. 2007).

METHODS

Hunting of Bears and Supplemental Feeding

In Slovenia, bears have access to supplemental food throughout the year. Supplemental feeding sites are not allowed within 2 km of human settlements, have a density of one every

400-700 ha, and all hunting occurs only from elevated stands, usually at feeding sites (Jerina 2012, Krofel et al. 2012). The Slovenian brown bear hunting season is between 1 October and 30 April, and the hunting quota is prescribed based on 3 body mass categories; <100 kg (minimum of 75 % of quota), 100-150 kg (maximum 15 % of quota), and >150 kg (maximum 10 % of quota) (Krofel et al. 2012). Hunting of bears in Slovenia has increased significantly during the last 10 years, because of an increasing trend in bear damages (Jerina and Adamič 2008), with an annual harvest rate during 1998-2008 of 20 % (Krofel et al. 2012). In Sweden, the bear harvest rate has shown a 3-fold increase during the last 10 years (Bischof et al. 2009a), and the quota was 322 animals in 2010, corresponding to a harvest rate of ca. 10 %. In Sweden, hunting bears at bait sites and supplemental or diversionary feeding is illegal. The hunting season is between 21 August and 31 October. Females with offspring are protected in both Slovenia and Sweden. Dependent young may be harvested in Slovenia, but not in Sweden.

The bear harvest in Slovenia is biased towards males and subadults (49% of hunter-killed bears are males <4 years old), in part due to harvest regulations (Krofel et al. 2012). However, in Sweden no hunter selectivity, in terms of sex and age distribution, seems to occur (Bischof et al. 2008, Bischof et al. 2009a). The protection of females with cubs from hunting in both countries may underestimate their occurrence when analyzing shot bears. Managers also may be more reluctant to kill problem females with offspring than solitary adult females (e.g. because of human safety and risks of orphaning cubs). This suggests that data on shot problem bears may underestimate the occurrence of females near settlements. Therefore, our data set is not suitable for explicitly testing differences in sex, or female reproductive status, between problem and nonproblem bears.

Data Collection

Two requirements had to be fulfilled for a bear to be considered a "problem" bear: 1) it had caused enough problems or incidents with people inside or in the immediate vicinity of settlement(s) to be reported to the authorities, and 2) it had to be killed because of being considered a problem bear by managers. Bears reported to be shot in self defense during hunting mostly other game species than bears were considered to be a separate category, and data were only available for Sweden.

Body measurements of killed bears were taken by managers from the Slovenia Forest Service in Slovenia and the Administrative County Boards in Sweden. We included 1,011 bears (134 problem bears, 877 nonproblem bears) killed during 1996-2010 in Slovenia, and 1,087 bears (15 problem bears, 1,021 nonproblem bears, and 51 bears shot in self defense) killed during 1990-2008 in Sweden. Data for shot bears were provided by the Slovenia Forest Service and the Swedish National Veterinary Institute, and included date of killing, coordinates, body mass, sex, front paw width, and the reason for the kill permit regarding problem bears. In Sweden, human densities were provided by Statistics Sweden (SCB), and the bear density indices by the Swedish Association for Hunting and Wildlife Management. In Slovenia, human and bear densities were provided by the Biotechnical Faculty, Department for Forestry at University of Ljubljana in Slovenia. Cubs-of-the-year were excluded from our study, because of their dependency on the mother. Age was determined using cementum annuli of an upper premolar of shot bears (Matson et al. 1993).

Densities of Humans and Bears

We used ArcView 3.2 and 9.3 (Environmental Systems Research Institute, Inc., Redlands, California) to extract densities of humans and bears. Human population densities were extracted within a 10 km-radius around the kill position for every bear in Sweden and Slovenia. Population density of Swedish bears was calculated as an index based on effort-

corrected annual observations by hunters averaged over a 3-year period and reported at the level of local management units (LMU) (Kindberg et al. 2009). The mean \pm SD size of LMUs where bears were shot was $2,208 \pm 1,576 \text{ km}^2$, which corresponds to the upper range of home range sizes in Swedish bears (Dahle and Swenson 2003b). Swedish bear population density indices were available for 590 bears shot between 1998 and 2006 (495 bears shot outside this period were excluded from analyses that included bear densities). Slovenian bear densities were estimated by combining four types of data: telemetry data from 33 GPS-equipped bears, 1,057 genetic samples derived from collection of feces during 2007, observations made from 165 counting sites during 2003-2010, and locations of killed bears during 1998-2010 (Jerina et al. 2013). Number of bears was extracted using an area of 120 km^2 around where bears were shot. This corresponds to the mean home range size of female bears in Slovenia (Jerina et al. 2012).

Body Condition Index (BCI)

Body condition indices (BCI) are commonly used by wildlife researchers when comparing productivity, diet, or habitat quality (Robbins et al. 2004). BCI of bears was calculated according to equation 1, where n is number of shot bears, e_{st} is standardized residual, BM is body mass (kg), PW is front paw width (cm), and d is Julian date:

$$BCI = e_{st} \sum_{i=1}^n \left(\frac{BM}{PW} \sim d \right) \quad (1).$$

We extracted standardized residuals separately for subadults and adults, because resource allocation may differ between age classes. The age of sexual maturity and of first litters in Slovenia is 4 years (Švigelj, 1961 cited in (Jerina et al. 2003)). In central Sweden, the mean age of primiparity is 4.7 years (Zedrosser et al. 2009). Therefore, we defined bears <4 years of age as subadults and bears ≥ 4 years of age as adults. We also extracted residuals separately for season (spring-summer and fall-winter) and country. Spring-summer was

defined as 1 March-15 July, i.e. starting with the onset of spring hunting season in Slovenia (Krofel et al. 2012), although Swedish bears have not yet emerged from their winter dens (Friebe et al. 2001, Manchi and Swenson 2005), and ending with the termination of the mating season in both Slovenia (Krofel et al. 2010) and Sweden (Dahle and Swenson 2003a). Fall-winter was defined as 1 August-15 February, i.e. starting after the onset of the hyperphagia period, and ending before den emergence in Sweden (Friebe et al. 2001, Manchi and Swenson 2005) and 2 weeks before start of the hunting season in Slovenia (Krofel et al. 2012). Few nonproblem bears were available during the spring in Sweden, because the hunting period only occurs during the fall. Therefore, we included body measurements from 507 nonproblem individual bears immobilized during April or May (between 1990 and 2008 by the Scandinavian Brown Bear Research Project (SBBRP), see Arnemo et al. (2011) for details on capture and handling), when calculating BCI for Swedish problem bears shot during spring. We used the front paw width as a body size estimate, because it is likely not influenced by interannual fluctuations in body mass and, thus, represents the true body size. Others have used body length as a measure of body size when calculating body condition index (Cattet et al. 2002, Oi et al. 2009, McLellan 2011). Bischof et al. (2009b) compared body size measurements taken by the SBBRP and showed that front paw width was a good predictor (and ranked higher than total body length) for overall size in bears. A high BCI in shot bears indicates high nutritional status and a low BCI indicates a low nutritional status. To verify if the BCI reflects body condition, we compared the ratio between body mass and paw width obtained from captured adult bears in Sweden with their proportional body fat content as obtained by bioelectrical impedance analysis (Farley and Robbins 1994).

Comparing Age Distribution and Body Condition among Bears

We constructed linear mixed models (LMM) to explain the variation in log-transformed age using the following fixed factors: sex, bear status (problem, nonproblem, or shot in self

defense), density of bears, density of people, and country. Year killed was included as a random effect. We analyzed the variation in log-transformed body mass/paw width with a LMM and the proportion of fat as a log-transformed fixed factor to compare body condition indices of captured bears. We included year as a random effect in this analysis. We analyzed the variation in BCI by using LMM with the following fixed factors: sex, age, bear status (problem, nonproblem, or shot in self defense), density index of bears, density of people, and country. Year killed was included as a random effect. We included interaction terms between country and densities of people and bears, between bear status and density of people, and between sex and age. The bear density index was standardized, and was only included as an interaction with country, because it was calculated differently between countries.

Predictability of food resources, expressed as variation in BCI, was compared between problem and nonproblem bears. A random subsample of nonproblem bears was used; generating equal numbers of problem and nonproblem bears, and the variation was calculated as absolute values of BCI subtracted by mean BCI. Variation in BCI between problem bears and nonproblem bears was tested using LMM, with a square-root transformed response, with bear status (problem or nonproblem) as a fixed factor, and included year killed as a random effect.

Number of Problem Bears and Seasonal Body Condition

We used generalized linear models (GLM) to test if annual numbers of shot problem bears could be explained by a seasonal mean BCI. Only nonproblem bears were used to calculate the mean BCI for a specific period, with residuals extracted separately for adults/subadults and country. We used four alternative periods to calculate seasonal mean BCI in relation to numbers of killed problem bears. Seasonal mean BCI was used as a fixed factor extracted for the fall-winter previous year, fall-winter same year, fall-winter previous year combined with spring-summer same year, and spring-summer combined with fall-winter same year, to test

for any delayed response in problem bear occurrence and food availability. We estimated annual bear population sizes during the period when problem bears were killed, based on methods and data used by Krofel et al. (2012) and Jerina et al. (2013) for the Slovenian bear population and by Kindberg and Swenson (2006;2010), and Kindberg et al. (2011) for the Swedish bear population. The annual population size estimates were used as a fixed factor to control for increasing bear populations in relation to annual numbers of killed problem bears.

Model Selection and Validation

All candidate models were constructed *a priori* to the model selection procedure. We evaluated the most parsimonious LMM to explain age distribution and BCI of killed bears based on Akaike's Information Criteria scores for small sample sizes (AIC_c) and AIC_c weights (AIC_{cw}) (Akaike 1973, Burnham and Anderson 2002). Number of problem bears in relation to seasonal mean BCI was analyzed assuming a Poisson distribution, and we controlled for potential overdispersion in our GLMs by using quasi-likelihood theory for AIC model selection (qAIC_c) (Richards 2008). All analyses were made in R.2.14.1 (R Development Core Team 2011). We used the package 'lme4' (Bates and Maechler 2010) for statistical modeling and generated β and its 95 % highest posterior density interval (HPD) for the fixed effects of the regression models with a Markov Chain Monte Carlo (MCMC) algorithm using 1,000 simulations, using the package 'LMERConvenienceFunctions' (Tremblay 2011). Effects were considered significant when the HPD 95 % around β did not include 0. Graphs of separate effects with 95 % confidence intervals for fixed factors were generated using the package 'effects'. Outliers were controlled for by using Cleveland dotplots, and multicollinearity by using variance inflation factors (Zuur et al. 2009).

RESULTS

Comparing Different Body Condition Indices

The ratio between body mass and paw width was positively related with the proportion of fat in the same bear with $\beta=0.31 \pm 0.11$ SE, based on measurements from 61 bears (this relationship was ranked as more parsimonious than an intercept model; $\Delta AIC_c=0.00$, $AIC_{cw}=0.67$) (Appendices 1 and 2 available online at www.onlinelibrary.wiley.com).

Descriptive Densities of Humans and Bears

Median (1st and 3rd quartiles) density of people in Slovenia was 40,000 (22,000-53,000) inhabitants per 1,000 km² where 877 nonproblem bears were shot, and 41,500 (33,250-51,750) inhabitants where 134 problem bears were shot, during 1996-2010. Median (1st and 3rd quartiles) density of people in Sweden was 12,400 (3,600-46,150) inhabitants per 1,000 km² where 1,019 nonproblem bears were shot, 183,800 (59,450-804,600) inhabitants where 15 problem bears were shot, and 13,700 (4,150-49,750) inhabitants where 51 bears were shot in self defense during 1990-2008.

Median (1st and 3rd quartiles) density of bears in Slovenia was 110 (67-156) bears per 1,000 km² where 726 nonproblem bears were shot and 123 (105-139) bears per 1,000 km² where 117 problem bears were shot during 1996-2010. Median (1st and 3rd quartiles) density index of bears in Sweden was 0.70 (0.40-1.12) bears per 1,000 observation hours where 553 nonproblem bears were shot, 0.85 (0.69-1.39) bears per 1,000 observation hours where 7 problem bears were shot, and 0.68 (0.43-1.38) bears per 1,000 observation hours where 30 bears were shot in self defense during 1998-2006.

Age Distribution of Problem/Nonproblem Bears

In Slovenia, the median (1st and 3rd quartiles) age was 2 (2-4) years for 877 hunter-killed nonproblem bears and 2 (1-3) years for 134 shot problem bears during 1996-2010. In Sweden, the median (1st and 3rd quartiles) age was 3 (2-7) years for 1,021 hunter-killed

nonproblem bears, 3 (2-10) years for 15 shot problem bears, and 7 (4-12) years for 51 bears shot in self defense during 1994-2008.

Bear status (i.e. problem, nonproblem, shot in self defense) and human density were included in the most parsimonious LMM to explain the age distribution among Slovenian and Swedish bears ($\Delta AIC_c=0.00$, $AIC_{cw}=0.94$, Appendix 3 available online at www.onlinelibrary.wiley.com). Bear density was not included in the most parsimonious LMM; the highest ranked model that included bear density had $\Delta AIC_c=12.82$, $AIC_{cw}<0.00$ (Appendix 3 available online at www.onlinelibrary.wiley.com). Therefore, we excluded the bear density index parameter and reran our candidate model set, thus increasing our sample size by 495 bears. Bear status and human density were again included in the most parsimonious LMM ($\Delta AIC_c=0.00$, $AIC_{cw}=0.98$, Table 1). Problem bears were 1.6 ± 1.2 (SE) years younger than nonproblem bears (log-transformed: $\beta=-0.198 \pm 0.071$ SE). Younger nonproblem and problem bears were shot more often than expected in areas with higher human densities in both Slovenia (log-transformed: $\beta=-0.125 \pm 0.016$ SE) and Sweden (log-transformed: $\beta=-0.027 \pm 0.010$ SE) (Table 2, Fig. 1). Bears shot in self defense in Sweden were 4.2 ± 1.3 (SE) years older than nonproblem bears (log-transformed: $\beta=0.619 \pm 0.116$ SE, Table 2).

Body Condition of Problem/Nonproblem Bears

Bear status (i.e. problem, nonproblem, shot in self defense) and human density were not included among the LMMs with highest support when analyzing BCI among Slovenian and Swedish bears; the highest ranked LMM including bear status or human density had $\Delta AIC_c=5.14$, $AIC_{cw}=0.05$, i.e. an evidence ratio 12.8 times less likely than the most parsimonious LMM (Table 3). Bear density was included in one of the two LMMs with highest support ($\Delta AIC_c=0.00$, $AIC_{cw}=0.64$, Table 3). BCI decreased with increasing bear density in Sweden with $\beta=-0.150 \pm 0.038$ (SE) kg/cm, whereas BCI among Slovenian bears

was not related with bear density ($\beta/\text{SE} < 0.5$, and HPD 95% interval of β included 0) (Table 4, Fig. 2).

Problem bear occurrence and seasonal body condition

The dates when problem bears were killed in Slovenia were distributed bimodally, with the first (considerably higher) peak during late spring-early summer (modus: June, with median (1st and 3rd quartiles) in 26 May (20 April-20 June), $n=75$) and the second peak during late autumn (modus: October, with median in 10 October (5 September-3 November), $n=59$). The distribution of dates when problem bears were killed in Sweden ($n=15$) was unimodal with modus: June and median (1st and 3rd quartiles) in 15 June (29 May-28 August). The median (1st and 3rd quartiles) dates when 51 Swedish bears were shot in self defense was 17 September (2 August-25 October).

The number of problem bears killed annually was not related with seasonal mean BCI in either Slovenia (1999-2010) or Sweden (1997-2008) using any of our four alternative periods (entire same year, same fall, previous fall, and previous fall combined with same spring), nor with annual population size, because our intercept model was ranked as most parsimonious ($\Delta\text{qAIC}_c=0.00$, $\text{qAIC}_c w=0.98$, Table 5). Variation in BCI (i.e. predictability of food resources) was not different between problem and nonproblem bears, because our intercept LMM was ranked as most parsimonious ($\Delta\text{AIC}_c=0.00$, $\text{AIC}_c w=0.97$, Table 6).

DISCUSSION

We found age differences between problem and nonproblem bears in both Slovenia and Sweden. Problem bears were 1.6 years ± 1.2 (SE) younger than nonproblem bears in both countries combined. In general, bears killed in areas with higher human density were younger, suggesting that younger bears have a higher likelihood of occurring closer to settlements than older conspecifics. The Slovenian hunting quotas prescribe lower body weight and more males than females (because females with offspring are protected), and, as a

consequence, more young and male bears are killed by hunters (49 % of hunting quota is <4-year-old males) (Krofel et al. 2012). This suggests that the true age difference between problem bears and the (nonproblem) standing population in Slovenia was larger than reported here and by Krofel et al. (2012). Several studies have reported a similar pattern, with younger bears closer to settlements or people than older conspecifics, in both North America (Dau 1989, Mattson et al. 1992, McLellan et al. 1999, Pease and Mattson 1999, Schwartz et al. 2006) and Europe (Kaczensky et al. 2006, Nellemann et al. 2007). If larger bears sought out settlements, because of their higher nutrient requirements due to larger body size (Robbins et al. 2004), we would have expected this age difference to be the opposite, with older (larger) bears shot in more populated areas. Therefore, food competition, in combination with predation avoidance, could explain the higher occurrence of young bears in areas with a higher human density (Elfström et al. 2013). Alternatively, younger bears may occur closer to settlements, because they are more naïve than older conspecifics (McLellan et al. 1999, Kaczensky et al. 2006). Naivety in young animals is expected to be more pronounced during dispersal and exploratory movements, and is typically triggered by avoiding resident conspecifics (i.e. a despotic distribution) (Støen et al. 2006, Zedrosser et al. 2007, Elfström et al. 2013).

In bear populations expanding towards areas with higher human densities, young dispersing individuals are expected to be more common in the expansion front than older animals (Swenson et al. 1998, Kojola et al. 2003, Jerina and Adamič 2008). Both the Slovenian and Swedish bear populations have increased in size and distribution during the study period (Kindberg et al. 2011, Krofel et al. 2012). However, the nonproblem bears we analyzed were not necessarily shot in or near any potential expansion fronts in either Slovenia or Sweden. Mortality from bear hunting may be higher in areas with higher bear densities in Sweden, because of increased hunting efforts and higher likelihood of encountering bears

where bear density is high. However, in Slovenia relative mortality rates have been reported to be higher in areas with lower bear density (Jerina et al. 2013), suggesting that bears may have lower survival probability in areas with higher human density. Thus, our reported age differences in relation to settlements in Slovenia could be due to lower survival in more populated areas (Mattson et al. 1992, Mueller et al. 2004). Therefore, we recommend documenting mortality rates due to bear hunting in relation to distance from settlements or human density, in order to separate the effects of human-induced mortality and adult avoidance of settlements on the observed spatial pattern of age distribution. Harvest rate, and sex and age composition of harvested bears may also change in relation to natural food availability (Noyce and Garshelis 1997).

Young bears have been considered or suggested to become food-conditioned or human habituated by acquiring their mother's behavior (Gilbert 1989, Pease and Mattson 1999) and, thus, the occurrence of mostly young bears near settlements could be explained by learned food-conditioning and not avoiding dominant conspecifics. However, social transmission from mother to offspring does not explain why the females with offspring occur more often near settlements than adult males (Steyaert et al. 2013), if a despotic distribution is not considered (Elfström et al. 2013).

Reports of bears utilizing garbage and other human-derived foods close to settlements (Gunther et al. 2004, Greenleaf et al. 2009, Hopkins et al. 2012) suggest that these food items are attractive and that bears may approach settlements in search of food. However, we found no differences in BCI between problem and nonproblem bears, which supports the safety-search/naivety hypothesis. Yamanaka et al. (2009) and Oi et al. (2009) also found no correlation between body condition and numbers of 'problem' Asiatic black bears (*Ursus thibetanus*) killed annually in Japan. The food-search/food-competition hypothesis predicts either an increased BCI in problem bears (e.g. utilizing high-nutritive and/or large amounts of

human-derived foods) or decreased BCI in problem bears (e.g. experiencing food shortage in remote areas in combination with food competition) compared to nonproblem bears. Bears' habitat quality in terms of food seemed not to be related with human density in either Slovenia or Sweden, because we found no relationship between human density and BCI among problem and nonproblem bears, supporting the safety-search/naivety hypothesis.

An alternative explanation for the lack of difference in BCI between problem and nonproblem bears may be that even well-nourished bears may experience hunger, as suggested by Yamanaka et al. (2009), and thus approach people. However, we would expect well-nourished bears to experience hunger less frequently than malnourished individuals and thus a generally lower BCI in problem than nonproblem bears. In addition, bears commonly avoid human activity and settlements (Mace and Waller 1996, Nellemann et al. 2007), perhaps because of human disturbance (Martin et al. 2010, Ordiz et al. 2011). Therefore, bears occurring near settlements must gain benefits which mitigate these costs. Thus, if bears primarily approach settlements because of hunger, this should be reflected by a difference in the BCI between problem and nonproblem bears and/or by a relation between BCI and human density. We also cannot rule out the possibility that some individual problem bears utilized human derived foods near settlements, but were shot before they had gained in body mass (i.e. increased in BCI). However, this does not explain the general lack of correlation between BCI and human density, because not all nonproblem bears would have been killed this early.

The ratio body mass/paw width was positively related with the proportion of fat in the same bear; thus our BCI seems to reflect variation in body condition. In Scandinavia, body condition measures fluctuate annually and are related to bear life history parameters; the probability of cub loss in primiparous females and size of female bears are negatively related

with an annual index of food condition (based on yearling body mass) (Zedrosser et al. 2006, Zedrosser et al. 2009).

BCI was negatively related to the bear density index among Swedish bears, suggesting competition among bears for food. Zedrosser et al. (2006) documented that size of female Scandinavian brown bears is positively related to food conditions and negatively related to bear density, which also suggests that food competition among bears where food resources are relatively evenly distributed, i.e. when foraging on berries. Another explanation for the negative relation between BCI and bear density index among Swedish bears could be higher natural food availability in areas with lower bear density, because bear density is generally lower closer to settlements (Nellemann et al. 2007). Thus, although we found no relation between BCI and human density, natural food availability could still be higher near settlements, which are located in more productive areas. However, effects from human disturbance (Martin et al. 2010, Ordiz et al. 2011) will probably constrain improvements in body condition. We found no relation between BCI and bear density among Slovenian bears, however, perhaps because the use of supplemental feeding in Slovenia reduces food competition, in combination with high (20 %) harvest rate of the bears (Krofel et al. 2012). Supplemental feeding may reduce seasonal variation in natural food availability. In Slovenia, the practice of supplemental feeding has been shown to decrease the home range size in red deer, *Cervus elaphus* (Jerina 2012). Alternatively, a despotic distribution may be amplified if dominant bears limit the access of predation-vulnerable conspecifics to these feeding sites and, if so, would explain why problem bears are younger than nonproblem bears, and why more problem bears are shot in Slovenia than Sweden. However, comparisons between countries must be viewed cautiously, because of different ecological conditions, public tolerance of bears, as well as management policies. The much higher human and bear densities in Slovenia than Sweden could also explain why more problem bears are shot in

Slovenia than Sweden. Another explanation for not finding any relationship between BCI and bear density in Slovenia, in contrast to in Sweden, may be the different methods and areas used.

Studies reporting a negative correlation between abundance of naturally occurring bear food and occurrence of bears damaging human property (Garshelis 1989, Mattson et al. 1992, Oka et al. 2004, Schwartz et al. 2006) suggest that food shortage causes bears to search for food close to settlements. However, we found no relation between problem bear occurrences and seasonal mean BCI in our study, which suggests that bears in general were not experiencing acute food shortage in either Slovenia or Sweden during our study period. Thus, our study period probably best elucidates factors behind the occurrence of bears near settlements during periods of “normal” food availability. However, food shortages may be more common in other areas. If extraordinary failures in food production would occur (Mattson et al. 1992, Oka et al. 2004), it is plausible that more bears would approach settlements in search of food.

Most problem bears were shot during the mating season, the period when most aggressive encounters among bears occur, although a smaller peak of shot problem bears also occurred during fall in Slovenia. Albert and Bowyer (1991) also reported a peak in bear occurrence near people during spring, whereas Gunther et al. (2004) reported that bear problems peaked later in the year, during the hyperphagic fall. We found no support for different variation in BCI (i.e. predictability of food availability or quality) between problem and nonproblem bears. This suggests that reasons other than food-search or food competition might explain why some bears approach settlements, independently of food availability and predictability. Our reported age difference in relation to settlements and lack of difference in BCI between problem and nonproblem bears indicate safety-search and naïve dispersal to be the primary mechanisms behind bear occurrence near settlements.

Bears shot in self defense were 4.2 ± 1.3 (SE) years older than nonproblem bears, probably because these incidents mostly occurred during hunting away from settlements, and older bears more often remain in their daybed when approached by people, whereas younger bears are more likely to leave the area (Moen et al. 2012). As expected, bears shot in self defense did not deviate in BCI from hunter-killed nonproblem bears, suggesting reasons other than food shortage to explain why some bears are involved in encounters with people. Most situations where bears were shot in self defense may have involved sudden, unexpected, encounters between hunters and bears, which the hunter interpreted as threatening. Shooting of bears in self defense may be more common in areas where hunters lack experience with them, and it is also possible that these shootings had been preceded by provocation of the bears by hunters' dogs (Kojola and Heikkinen 2012).

MANAGEMENT IMPLICATIONS

We did not find support for the hypothesis that bears approach settlements in search of food in either Slovenia or Sweden during years with no acute food failure and, thus, managers in these countries must also consider other factors than food to explain bear occurrence near settlements. The age difference among hunted bears in relation to human density, younger problem than nonproblem bears, lack of differences in BCI between problem and nonproblem bears and in relation to human density, and no correlation between problem bear occurrence and seasonal mean BCI, all support the safety-search/naivety hypothesis. We conclude that younger bears occur closer to settlements as a result of dispersal and to avoid intraspecific predation or aggression, rather than because of food search or food competition. However, other mechanisms may operate if food failures occur. The BCI of Swedish bears was negatively related to bear density indices, with no supplemental feeding, whereas no correlation was found among Slovenian bear densities, where feeding is a common practice.

This suggests that supplementary feeding, in combination with high harvest rate, may reduce potential competition for food among bears.

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LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. B. Petrov, and F. Caski, eds. Proceeding of the Second International Symposium on Information Theory:267-281.
- Albert, D. M., and R. T. Bowyer. 1991. Factors related to grizzly bear-human interactions in Denali National Park. *Wildlife Society Bulletin* 19:339-349.
- Arnemo, J. M., A. Evans, Å. Fahlman, P. Ahlqvist, H. Andrén, S. Brunberg, O. Liberg, J. D. C. Linnell, J. Odden, P. Persson, H. Sand, P. Segerström, K. Sköld, T. H. Strømseth, O.-G. Støen, J. E. Swenson, and P. Wabakken. 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway:14.
- Bates, D. M., and M. Maechler. 2010. lme4: Linear mixed-effects models using Eigen and R syntax. package version 0.999375-37. <http://CRAN.R-project.org/package=lme4>:29.
- Beckmann, J. P., C. W. Lackey, and J. Berger. 2004. Evaluation of deterrent techniques and dogs to alter behavior of "nuisance" black bears. *Wildlife Society Bulletin* 32:1141-1146.

- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465-474.
- Bischof, R., R. Fujita, A. Zedrosser, A. Söderberg, and J. E. Swenson. 2008. Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. *Journal of Wildlife Management* 72:79-88.
- Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009a. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78:656-665.
- Bischof, R., A. Zedrosser, S. Brunberg, and J. E. Swenson. 2009b. A Note on Opportunism and Parsimony in Data Collection. *Journal of Wildlife Management* 73:1021-1024.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. New York, Springer-Verlag.
- Cattet, M. R. L., N. A. Caulkett, M. E. Obbard, and G. B. Stenhouse. 2002. A body-condition index for ursids. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80:1156-1161.
- Craighead, J. J., J. Sumner, and J. A. Mitchell. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959-1992. 517pp. Island Press, Washington D.C., USA.
- Dahle, B., and J. E. Swenson. 2003a. Family break-up in brown bears; are young forced to leave? *Journal of Mammalogy* 84:536-540.
- Dahle, B., and J. E. Swenson. 2003b. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* 260:329-335.

- Dau, C. P. 1989. Management and biology of brown bears at Cold Bay, Alaska. Bear–people conflicts: proceedings of a symposium on management strategies. Pages 19-26 in M Bromley, ed. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Elfström, M., A. Zedrosser, O.-G. Støen, and J. E. Swenson. 2013. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review* in press.
- Enserink, M., and G. Vogel. 2006. Wildlife conservation - The carnivore comeback. *Science* 314:746-749.
- Farley, S. D., and C. T. Robbins. 1994. Development of two methods to estimate body composition of bears. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 72:220-226.
- Friebe, A., J. E. Swenson, and F. Sandegren. 2001. Denning chronology of female brown bears in central Sweden. *Ursus* 12:37-45.
- Garshelis, D. L. 1989. Nuisance bear activity and management in Minnesota. Bear–people conflicts: proceedings of a symposium on management strategies. Pages 169-180 in M. Bromley, ed. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Gilbert, B. 1989. Behavioural plasticity and bear-human conflicts. Bear–people conflicts: proceedings of a symposium on management strategies. Pages 1-8 in M. Bromley, ed. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Greenleaf, S. S., S. M. Matthews, R. G. Wright, J. J. Beecham, and H. M. Leithead. 2009. Food habits of American black bears as a metric for direct management of human–

- bear conflict in Yosemite Valley, Yosemite National Park, California. *Ursus* 20:94-101.
- Gunther, K. A., M. A. Haroldson, K. Frey, S. L. Cain, J. Copeland, and C. C. Schwartz. 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992-2000. *Ursus* 15:10-22.
- Herrero, S., T. Smith, T. D. DeBruyn, K. Gunther, and C. A. Matt. 2005. From the field: brown bear habituation to people - safety, risks, and benefits. *Wildlife Society Bulletin* 33:362-373.
- Hobson, K. A., B. N. McLellan, and J. G. Woods. 2000. Using stable carbon ($\delta C-13$) and nitrogen ($\delta N-15$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78:1332-1339.
- Hopkins, J. B., P. L. Koch, C. C. Schwartz, J. M. Ferguson, S. S. Greenleaf, and S. T. Kalinowski. 2012. Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. *Journal of Wildlife Management* 76:703-713.
- Huber, D., and H. U. Roth. 1997. Denning of brown bears in Croatia. *Ursus* 9:79-83.
- Jerina, K., M. Debeljak, S. Džeroski, A. Kobler, and M. Adamič. 2003. Modeling the brown bear population in Slovenia - A tool in the conservation management of a threatened species. *Ecological Modelling* 170:453-469.
- Jerina, K., and M. Adamič. 2008. Fifty years of brown bear population expansion: effects of sex-biased dispersal on rate of expansion and population structure. *Journal of Mammalogy* 89:1491-1501.
- Jerina, K. 2012. Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. *Journal of Mammalogy* 93:1139-1148.

- Jerina, K., M. Krofel, M. Stergar, and U. Videmšek. 2012. Factors affecting brown bear habituation to humans: a GPS telemetry study. Final report—summary for users. University of Ljubljana, Biotechnical Faculty, Ljubljana.
- Jerina, K., M. Jonožovič, M. Krofel, and T. Skrbinšek. 2013. Range and local population densities of brown bear *Ursus arctos* in Slovenia. *European Journal of Wildlife Research* In press.
- Kaczensky, P., D. Huber, F. Knauer, H. Roth, A. Wagner, and J. Kusak. 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *Journal of Zoology* 269:474-485.
- Kindberg, J., and J. Swenson. 2006. Populationsberäkning av björnstammen i Sverige 2005 [Estimate of the bear population in Sweden in 2005] Report No. 2006-2 [In Swedish].
- Kindberg, J., G. Ericsson, and J. E. Swenson. 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. *Biological Conservation* 142:159-165.
- Kindberg, J., and J. Swenson. 2010. Skattning av björnstammens storlek i Sverige åren 1994 och 2000 [Estimate of the bear population in Sweden for the years 1994 and 2000] Report No. 2006-2 [In Swedish].
- Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear *Ursus arctos* population. *Wildlife Biology* 17:114-123.
- Kojola, I., P. I. Danilov, H.-M. Laitala, V. Belkin, and A. Yakimov. 2003. Brown bear population structure in core and periphery: analysis of hunting statistics from Russian Karelia and Finland. *Ursus* 14:17-20.

- Kojola, I., and S. Heikkinen. 2012. Problem brown bears *Ursus arctos* in Finland in relation to bear feeding for tourism purposes and the density of bears and humans. *Wildlife Biology* 18:258-263.
- Krofel, M., S. Filacorda, and K. Jerina. 2010. Mating-related movements of male brown bears on the periphery of an expanding population. *Ursus* 21:23-29.
- Krofel, M., M. Jonožovič, and K. Jerina. 2012. Demography and mortality of removed brown bears in a heavily exploited population. *Ursus* 23:91-103.
- Kryštufek, B., and H. I. Griffiths. 2003. Anatomy of a human–brown bear conflict. Case study from Slovenia in 1999–2000. In B. Kryštufek, B. Flajšman, H.I. Griffiths, eds *Living with bears, a large European carnivore in a shrinking world* 368pp. Ecological Forum of the Liberal Democracy of Slovenia, Ljubljana, Slovenia:126-153.
- Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4:345-349.
- Mace, R. D., and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. *Wildlife Society Bulletin* 24:461-467.
- Manchi, S., and J. E. Swenson. 2005. Denning behavior of male Scandinavian brown bears (*Ursus arctos*). *Wildlife Biology* 11:123-132.
- Martin, J., M. Basille, B. Van Moorter, J. Kindberg, D. Allaine, and J. E. Swenson. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology* 88:875-883.
- Matson, G. M., L. Van Daele, E. Goodwin, A. Aumiller, H. V. Reynolds, and H. Hristienko. 1993. A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth. Matson's Laboratory, Milltown, Montana, USA.
- Mattson, D. 1990. Human impacts on bear habitat use. *Ursus* 8:33-56.

- Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Ursus* 7:259-273.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* 56:432-442.
- McCullough, D. R. 1982. Behavior, bears, and humans. *Wildlife Society Bulletin* 10:27-33.
- McLellan, B. 1994. Density-dependent population regulation of brown bears. In M. Taylor, ed. *Density-dependent population regulation of black, brown, and polar bears*. 43pp. *Ursus*. Monograph Series 3:15-24.
- McLellan, B. N., F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *Journal of Wildlife Management* 63:911-920.
- McLellan, B. N. 2005. Sexually selected infanticide in grizzly bears: the effects of hunting on cub survival. *Ursus* 16:141-156.
- McLellan, B. N. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 89:546-558.
- Moen, G. K., O. G. Stoen, V. Sahlen, and J. E. Swenson. 2012. Behaviour of solitary adult Scandinavian brown bears (*Ursus arctos*) when approached by humans on foot. *Plos One* 7.
- Mueller, C., S. Herrero, and M. L. Gibeau. 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15:35-47.

- Nellemann, C., O. Støen, J. Kindberg, J. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157-165.
- Nevin, O. T., and B. K. Gilbert. 2005. Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? *Biological Conservation* 121:611-622.
- Noyce, K. V., and D. L. Garshelis. 1997. Influence of natural food abundance on black bear harvests in Minnesota. *Journal of Wildlife Management* 61:1067-1074.
- Oi, T., N. Ohnishi, H. Furusawa, and T. Fujii. 2009. Nutritional condition and dietary profile of invasive bears in Hiroshima Prefecture, western Japan. Toru Oi, Naoki Ohnishi, Toru Koizumi, Isamu Okochi eds. FFPRI Scientific Meeting Report 4 "Biology of Bear Intrusions". Forestry and Forest Products Research Institute, Ibaraki, Japan:44-47.
- Oka, T., S. Miura, T. Masaki, W. Suzuki, K. Osumi, and S. Saitoh. 2004. Relationship between changes in beechnut production and Asiatic black bears in northern Japan. *Journal of Wildlife Management* 68:979-986.
- Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears *Oecologia* 166:59-67.
- Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. *Ecology* 80:957-975.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>. Version.
- Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology* 45:218-227.

- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15:161-171.
- Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128:62-71.
- Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636-2646.
- Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population dynamics of black bears in northeastern Minnesota. *Wildlife Monographs* 97:1-72.
- Rogers, L. L. 2011. Does diversionary feeding create nuisance bears and jeopardize public safety? *Human-Wildlife Interactions* 5:287-295.
- Røskaft, E., T. Bjerke, B. Kaltenborn, J. D. C. Linnell, and R. Andersen. 2003. Patterns of self-reported fear towards large carnivores among the Norwegian public. *Evolution and Human Behavior* 24:184-198.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1-68.
- Skrbinšek, T., M. Jelenčič, H. Potočnik, P. Trontelj, and I. Kos. 2008. Analiza medvedov odvzetih iz narave in genetsko-molekularne raziskave populacije medveda v Sloveniji. I. Del. Varstvena genetika in ocena številčnosti medveda 2007. [Analysis of removed brown bears and genetic-molecular studies on brown bear population in Slovenia. Part I. Conservation genetics and bear population size estimate for 2007.].

- Final report. Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia. [In Slovenian].
- Spencer, R. D., R. A. Beausoleil, and D. A. Martorello. 2007. How agencies respond to human-black bear conflicts: a survey of wildlife agencies in North America. *Ursus* 18:217-229.
- Steyaert, S. M. J. G., J. Kindberg, J. Swenson, and A. Zedrosser. 2013. Male reproductive strategy explains spatiotemporal segregation in brown bears. *Journal of Animal Ecology* 82:836-845.
- Støen, O.-G., A. Zedrosser, S. Sæbø, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* 148:356-364.
- Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67:819-826.
- Swenson, J. E., B. Dahle, and F. Sandegren. 2001a. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12:81-92.
- Swenson, J. E., B. Dahle, and F. Sandegren. 2001b. Intraspecific Predation in Scandinavian Brown Bears Older than Cubs-of-the-Year. *Ursus* 12:81-91.
- Swenson, J. E., M. Adamič, D. Huber, and S. Stokke. 2007. Brown bear body mass and growth in northern and southern Europe. *Oecologia* 153:37-47.
- Tremblay, A. 2011. A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. <http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html>.
- Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. *Ecology* 78:1105-1119.

- Wielgus, R. B., and F. L. Bunnell. 1994. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405-413.
- Yamanaka, A., M. Asano, M. Suzuki, T. Mizoguchi, M. Shimosuru, and T. Tsubota. 2009. Is there any relationship between the number of nuisance-killed Japanese black bears (*Ursus thibetanus japonicus*) and their nutritional condition? . In T. Oi, N. Ohnishi, T. Koizumi, I. Okochi eds. FFPRI Scientific Meeting Report 4 "Biology of Bear Intrusions". Forestry and Forest Products Research Institute, Ibaraki, Japan:48-51.
- Zedrosser, A., B. Dahle, J. E. Swenson, and N. Gerstl. 2001. Status and management of the brown bear in Europe. *Ursus* 12:9-20.
- Zedrosser, A., B. Dahle, and J. E. Swenson. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87:510-518.
- Zedrosser, A., O. Støen, S. Sæbø, and J. Swenson. 2007. Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour* 74:369-376.
- Zedrosser, A., B. Dahle, O.-G. Støen, and J. E. Swenson. 2009. The effects of primiparity on reproductive performance in the brown bear. *Oecologia* 160:847-854.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York 1st edition:532-536.

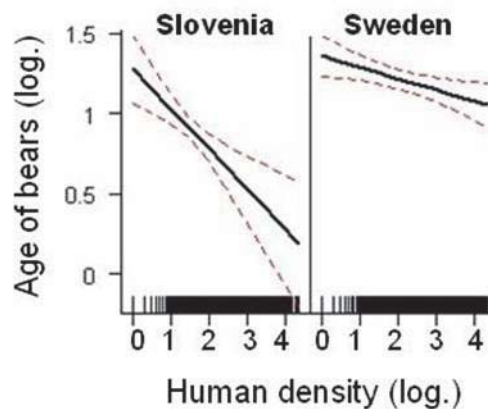


Figure 1. Separate effects, and 95 % confidence intervals, on age distribution in relation to human density among shot brown bears in Slovenia and Sweden between 1990 and 2010; 149 (134 Slovenian, 15 Swedish) problem bears, 47 Swedish bears shot in self defense, and 1,896 (877 Slovenian, 1,019 Swedish) nonproblem bears, based on the linear mixed model with highest support ($\Delta AIC_c=0.00$, $AIC_c w=0.98$, Table 2). Variables are log transformed.

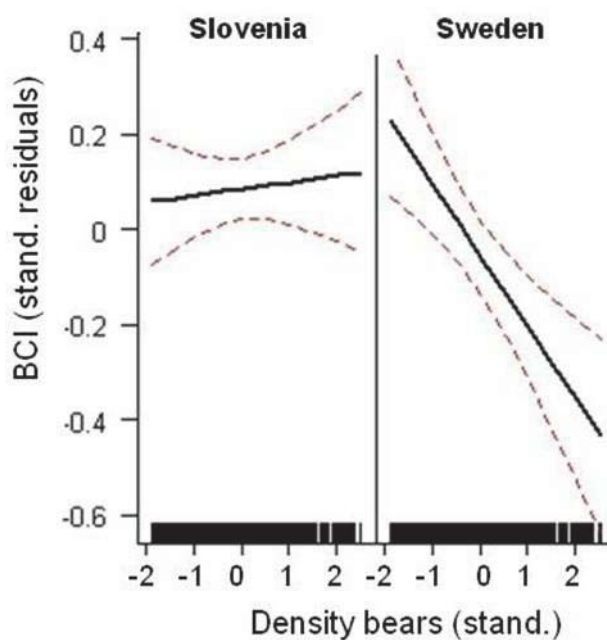


Figure 2. Separate effects, and 95 % confidence intervals, on body condition index (BCI) distribution in relation to standardized density of bears among shot brown bears in Slovenia and Sweden between 1996 and 2010; 124 (117 Slovenian, 7 Swedish) problem bears, 30 Swedish bears shot in self defense, 1,279 (726 Slovenian, 553 Swedish) nonproblem bears, based on the linear mixed model with highest support ($\Delta AIC_c=0.00$, $AIC_c w=0.64$, Table 4). Density of bears was calculated differently between Slovenia and Sweden.

Table 1. Model selection based on AIC_c values (w_i =AIC_c weights) finding the most parsimonious linear mixed model when fitting age distribution of 2,096 brown bears shot in Slovenia and Sweden (1990-2010), with year shot as random effect and bear density excluded (response is log transformed). A variable on gray background and strikethrough represents its exclusion. S=sex, PrD= problem bear status (nonproblem, problem, or shot in self defense), HD=human density (log-tr.), and C=country.

Candidate models	K	AICc	ΔAICc	w_i	w_i cum.
S + PrD + HD:C + C	8	5063.86	0.00	0.98	0.98
S + PrD : HD: C + C	8	5072.14	8.29	0.02	1.00
S + PrD : HD:C + C	5	5099.09	35.23	0.00	1.00
Intercept only	3	5188.71	124.86	0.00	1.00

Table 2. Log-transformed age distribution among shot bears in Slovenia and Sweden between 1990 and 2010, in relation to 149 (134 Slovenian, 15 Swedish) problem bears, 51 Swedish bears shot in self defense, and 1,896 (877 Slovenian, 1,019 Swedish) nonproblem bears, and density of people, with year shot as a random effect. Variances of random effects are 0.0045 for year shot and 0.6406 for residuals, based on the most parsimonious linear mixed model (Table 1). Markov Chain Monte Carlo (MCMC)-simulated β and its 95 % highest posterior density interval (HPD) are given with β and standard errors (SE) based on a t -distribution.

$\Delta AIC_c = 0.00, w = 0.98$	β	SE	β_{MCMC}	HPD 95 %	HPD 95 %
				lower	upper
(Intercept)	1.359	0.059	1.362	1.250	1.480
Males	-0.038	0.035	-0.039	-0.104	0.031
Problem bears	-0.198	0.071	-0.201	-0.339	-0.064
Self defense	0.619	0.116	0.619	0.399	0.835
Slovenia :					
Density people(log.)	-0.125	0.016	-0.125	-0.154	-0.091
Sweden :					
Density people(log.)	-0.027	0.010	-0.028	-0.049	-0.010

Table 3. Model selection based on AICc values (w_i =AICc weights) finding the most parsimonious linear mixed model when fitting body condition index (BCI) among 1,433 brown bears shot in Slovenia and Sweden (1996-2010), with year shot included as a random effect. The response is the standardized residual of BCI regressed on date shot, extracted separately for subadults and adults, spring and fall, and country. A variable on gray background and strikethrough represents its exclusion. A=age (log-tr.), S=sex, C=country, PrD= problem bear status (nonproblem, problem, or shot in self defense), HD=human density (log-tr.), BD=bear density (standardized).

Candidate models	K	AICc	Δ AICc	w_i	w_i cum.
S*A + C + PrD + HD:C + BD:C	9	3852.92	0.00	0.64	0.64
S*A + C + PrD + HD:C + BD:C	7	3854.96	2.04	0.23	0.88
S*A + C + PrD + HD:C + BD:C	13	3858.06	5.14	0.05	0.92
S*A + C + PrD + HD:C + BD:C	11	3858.84	5.92	0.03	0.96
S*A + C + PrD : HD:C + BD:C	10	3859.38	6.45	0.03	0.98
S*A + C + PrD : HD:C + BD:C	12	3860.24	7.32	0.02	1.00
Intercept only	3	4152.23	299.31	0.00	1.00

Table 4. Body condition index (BCI) among brown bears shot in Slovenia and Sweden between 1996 and 2010, in relation to standardized density of bears, sex, age, and with year shot as a random effect. The factors human density and bear status are not included, when analyzing 124 (117 Slovenian, 7 Swedish) problem bears, 30 Swedish bears shot in self defense, and 1,279 (726 Slovenian, 553 Swedish) nonproblem bears (based on AIC_c values, Table 4). Variances for random effects for year shot and residuals, respectively, are <0.0000 and 0.8356, and <0.0000 and 0.8437, based on the 2 most parsimonious linear mixed models (Table 3). Markov Chain Monte Carlo (MCMC)-simulated β and its 95 % highest posterior density interval (HPD) are given with β and standard errors (SE) based on a *t*-distribution.

	β	SE	β_{MCMC}	HPD 95 % lower	HPD 95 % upper
$\Delta\text{AIC}_c = 0.00$; $w = 0.64$					
(Intercept)	-0.434	0.060	-0.433	-0.549	-0.321
Males	0.190	0.076	0.188	0.038	0.337
Age (log.)	0.202	0.047	0.204	0.108	0.297
Sweden	-0.138	0.052	-0.144	-0.252	-0.043
Males:Age(log)	0.402	0.061	0.404	0.285	0.534
Density bears(stand):Slovenia	0.014	0.031	0.015	-0.048	0.070
Density bears(stand):Sweden	-0.150	0.038	-0.151	-0.222	-0.075
$\Delta\text{AIC}_c = 2.04$; $w = 0.23$					
(Intercept)	-0.444	0.060	-0.445	-0.562	-0.324
Males	0.202	0.076	0.204	0.061	0.362
Age (log.)	0.202	0.047	0.202	0.113	0.299
Sweden	-0.140	0.052	-0.141	-0.256	-0.043
Males:Age(log)	0.410	0.062	0.410	0.287	0.524

Table 5. Model selection based on quasi-AICc values ($w_i = qAIC_c$ weights) finding the most parsimonious generalized linear model when fitting averaged body condition index (FAI) for different seasons among years ($n=22$), in relation to number of problem brown bears shot in Slovenia (1999-2010) and Sweden (1997-2008). The response is assumed a poisson distribution. C=country, Pop= population size.

Candidate models	K	qAICc	$\Delta qAICc$	w_i	w_i cum.
Intercept only	3	6.29	0.00	0.99	0.99
Pop:C	5	14.87	8.59	0.01	1.00
Fall _{prev} & Spring _{conc.} * C +Pop:C	8	26.53	20.24	0.00	1.00
Spring _{conc} & Fall _{conc.} * C+Pop:C	8	26.74	20.45	0.00	1.00
Fall _{conc.} * C +Pop:C	8	26.81	20.52	0.00	1.00
Fall _{prev} * C +Pop:C	8	27.41	21.13	0.00	1.00

Table 6. Model selection based on AICc values (w_i =AICc weights) finding the most parsimonious linear mixed model when fitting variation in body condition index (BCI) in relation to 129 problem and 129 nonproblem brown bears in Slovenia (1996-2010) and Sweden (1994-2008). Year bears were shot is included as a random effect. The response was square-root transformed.

Candidate models	K	AICc	ΔAICc	w_i	w_i cum.
Intercept only	3	-0.61	0.00	0.97	0.97
Problem vs. nonproblem bears	4	6.55	7.15	0.03	1.00

SUPPLEMENTAL MATERIAL

APPENDIX 1. Model selection based on Akaike's Information Criteria scores for small sample sizes (AIC_c , $w_i=AIC_c$ weights) finding the most parsimonious linear mixed model when fitting the ratio between body mass and paw width against log-transformed proportion of fat in 61 brown bears immobilized in Sweden (2001-2006), with year bear was captured as a random effect (response is log transformed).

Candidate models	K	AICc	$\Delta AICc$	w_i	w_i cum.
Fat (% , log.)	4	27.04	0.00	0.67	0.67
Intercept only	3	28.42	1.38	0.33	1.00

APPENDIX 2. Log-transformed ratio between body mass and paw width against log-transformed proportion of fat in 61 brown bears immobilized in Sweden (2001-2006), with year immobilized as a random effect. Variances of random effects are 0.0045 for year captured and 0.0697 for residuals, based on the most parsimonious linear mixed model (Appendix 1). Markov Chain Monte Carlo (MCMC)-simulated β and its 95 % highest posterior density interval (HPD) are given with β and standard errors (SE) based on a t -distribution.

$\Delta AIC_c = 0.00$, $w=0.67$	β	SE	β_{MCMC}	HPD 95 %	HPD 95
				lower	% upper
(Intercept)	1.331	0.327	1.350	0.656	2.036
Fat (% , log.)	0.314	0.115	0.312	0.080	0.554

APPENDIX 3. Model selection based on Akaike's Information Criteria scores for small sample sizes (AIC_c , $w_i=AIC_c$ weights) finding the most parsimonious linear mixed model when fitting age distribution of 1,601 brown bears shot in Slovenia and Sweden (1996-2010), with year shot as random effect (response is log transformed). A variable on gray background and strikethrough represents its exclusion. S=sex, PrD=bear status (nonproblem, problem, shot in self defense), HD=human density (log-tr.), BD=bear density (standardized), and C=country.

Candidate models	K	AICc	$\Delta AICc$	w_i	w_i cum.
S + PrD + HD : C + BD:C + C	8	3757.94	0.00	0.94	0.94
S + PrD : HD : C + BD:C + C	8	3763.35	5.41	0.06	1.00
S + PrD + HD : C + BD:C + C	10	3770.76	12.82	0.00	1.00
S + PrD : HD : C + BD:C + C	10	3774.78	16.84	0.00	1.00
S + PrD + HD : C + BD:C + C	5	3779.04	21.10	0.00	1.00
Intercept only	3	3848.40	90.46	0.00	1.00
S + PrD + HD : C + BD:C + C	6	3862.75	104.81	0.00	1.00

PAPER IV

Gut retention time in captive brown bears *Ursus arctos*

Marcus Elfström, Ole-Gunnar Støen, Andreas Zedrosser, Ian Warrington & Jon E. Swenson

Knowing animals' gut retention time (GRT) for important food items is critical when using non-invasive studies based on faecal remains, e.g. when analysing nutritive quality of food, or relating diet or behaviour to movements. We analysed GRT in six captive brown bears *Ursus arctos*, after feeding on either berries (a mixture of bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea*) or animal carcasses (either reindeer *Rangifer tarandus*, European rabbit *Oryctolagus cuniculus*, domestic pig *Sus scrofa domestica*, cattle *Bos taurus* or horse *Equus ferus caballus*). Median GRT_{50%} (i.e. when 50% of all faeces containing experimental food had been defecated) was 5 hours and 47 minutes (1st and 3rd quartiles = 4 hours and 36 minutes and 7 hours and 3 minutes; N = 20) after feeding on berries and 14 hours and 30 minutes (1st and 3rd quartiles = 10 hours and 9 minutes and 16 hours and 57 minutes; N = 20) after feeding on carcasses. Median GRT_{min} (i.e. first defecation comprised of experimental food) was 3 hours and 5 minutes (1st and 3rd quartiles = 1 hour and 51 minutes and 4 hours and 12 minutes; N = 21) for berries and 8 hours and 2 minutes (1st and 3rd quartiles = 6 hours and 14 minutes and 10 hours and 44 minutes; N = 20) for carcasses. Median GRT_{max} (i.e. last defecation comprised of experimental food) was 15 hours and 27 minutes (1st and 3rd quartiles = 11 hours and 36 minutes and 17 hours and 16 minutes; N = 21) for berries and 16 hours and 16 minutes (1st and 3rd quartiles = 12 hours and 11 minutes and 17 hours and 27 minutes; N = 20) for carcasses. A carcass diet had 6 hours and 26 minutes \pm 1 hour and 56 minutes (SE) longer GRT_{50%} than a berry diet (N = 39), despite low variation in food intake. Activity level, feeding time (midday/midnight), sex, age (subadult/adult), ingested amounts of food, prior food remains processed by the gut (i.e. cumulative faeces weight) and defecation rate did not influence the GRT_{50%}. Our reported GRT estimates are reliable values to be used within research and management to relate diet based on faecal remains to habitat use for common and important food items used by Scandinavian brown bears.

Key words: brown bear, digestibility, food intake, gastrointestinal, gut retention time, ingestion passage, transit, *Ursus arctos*

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Analyses of faecal remains allow non-invasive studies of, for instance, a species' distribution, habitat use and diet (Putman 1984). Data based on faecal remains can also be related to animal movements (e.g. using GPS positions). However, these studies often require knowledge of the time for ingested food

to pass through the digestive tract, hereafter called gut retention time (GRT). Therefore, knowledge of the GRT is valuable for many types of studies. Knowing the GRT allows sampling faeces within a defined time frame, thus uniting feeding patterns with spatio-temporal data of individuals. In domestic

pigs *Sus scrofa domestica*, a short GRT is associated with increasing proportions of ingested fibre (Partanen et al. 2007). When problem carnivores are shot (e.g. because of depredation incidents), the GRT also defines the time frame during which depredated foods are expected to be found in the digestive tract of destroyed animals. The GRT has been studied for several aquatic and terrestrial carnivores (Edwards et al. 2001, Hall-Aspland et al. 2011), as well as for omnivores (Tsuji et al. 2011). In bears, Ursidae, the GRT has been studied in omnivores with mainly a vegetative diet (giant pandas *Ailuropoda melanoleuca*; Dierenfeld et al. 1982), almost exclusively carnivores (polar bears *Ursus maritimus*; Best 1985), and omnivores with relatively large variation in their diet (Asiatic black bears *Ursus thibetanus*; Koike et al. 2010, and brown bears *Ursus arctos*; Pritchard & Robbins 1990). Pritchard & Robbins (1990) estimated the GRT for hair when feeding on carcasses and (chromium-marked) clover *Trifolium repens* in North American brown bears confined in small cages.

We analysed the GRT of captive Scandinavian brown bears for two common food items; berries and meat from carcasses. Meat (i.e. newborn calves of reindeer *Rangifer tarandus* and moose *Alces alces*) and berries (i.e. bilberry *Vaccinium myrtillus*, crowberry *Empetrum nigrum* and lingonberry *Vaccinium vitis-idaea*) constitute important foods for Scandinavian brown bears during spring and autumn, respectively (Dahle et al. 1998, Persson et al. 2001). Thus, although bears may have a mixed diet, they often feed on animals and berries during separate periods of the year. We compared GRT in relation to sex and age classes of bears, feeding time (midday/midnight), activity, diet (berry/carcass), weights of experimental food and supplemental food, cumulative weight of faeces and defecation rate. We hypothesised a longer GRT for a carcass than a berry diet, because Pritchard & Robbins (1990) reported higher digestibility (i.e. less material to be processed by the gut) and lower fibre content for meat than for berries.

Material and method

We studied GRT on six captive animals, three females (two subadults 2.5-year old and one adult 8.5-year old) and three males (two subadults 3.5-year old and one adult 10.5-year old) in the Orsa Bear Park, Sweden, during August of 2010. For none of the animals there were earlier reports or indications

of gastrointestinal diseases. The four subadult bears were kept together in the same enclosure, whereas the two adults were kept together in a separate enclosure, both encompassing approximately 10,000 m². We used two individuals per experiment, and consecutive experiments were separated by a minimum of 48 hours for each individual.

During an experiment, bears were confined to an enclosure encompassing 400 m² for 24 hours. In order to standardise and improve the detection of experimental foods, individuals were given no food, except for ca 200 g of dog food pellets provided immediately after entering the experimental enclosure, and after four hours they were given the experimental foods. Bears were either given their experimental foods at midday (12:00) or at midnight (00:00) in order to control for last routine feeding between experiments and diel behaviour (Moe et al. 2007), which may affect gastrointestinal functions (Bron & Furness 2009). Between the experiments, bears were fed fruits (i.e. grapes *Vitis vinifera*, apples *Malus* sp. and oranges *Citrus* sp.) and bread daily at 14:00. Thus, ingestion of experimental food at midday took place ca 22 hours and midnight feeding ca 10 hours after the last routine feeding. Bears had access to carcasses (parts of domestic pig, cattle *Bos taurus* or horse *Equus ferus caballus*) within 12 hours before two experiments on carcass diet and one experiment on berry diet. Bears always had access to water and were given corn *Zea mays* weighed as fed after the experimental food had been consumed.

We mixed the experimental foods with 50-100 g plastic beads (of 5 mm in diameter), which functioned as solid markers to assist detection of experimental food items in the faeces and to confirm that faecal remains were derived from experimental foods. Experimental feeding of berries was comprised of a mixture of bilberry and lingonberry with a large proportion of the former. Experimental feeding of carcasses was comprised of meat, bones and fur from either bear-killed domestic reindeer calves, domestic rabbits *Oryctolagus cuniculus* or parts of domestic pigs, cattle or horses. All provided experimental food was consumed except larger pieces of bones or fur, which were subtracted from the weight as fed after the experiments. We only used data from experiments in which bears finished consuming the experimental food within two hours.

We video-recorded the animals during each experiment, using light-equipped cameras and recording capability within infrared wavelengths, noted start and end time of feeding, time of defecation,

measured with an accuracy ± 1 second and scored an activity level every 10 minutes as active (standing/moving) or passive (laying/sitting down). After the bears had been released back into their main enclosures, all faeces were collected, labelled in order to relate each faeces to the time of defecation and bear identity (based on the video-recordings) and immediately weighed on an electronic scale. We examined faecal remains to detect the presence of markers, and we separated faeces containing experimental food item, i.e. berry or carcass, from those containing only corn. No corn defecation occurred before the first defecation containing remains of ingested experimental food, and the last defecation during experiments contained corn. The mean \pm SD air temperature during the experiments was $15^{\circ}\text{C} \pm 4$ (SD) at 12:00 and $12^{\circ}\text{C} \pm 3$ (SD) at 00:00. Our study was approved by the Ethical Committee of Animal Research in Umeå, Sweden (permit D nr A 75-10).

Data analysis

We used both start and end times of feeding to calculate GRT. GRT_{\min} denotes the time elapsed before the first defecation containing experimental food with markers, and GRT_{\max} denotes the time elapsed before the last defecation containing experimental food with markers, after the ingestion of experimental food. $\text{GRT}_{50\%}$ denotes the time when 50% of the cumulative weight of faecal remains of experimental food with markers had been defecated after the ingestion of experimental food. We report median values, because distributions were non-normal, and to avoid overestimating the GRT (Ormseth & Ben-David 2000).

We estimated GRT_{\min} , GRT_{\max} and $\text{GRT}_{50\%}$ using only faeces with confirmed presence of experimental foods and markers. However, the total amount of material processed in the gut during and after the time of ingesting the experimental food affects the available volume in the gut before the next defecation (e.g. the $\text{GRT}_{50\%}$). Thus, material processed by the gut, measured as defecation rate and cumulative weight of defecations after ingesting experimental food prior to the $\text{GRT}_{50\%}$, may affect $\text{GRT}_{50\%}$. Therefore, when calculating defecation rate and cumulative weight of defecations prior to the $\text{GRT}_{50\%}$ defecation, we included all defecations (i.e. also faecal remains of corn and not containing experimental food or markers). We used linear mixed models (LMM) to analyse $\text{GRT}_{50\%}$ in relation to the following fixed factors: sex, age class (adult/sub-adult), activity score (% active), feeding time (mid-

day/midnight), diet (berry/carcass), weight of ingested experimental food, weight of ingested supplemental food (corn), cumulative weight of defecations prior to $\text{GRT}_{50\%}$ and defecation rate prior to $\text{GRT}_{50\%}$. We included an interaction term between sex and age classes to control for potential differences among these classes, because bears are sexually dimorphic (Rode et al. 2006) and body size has been suggested to influence the GRT among herbivores (Demment & Van Soest 1985). We calculated the defecation rate prior to the $\text{GRT}_{50\%}$ as the number of defecations divided by the period from midpoint of feeding (between start and end times) until the $\text{GRT}_{50\%}$ defecation occurred. We calculated $\text{GRT}_{50\%}$ using the midpoint between the start and end of feeding in our LMM. We used bear identity and experiment as random effects.

We constructed a candidate set of 14 LMMs *a priori* and selected the most parsimonious LMM based on Akaike's Information Criteria scores for small sample sizes (AIC_c) and AIC_c weights ($\text{AIC}_c w$; Akaike 1973, Burnham & Anderson 2002). We used the 'lme4' package (Bates & Maechler 2010) for statistical modelling and generated β and its 95% highest posterior density interval (HPD) for the fixed effects of the regression models with a Markov Chain Monte Carlo algorithm (MCMC) using 1,000 simulations, package 'LMERConvenienceFunctions' (Tremblay 2011) in R.2.14.1 (R Development Core Team 2009). We considered effects significant when the HPD 95% around β did not include 0. Outliers were controlled for by using Cleveland dotplots and multicollinearity by using variance inflation factors (Zuur et al. 2009). The number of observations (N) deviated among analyses, because the factor activity score was missing for one animal during one experiment, and weights of faeces were missing for one animal during another experiment.

Results

Gut retention times and defecation rates for berries and carcasses

Median $\text{GRT}_{50\%}$ from the midpoint time of feeding was 5 hours and 47 minutes (1st and 3rd quartiles = 4 hours and 36 minutes and 7 hours and 3 minutes; $N = 20$) for berry diet and 14 hours and 30 minutes (1st and 3rd quartiles = 10 hours and 9 minutes and 16 hours and 57 minutes; $N = 20$) for carcass diet (Fig. 1). Median GRT_{\min} from the midpoint time of feeding was 3 hours and 5 minutes (1st and 3rd

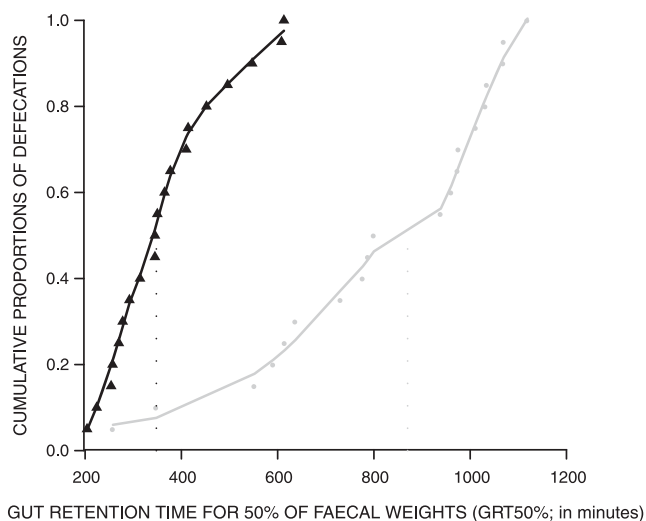


Figure 1. Cumulative proportions of defecations in relation to gut retention time when 50% of the cumulative weight of all faeces after 20 feedings of berry (▲) and 20 feedings of carcasses (•) had been defecated ($GRT_{50\%}$), for six captive Scandinavian brown bears in the Orsa Bear Park, Sweden, during 2010. Dashed vertical lines represent median $GRT_{50\%}$, and the x-axis has a minimum value of 200 minutes.

quartiles = 1 hour and 51 minutes and 4 hours and 12 minutes; $N = 21$) for berry diet and 8 hours and 2 minutes (1st and 3rd quartiles = 6 hours and 14 minutes and 10 hours and 44 minutes; $N = 20$) for carcass diet. Median GRT_{max} from the midpoint time of feeding was 15 hours and 27 minutes (1st and 3rd quartiles = 11 hours and 36 minutes and 17 hours and 16 minutes; $N = 21$) for berry diet and 16 hours and 16 minutes (1st and 3rd quartiles = 12 hours and 11 minutes and 17 hours and 27 minutes; $N = 20$) for carcass diet. Descriptive estimates of GRT_{min} , GRT_{max} and $GRT_{50\%}$ are shown in relation to start and end points of feeding experimental foods in Table 1.

Median (1st and 3rd quartiles) defecation rate between start of feeding and last defecation of experimental food among experiments and individuals was 7.1 defecations/24 hours (6.1 and 9.4; $N = 21$) for berry feedings and 4.0 defecations/24 hours (1.2 and 5.4; $N = 20$) for carcass feedings.

Effects of diet, activity, sex, age, weights of food and faeces and defecation rate on $GRT_{50\%}$

The most parsimonious LMM included sex, age, (adult/subadult), feeding time (midday/midnight),

Table 1. Gut retention time (GRT; in hours:minutes) in six captive Scandinavian brown bears (two 2-year-old and one 8-year-old female; two 3-year-old and one 10-year-old male), after feeding on either berries or carcass (meat with bones and fur), at the Orsa Bear Park, Sweden, during 2010. GRT is combined between feeding at midday and midnight. Maximum time elapsed between start and end times of feeding was 1 hour and 39 minutes. GRT_{min} and GRT_{max} are based on 21 berry feedings and 20 carcass feedings, and $GRT_{50\%}$ is based on 20 berry feedings and 20 carcass feedings.

	Berry ^a		Carcasses ^b	
	Feeding		Feeding	
	Start	End	Start	End
GRT_{min} (First defecation)				
Median	3:09	2:38	8:21	7:39
Quartiles 1-3	2:25-4:19	1:46-4:06	6:35-11:09	5:45-10:16
Mean	3:41	3:08	9:21	8:39
SD	1:55	1:59	4:03	4:09
GRT_{max} (Last defecation)				
Median	15:38	15:17	16:41	15:56
Quartiles 1-3	12:00-17:53	11:23-16:48	12:42-17:54	11:26-17:11
Mean	14:27	13:53	14:46	14:03
SD	3:57	3:46	4:21	4:15
$GRT_{50\%}$ ^c				
Median	6:15	5:38	14:51	14:15
Quartiles 1-3	5:06-7:16	4:19-6:57	10:34-17:00	9:43-16:47
Mean	6:28	5:53	13:43	13:01
SD	2:03	2:00	4:26	4:21

^a Mixture of bilberry and lingonberry.

^b Either reindeer, European rabbit, domestic pig, cattle or horse.

^c Denotes time elapsed when 50% of cumulative weight of all faeces had been defecated.

Table 2. Model selection based on AIC_c values ($w_i = AIC_c$ weights), finding the most parsimonious linear mixed model when fitting gut retention time when 50% of faeces with experimental foods had been defecated ($GRT_{50\%}$) for six captive Swedish brown bears, with bear ID and experiment as random effects, using *a priori* set of 14 candidate models. A variable on grey background represents its exclusion. A = subadult or adult, Ac = Activity score, CB = carcass or berry diet, DN = midday or midnight feeding, Dr = defecation rate, S = sex, Wc = cumulative weight of faeces, We = weight of experimental food, Ws = weight of supplemental food and * = an interaction between two factors.

Candidate models	K	AIC_c	ΔAIC_c	w_i	w_{icum}
S*A+DN+Ac+ We + Ws + Wc +Dr+CB	11	475.86	0.00	0.97	0.97
S*A+DN+Ac+ We + Ws + Wc +Dr+CB	13	483.44	7.58	0.02	0.99
S*A+DN+Ac+ We + Ws + Wc +Dr+CB	13	484.79	8.93	0.01	1.00
S*A+DN+Ac+ We + Ws + Wc +Dr+CB	13	491.29	15.43	0.00	1.00
S*A+DN+Ac+ We + Ws + Wc +Dr+CB	14	491.70	15.84	0.00	1.00
S*A+DN+ Ac + We + Ws + Wc +Dr+CB	13	499.64	23.78	0.00	1.00
S*A+ DN +Ac+ We + Ws + Wc +Dr+CB	13	500.47	24.61	0.00	1.00
S*A+DN+Ac+ We + Ws + Wc + Dr +CB	13	501.21	25.36	0.00	1.00
S *A+DN+Ac+ We + Ws + Wc +Dr+CB	12	507.91	32.05	0.00	1.00
S *A+DN+Ac+ We + Ws + Wc +Dr+CB	12	508.48	32.62	0.00	1.00
S*A+ DN + Ac + We + Ws + Wc +Dr+CB	12	508.85	32.99	0.00	1.00
S*A+DN+Ac+ We + Ws + Wc +Dr+ CB	13	512.01	36.15	0.00	1.00
S *A+DN+Ac+ We + Ws + Wc +Dr+CB	11	515.53	39.68	0.00	1.00
Intercept model	4	560.98	85.12	0.00	1.00

activity score, prior defecation rate, diet (berry/carcass) and the interaction between sex and age class based on AIC_c ($\Delta AIC_c = 0.00$ and $AIC_{cw} = 0.97$; Table 2). Thus, this LMM excluded weight of experimental foods, supplemental food and prior cumulative faeces weight (see Table 2). Diet (berry or carcass) was the only fixed factor with a HPD 95% interval around β_{MCMC} that did not include 0; it had a β/SE of 3.3. A carcass diet had 6 hours and 26 minutes ± 1 hour and 56 minutes (SE) longer $GRT_{50\%}$ than berries ($N = 39$ feedings; Table 3). All other fixed factors in this model had HPD 95% intervals around β_{MCMC} that included 0, and β/SE ratios were ≤ 2.0 ; i.e. sex had $\beta/SE = 2.0$, age (adult/subadult) had $\beta/SE = 1.0$, feeding time (midday/

midnight) had $\beta/SE = 0.7$, activity score had $\beta/SE = 0.5$, prior defecation rate had $\beta/SE = 0.1$ and interaction between sex and age class had $\beta/SE = 1.3$ ($N = 39$ feedings; see Table 3). Descriptive estimates for continuous fixed factors used in our LMM data set are shown in Table 4.

Discussion

We found no relationship between $GRT_{50\%}$ and activity levels of the animals, which were constrained within ca 400 m² during the experiments. Our reported median $GRT_{50\%}$ of 14 hours and 30 minutes after feeding on carcasses is similar to a

Table 3. Factors explaining gut retention time (in decimal minutes) when 50% of faeces with experimental foods had been defecated ($GRT_{50\%}$) after 39 feedings of six captive brown bears in Sweden 2010, in relation to diet of berries or carcasses, activity score, midday or midnight feeding, cumulative faeces weight, the interaction term between sex and subadult/adult and with bear ID and experiment as random effects based on the most parsimonious linear mixed model (see Table 2). Variances of random effects are < 0.0 for bear ID, 7,965.2 for experiment, and 35,474.4 for residuals. Markov Chain Monte Carlo (MCMC)-simulated β and its 95% highest posterior density interval (HPD) are given with β and standard errors (SE) based on a t-distribution.

$\Delta AIC_c = 0.00, w = 0.97$	β	SE	β_{MCMC}	HPD 95%	
				Lower	Upper
(Intercept)	299.80	168.63	313.53	-55.55	637.42
Males	257.22	128.88	272.67	-90.49	620.10
Subadults	140.65	139.00	179.66	-143.84	490.41
Midnight feeding	-57.16	76.70	-53.92	-190.30	87.81
Defecation rate	21.96	191.80	15.53	-424.67	397.61
Carcass	385.99	115.94	367.83	162.66	597.17
Activity score	-117.31	240.77	-174.57	-665.24	288.36
Males:Subadults	-194.63	149.10	-231.03	-628.17	192.94

Table 4. Mean and standard deviation for fixed factors used to analyse effects on gut retention time on six captive bears after having a diet comprised of either berries (20 feedings) or carcasses (19 feedings). Bears were either given their experimental foods at midday (N = 22) or at midnight (N = 17).

	Ingested		Weight of prior faeces (g wet matter)	Defecation rate ^a (/hour)	Activity scores ^b (% of total)
	Experimental food (g as fed)	Supplemental food of corn (g as fed)			
Berry					
Median	5909	1810	837	0.29	51.5
Quartiles 1-3	2200-6018	950-2020	357-1248	0.18-0.60	38.3-70.3
Mean	4693	1627	813	0.36	55.6
SD	1784	643	534	0.26	21.6
Carcasses					
Median	4691	1704	265	0.16	34.5
Quartiles 1-3	4260-5425	1500-1962	0-461	0.00-0.20	30.3-38.3
Mean	4607	1682	307	0.14	33.4
SD	1004	342	300	0.14	9.8

^a Number of defecations prior to when 50% of all faecal weight was defecated.

^b The animal was active if standing/walking and passive if laying/sleeping, and was recorded every 10 minutes.

mean GRT for hair ingested by North American brown bears when feeding on carcass, based on amount of digested marked and unmarked hairs per defecation, 13 hours \pm 2 hours (SD; Pritchard & Robbins 1990). However, Pritchard & Robbins (1990) used animals constrained within cages with a maximum dimension of 2.4 m. This suggests that GRT is not related to activity levels, and that our estimates of GRT_{50%} are reliable values to use within research (e.g. to compare diet based on faecal remains with movements) and management (e.g. for how long to expect to find ingested livestock in the gut of shot bears) for common food items used by brown bears.

We found no relation between GRT_{50%} and feeding time (midnight or midday). The main sleeping period of the bears used in this experiment was between midnight and sunrise, whereas the last routine feeding took place 22 hours before experimental feeding at midday and 10 hours before experimental feeding at midnight. This suggests that there is no effect from a circadian activity pattern on GRT_{50%} and/or effects from last ingestion before our experiments of GRT_{50%}.

We provided the same amount of food during all experiments, and this may explain why we found no relationship between food intake (i.e. weight of ingested experimental or supplemental food) and GRT_{50%}, as well as no relationship between cumulative faecal weights or defecation rate prior to the GRT_{50%} defecation and GRT_{50%}. In the carnivorous leopard seal *Hydrurga leptonyx*, Trumble et al. (2003) reported similar GRT among experiments

with different feeding frequency. However, it is possible that a larger variation in food intake would have had a larger effect on the GRT in our study, because larger food intake may shorten the GRT due to gut volume constraints. A negative correlation between food intake and GRT has been reported in omnivores, e.g. mice (McClelland et al. 1999) and herbivores (Clauss et al. 2007).

We found no differences in GRT_{50%} between subadults and adults, nor between female and male bears (i.e. groups with smaller and larger body sizes), even though foraging efficiency may decrease with increasing body size in bears (Welch et al. 1997, Rode et al. 2001). GRT does not change with body size in dogs *Canis familiaris* (Boillat et al. 2010) and primates (Lambert 1998). Steuer et al. (2011) concluded that body mass alone poorly explained differences in GRT between small and large herbivorous ungulates.

The GRT_{50%} for the carcass diet was 6 hours and 26 minutes \pm 1 hour and 56 minutes (SE) longer than of berries, despite low variation in food intake. Pritchard & Robbins (1990) reported higher digestibility for carcasses (93%) than for blueberries *Vaccinium corymbosum* (64%). A higher digestibility of carcasses compared to berries results in a reduced amount of faecal remains and, hence, the gut can contain more faecal remains before the gut volume is filled and defecation occurs after feeding on carcass. Giant pandas feeding on bamboo *Phyllostachys aureosulcata*, which is rich in fibre content, have short GRT, probably because they ingest large amounts of poorly digestible food (Dierenfeld et al.

1982). Partanen et al. (2007) reported a shorter GRT and lower digestibility with increasing proportions of ingested fibre for pigs that were fed the same amounts of food. In humans, ingested fibre is known to improve bowel movements and produce softer faeces (Klosterbuer et al. 2011) and fresh bilberry has been described as having a laxative function (Jaric et al. 2007). In birds, ingested seeds have been suggested to have a chemical laxative function by shortening the GRT (Murray et al. 1994). The dietary fibre content of berries is five times higher than in carcasses (Pritchard & Robbins 1990). Thus, the much shorter GRT_{50%} for berries compared to carcasses in our study may be a result of lower digestibility in combination with increased gastrointestinal activity after ingesting berries.

Berries constitute the most important food item for Scandinavian bears during hyperphagia in summer and autumn (Dahle et al. 1998). The potential median and maximum seed dispersal distances for berries, based on our GRT_{50%} and GRT_{max} for berries, are 4.2 km and 11.1 km, respectively, when combining our results with a reported median rate of movement of 0.72 km/hour by Scandinavian brown bears (Moe et al. 2007). We found that the median (1st and 3rd quartiles) defecation rate of 7.1 (6.1 and 9.4) defecations/24 hours when bears foraged on berries is similar to the 7.2 defecations/day during autumn reported by Roth (1980) in captive brown bears fed a diet of mostly plants.

Conclusions

Our results suggest that GRT estimates are reliable to use in research where GRT after berry/carcass diet of bears are required. When combined with positioning data, GRT constitutes an important tool for determining where food remains found in faeces have been consumed and where remains of consumed foods will be excreted. The GRT also constitutes an important tool for management by defining a time frame in which to expect finding particular food remains in bears, e.g. livestock remains.

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References

- Akaike, H. 1973: Information theory and an extension of the maximum likelihood principle. - In: Petrov, B & Caski, F. (Eds.); Proceeding of the Second International Symposium on Information Theory: 267-281.
- Bates, D.M. & Maechler, M. 2010: lme4: Linear mixed-effects models using S4 classes - R package version 0.999375-37. - Available at: <http://CRAN.R-project.org/package=lme4>:29 (Last accessed on 27 July 2012).
- Best, R.C. 1985: Digestibility of ringed seals by the polar bear. - Canadian Journal of Zoology - Revue Canadienne De Zoologie 63: 1033-1036.
- Boillat, C.S., Gaschen, F.P. & Hosgood, G.L. 2010: Assessment of the relationship between body weight and gastrointestinal transit times measured by use of a wireless motility capsule system in dogs. - American Journal of Veterinary Research 71: 898-902.
- Bron, R. & Furness, J.B. 2009: Rhythm of digestion: keeping time in the gastrointestinal tract. - Clinical and Experimental Pharmacology and Physiology 36: 1041-1048.
- Burnham, K.P. & Anderson, D.R. 2002: Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. - Springer-Verlag, New York, New York, USA, 488 pp.
- Clauss, M., Streich, W.J., Schwarm, A., Ortmann, S. & Hummel, J. 2007: The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. - Oikos 116: 209-216.
- Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E. & Sandegren, F. 1998: The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. - Wildlife Biology 4(3): 147-158.
- Demment, M.W. & Van Soest, P.J. 1985: A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. - American Naturalist 125: 641-672.
- Dierenfeld, E.S., Hintz, H.F., Robertson, J.B., Van Soest, P.J. & Oftedal, O.T. 1982: Utilization of bamboo by the giant panda. - Journal of Nutrition 112: 636-641.
- Edwards, M.S., Gaffney, M. & Bray, R.E. 2001: Influence of fiber source on apparent digestibility, rate of passage and fecal consistency in small felids fed a beef-based carnivore diet. - In: Edwards, M.S., Lisi, K.J., Schlegel, M.L. & Bray, R.E. (Eds.); Fourth Nutrition Advisory Group Conference on Zoo and Wildlife Nutrition. Proceedings of the American Zoo and Aquarium Association, Walt Disney World Resort, Florida, USA 4: 71-80.
- Hall-Aspland, S., Rogers, T., Canfield, R. & Tripovich, J. 2011: Food transit times in captive leopard seals (*Hydrurga leptonyx*). - Polar Biology 34: 95-99.
- Jaric, S., Popovic, Z., Macukanovic-Jovic, M., Djurdjevic, L., Mijatovic, M., Karadzic, B., Mitrovic, M. & Pavlovic,

- P. 2007: An ethnobotanical study on the usage of wild medicinal herbs from Kopaonik Mountain (Central Serbia). - *Journal of Ethnopharmacology* 111: 160-175.
- Klosterbuer, A., Roughead, Z.F. & Slavin, J. 2011: Benefits of dietary fiber in clinical nutrition. - *Nutrition in Clinical Practice* 26: 625-635.
- Koike, S., Masaki, T., Nemoto, Y., Kozakai, C., Yamazaki, K., Kasai, S., Nakajima, A. & Kaji, K. 2010: Estimate of the seed shadow created by the Asiatic black bear *Ursus thibetanus* and its characteristics as a seed disperser in Japanese cool-temperate forest. - *Oikos* 120: 280-290.
- Lambert, J.E. 1998: Primate digestion: Interactions among anatomy, physiology, and feeding ecology. - *Evolutionary Anthropology* 7: 8-20.
- McClelland, K.L., Hume, I.D. & Soran, N. 1999: Responses of the digestive tract of the omnivorous northern brown bandicoot, *Isodon macrourus* (Marsupialia: Peramelidae), to plant- and insect-containing diets. - *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 169: 411-418.
- Moe, T.F., Kindberg, J., Jansson, I. & Swenson, J.E. 2007: Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). - *Canadian Journal of Zoology* 85: 518-525.
- Murray, K.G., Russell, S., Picone, C.M., Winnettmurray, K., Sherwood, W. & Kuhlmann, M.L. 1994: Fruit laxatives and seed passage rates in frugivores - consequences for plant reproductive success. - *Ecology* 75: 989-994.
- Ormseth, O.A. & Ben-David, M. 2000: Ingestion of crude oil: effects on digesta retention times and nutrient uptake in captive river otters. - *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 170: 419-428.
- Partanen, K., Jalava, T. & Valaja, I. 2007: Effects of a dietary organic acid mixture and of dietary fibre levels on ileal and faecal nutrient apparent digestibility, bacterial nitrogen flow, microbial metabolite concentrations and rate of passage in the digestive tract of pigs. - *Animal* 1: 389-401.
- Persson, I.L., Wikan, S., Swenson, J.E. & Mysterud, I. 2001: The diet of the brown bear *Ursus arctos* in the Pasvik Valley, northeastern Norway. - *Wildlife Biology* 7(1): 27-37.
- Pritchard, G.T. & Robbins, C.T. 1990: Digestive and metabolic efficiencies of grizzly and black bears. - *Canadian Journal of Zoology - Revue Canadienne De Zoologie* 68: 1645-1651.
- Putman, R.J. 1984: Facts from feces. - *Mammal Review* 14: 79-97.
- R Development Core Team 2009: R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/> (Last accessed on 19 July 2012).
- Rode, K.D., Farley, S.D. & Robbins, C.T. 2006: Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. - *Ecology* 87: 2636-2646.
- Rode, K.D., Robbins, C.T. & Shipley, L.A. 2001: Constraints on herbivory by grizzly bears. - *Oecologia* 128: 62-71.
- Roth, H.U. 1980: Defecation rates of captive brown bears. - *Ursus* 4: 249-253.
- Steuer, P., Südekum, K.-H., Müller, D.W.H., Franz, R., Kaandorp, J., Clauss, M. & Hummel, J. 2011: Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates. - *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* 160: 355-364.
- Tremblay, A. 2011: A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. - Available at: <http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html> (Last accessed on 8 August 2012).
- Trumble, S.J., Barboza, P.S. & Castellini, M.A. 2003: Digestive constraints on an aquatic carnivore: effects of feeding frequency and prey composition on harbor seals. - *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 173: 501-509.
- Tsuji, Y., Shiraishi, T. & Miura, S. 2011: Gastrointestinal passage time of seeds ingested by captive Japanese martens *Martes melampus*. - *Acta Theriologica* 56: 353-357.
- Welch, C.A., Keay, J., Kendall, K.C. & Robbins, C.T. 1997: Constraints on frugivory by bears. - *Ecology* 78: 1105-1119.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009: Mixed Effects Models and Extensions in Ecology with R. 1st edition. - Springer, New York, New York, USA, pp. 532-536.

PAPER V

Do Scandinavian brown bears approach settlements to obtain high-quality food?

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Abstract

Large carnivores, such as bears, that approach human settlements are usually considered to be a problem and a threat to human property and safety. The prevailing paradigm is that such 'problem' bears approach settlements in search of food. Based on fecal remains, we compared the diet of individual brown bears (*Ursus arctos*) in south-central Sweden in relation to settlements. Nutritive quality was quantified as crude fat, protein, and lignin/neutral detergent fiber content, using near-infrared spectroscopy, and food items were identified using a DNA metabarcoding approach. We analyzed 36 bear visits <150 m from settlements by 21 individuals equipped with GPS/GSM, and the corresponding diet when the same bears were >600 m from settlements (i.e. constituting 95 % of bears' habitat use). The food-search hypothesis predicted a different and higher-quality diet when an individual bear was close to settlements than when in a remote area.

We found no significant difference in the composition or quality of the bears' diet between settlements and remote areas; <1.9 % of the variation in dietary composition was associated with settlements. Thus, we found no support for a food-search hypothesis to explain bear occurrence near settlements. However, within 48 hours prior to a settlement visit and while >150 m from any settlements, bears more often exploited pig remains compared to when near settlements or in remote areas. Diet composition and quality did not differ between subadults and adult males, suggesting no effects from interference competition. Diet quality of females with cubs-of-the-year was not different and their diet composition was in general not different from adult males. However, females with yearlings had 5.1 ± 2.9 (SE) % lower fecal protein content than adult males. Females with cubs-of-the-year and females with yearlings exploited pig remains less often than other bears. This suggests that the distribution of predation-vulnerable bears may have been affected to some degree by despotic behavior of dominant bears.

Introduction

Large carnivores have increased in numbers and range (Linnell et al. 2001), but they commonly avoid human activity and settlements (Woodroffe and Ginsberg 1998, Frid and Dill 2002). However, large carnivores do sometimes occur close to settlements, and are often considered to be a problem, because people fear them (Røskoft et al. 2003, Johansson et al. 2012) and property may be damaged or even humans injured (Woodroffe and Ginsberg 1998). Several authors have proposed that brown bears (*Ursus arctos*) approach settlements in search of food, which can result in food-conditioning, i.e. the learning process to associate people with easily-accessible and/or attractive foods (McCullough 1982, Gunther et al. 2004), even though bears generally avoid human activity and settlements (Mace and Waller 1996, Nellemann et al. 2007). Nevertheless, if bears gain access to high-quality foods near settlements (Hobson et al. 2000), this may explain why some bears tolerate the disturbance associated with human activity and approach settlements.

The distribution of brown bears is affected by food availability, anthropogenic disturbances, and intraspecific interactions, among them aggression or predation from dominant conspecifics (McLoughlin et al. 2002, Ciarniello et al. 2007, Roever et al. 2008, Steyaert et al. 2013). This suggests that the distribution of individuals in bear populations follows a despotic pattern, where human settlements may supply food resources for smaller/subdominant bears, due to interference competition, and/or predation refuges for smaller/subdominant bears, due to avoidance of aggression (Elfström et al. 2013b). Subadults and females with offspring seem to exploit habitats with lower diet quality than adult males (Stelmock and Dean 1986, Mattson et al. 1987, Blanchard and Knight 1991, Mattson et al. 1992, Wielgus and Bunnell 1994;1995, Ben-David et al. 2004). Smaller bears have lower nutritional requirements than larger bears, due to their smaller absolute energetic requirements and relatively large intake capability (Welch et al. 1997, Rode et al. 2001).

Thus, large adult males may require more abundant foods or higher food quality than other sex/age categories of bears (Robbins et al. 2004). Yet, the bears most often involved in incidents with people are subadults (Schwartz et al. 2006, Hristienko and McDonald 2007, Elfström 2013) and females with offspring (Kaczensky et al. 2006, Rode et al. 2006b), whereas adult males more often are found in more remote areas during both the nondenning period (Mattson et al. 1987, Mattson et al. 1992, Gibeau et al. 2002, Rode et al. 2006a, Nellemann et al. 2007, Steyaert et al. 2013) and the denning period (Elfström and Swenson 2009).

Our objective was to establish if the diet of individual brown bears of different sex, age, and reproductive categories was different and of higher quality when they were feeding near human settlements compared to in remote areas. If individual bears gain a nutritional advantage by using areas close to settlements, the food-search hypothesis predicts that, bears would have a different diet and consume foods with higher nutritive value when near settlements than in remote areas (Hobson et al. 2000, Hopkins et al. 2012), independently of sex, age, or reproductive categories. If individual bears use areas close to settlements to avoid intraspecific aggression, or alternatively, because they are naive (i.e. lack experience with people), diet composition or quality should be similar when near settlements or in remote areas. We documented habitat use based on relocations of GPS/GSM-collared brown bears. We collected fecal samples from these bears and analyzed fecal nutritive constituents using near-infrared reflectance spectroscopy (NIRS) (Cen and He 2007, Steyaert et al. 2012), and diet composition by identification of short fecal DNA sequences against a reference database, i.e. the DNA metabarcoding concept (Valentini et al. 2009, Taberlet et al. 2012).

Methods

Study area

Our study area was situated in south-central Sweden (~61° N, 15° E), and encompasses ~12,000 km² (Dahle and Swenson 2003). More than 80% of the area consists of intensively managed boreal forest, with Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*), and downy birch (*B. pubescens*) as the dominant tree species; the remaining area is mainly covered by bogs or lakes (Moe et al. 2007). The forest floor is dominated by lichens, heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea*), and crowberry (*Empetrum hermaphroditum*) (Swenson et al. 1999).

Elevations range between 200 to 1000 meters above sea level, most of the area (90 %) lies below the timberline (~750 m a.s.l.) (Dahle and Swenson 2003), and the slopes are <8° in >90 % of the area (Elfström et al. 2008). The area is sparsely populated, with few settlements and isolated houses (Martin et al. 2010). There are six towns and settlements, ranging from 3,000–11,000 inhabitants, and two major tourist resort areas with cabins (Nellemann et al. 2007). 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).

Study design

We studied brown bear diet using fecal remains found at GPS relocations in relation to human settlements, between 1 May and 1 October, 2010. We monitored 49 bears equipped with GPS/GSM-collars with relocations scheduled at 10- or 30-minute intervals (VECTRONIC Aerospace GmbH, Berlin, Germany). Details for capturing and handling of bears are described in Arnemo et al. (2011). Bears were categorized according to their sex, age, and reproductive status. Males ≥5 years of age were defined as adult males (AM) and

males <5 years of age and nullparous females as subadults (SUB). After having given birth, females were categorized as lone parous females (LF), females with cubs-of-the-year (FC), and females with dependent offspring, 1-2 years of age (FY) (Dahle and Swenson 2003, Zedrosser et al. 2007).

We used ArcGIS 9.2 (Environmental Systems Research Institute, Inc., Redlands, California) for spatial analyses. We defined settlements as inhabited building(s) with registered garbage collection. The County Administrative Boards of Dalarna and Gävleborg provided digital maps (GSD Fastighetskartan) of buildings (D nr 501-6993-09 and 09910-2009, respectively). Registers of garbage collection were provided by the municipalities of Ljusdal, Mora, Orsa, Ovanåker, Rättvik and Älvdalen, in corporation with the following garbage disposal companies; Bollnäs Ovanåkers Renhållnings AB (BORAB), Dala Vatten och Avfall AB, Norra Dalarna Vatten och Avfall (NODAVA), and SITA Sverige. Human presence was scored at settlements visited by bears, based on signs of occasional or regular human activity, e.g. presence/absence of people, cars, mowed lawn, as confirmed human presence, no human presence, and unknown. Minimum duration of settlement visits was measured as the time period elapsed between first and last GPS relocations <150 m from a settlement.

A settlement visit was defined as a bear occurring within a 150-m radius of a settlement for a minimum of 2 consecutive GPS relocations. The 150-m cut-off around settlements was based on bear movements and distances between residential houses and their garbage bins. Bears in our study area have a reported upper range of movement, i.e. quartile 3, median, of 600 m/30 min while they are active (Moe et al. 2007). Thus, an upper-range movement from a settlement and back between two close GPS relocations separated by a maximum of 30 minutes corresponds to 300 m. Garbage bins are recommended not to be located more than 450 m from rural residential houses, according to two decisions made by

the Swedish Environmental Supreme Court (case number M 7725-05 in 2006, case number M 583-06 in 2007). Thus, our 150-m radius around settlements probably excludes unknown bear movements between consecutive GPS relocations that exceed the maximum recommended distance between garbage bins and residential houses.

We collected fecal samples only from the bears' bed sites, identified as clusters of GPS relocations <20 m apart and used by the bear ≥ 60 minutes, starting 1 hour after the first GPS relocation occurred <150 m from a settlement, and until 24 hours after the first GPS relocation occurred again >150 m from the settlement. Thus, we sampled fecal remains deposited during a minimum period of 24 hours after a bear approached a settlement, which overlaps reported gut retention times of 6 and 14.5 hours for captive Scandinavian brown bears fed berry and meat diets, respectively (Elfström et al. 2013a), i.e. diets with different fiber content and digestibility (Pritchard and Robbins 1990). Feces deposited while bears were not using a resting site were not sampled.

A remote area was defined as an area with no GPS relocations within 600 m of any settlements, and corresponded to 95 % of the habitat used by GPS-collared bears in our study area during 2006-2009. We randomly selected 2 beds from the same individual to sample remote fecal remains a minimum of 48 hours after a bear visited a settlement, and only if all GPS relocations had been in remote areas for a minimum of 24 hours prior to collection.

We also analyzed diet composition and quality from fecal samples defecated in the 24 hours prior to a bear-visit near a settlement. Only if no GPS relocations had occurred within the settlement areas for a minimum of 48 hours before the settlement visit occurred, we included samples from 2 randomly selected bed sites from the same individual. Thus, we analyzed bears' diet while occurring away (>150m) from settlements, and independently of bear use in remote areas, reflecting feeding behavior between remote and settlement areas.

We collected ca. 1 cm³ from all fecal remains found within 5 m of bed sites, mixed all samples, and preserved 1 sample per bed site in ethyl alcohol for DNA analysis. If multiple feces were present at bed sites, we only sampled the fecal deposit found closest to the bed for diet quality analysis. We estimated maximum duration of fecal field exposure, i.e. the time period elapsed from first GPS relocation by a bear at a cluster until time of fecal sampling, because it may affect the fecal nutritive constituents (Steyaert et al. 2012). Details for nutritive sampling procedure, treatment and analysis followed descriptions by Steyaert et al. (2012).

Diet composition analysis

We extracted, cleaned and purified total DNA from about 10 mg of sample using the DNeasy Blood and Tissue Kits (QIAGEN GmbH), according to the DNeasy Blood and Tissue Handbook, 7/2006, QIAGEN. Mock extractions were systematically performed to monitor for possible contaminations. We amplified DNA metabarcoding regions for plants, vertebrates, and invertebrates by polymerase chain reaction (PCR) in two multiplexed reactions using universal primers for the targeted taxonomic groups, as described by M. De Barba (unpublished). The first multiplex PCR contained the primer sets g/h (amplifying the P6 loop of the chloroplast trnL (UAA) intron in angiosperms and gymnosperms (Taberlet et al. 2007, Valentini et al. 2009)), 12SV5F/12SV5R (amplifying the V5 loop of the mitochondrial 12S gene in vertebrates (Riaz et al. 2011)), and MAVF/MAVR (targeting a short portion of the mitochondrial 16S gene of mollusks, annelids, and vertebrates; unpublished) with the *Ursus* V5 blocking primer, mammalian MAVB1 blocking primer, and *Homo* blocking primer to prevent amplification of bear and human DNA in the vertebrate samples, and mammalian DNA in the invertebrate samples. The second multiplex PCR contained the primer sets ITS1-F/ITS1Poa-R (Poaceae ITS1 (Baamrane et al. 2012)), ITS1-F/ITS1Ast-R (Asteraceae ITS1 (Baamrane et al. 2012)), ITS1-F/ITS1Cyp-R (Cyperaceae

ITS1(P. Taberlet unpublished)) targeting a short fragment of the internal transcribed spacer region 1 (ITS1) of nuclear ribosomal DNA of the Asteraceae, Cyperaceae, and Poaceae, and ITSrosF/ITSrosR (Rosaceae ITS2 (M. De Barba unpublished) amplifying a short fragment of the internal transcribed spacer region 2 (ITS2) of nuclear ribosomal DNA of the Rosaceae. We conducted four replicate PCRs per multiplex PCR for each fecal sample, and conditions for both reactions were as described in M. De Barba (unpublished). We uniquely tagged universal primers (each tag was composed by CC or GG followed by eight variable nucleotides and was added on the 5' end of the primers) to allow for individual sample recognition in downstream bioinformatic analyses after pooling of PCR products for sequencing (Coissac et al. 2012). PCR products of multiplex 1 and multiplex 2 were purified, mixed together in equimolar concentration (M. De Barba unpublished) and sequenced on one region of the Illumina HiSeq 2000 (Illumina Inc.), following the manufacturer's instructions. We sequenced a total of 100 nucleotides on each extremity of the DNA fragments.

We processed sequences using the OBITools program (available at: <http://www.grenoble.prabi.fr/trac/OBITools>) suite of python scripts. The direct and reverse reads corresponding to single molecules were aligned and a consensus sequence and quality score were generated using the *solexaPairEnd* script. We identified primers and tags using *ngsfilter*, and excluded those sequences with errors in the tags and a maximum of two errors in the primers from further analysis. The amplified regions, excluding primers and tags, were kept for further analysis. For each marker dataset, identical sequences were clustered using *obiuniq*, while still keeping the information about their distribution among samples. We excluded sequences shorter than 10 bp (gh, mav, cyp, ros markers) or 30 bp (v5, ast, poa markers), or with occurrence <1000 from the dataset using the *obigrep* script. The *obiclean* script was implemented to detect PCR and sequencing errors: each unique sequence within a PCR product was given the status "head" (most common sequence among all those sequences

that can be linked by a single indel or substitution), “singleton” (no other variant with a single difference in the relevant PCR product), or “internal” (all other sequences not being “head” or “singleton”, i.e. corresponding to amplification/sequencing errors). We excluded all sequences designated more often as “internal” than “head” or “singleton” from further analysis.

We gave each unique sequence a taxonomic assignment using the *ecoTag* script for all amplified regions. The *ecoTag* script identifies the taxon corresponding to the last common ancestor node of the NCBI (National Center for Biotechnology Information) taxonomic tree of all the taxids annotating those sequences matching the query in a marker-specific reference database generated by extracting the relevant part of the EMBL (European Molecular Biology Laboratory) nucleotide database using the *ecoPCR* script (Ficetola et al. 2010). We then conducted a final filtering of the dataset. We removed unique sequence groups from the dataset that 1) occurred in <3 of the four PCR replicates, 2) had a best identity match <0.95, 3) accounted for <1% of the total sequences generated for that marker across all samples (presumably items of little dietary significance), or 4) were identified as human or bear. Those unique sequence groups within the chloroplast trnL marker dataset that were identified as belonging to the Asteraceae, Cyperaceae, Poaceae, or Rosaceae were excluded to avoid overlap in detection with the family-specific ITS marker datasets. Finally, we collapsed unique sequence groups with identical taxonomic assignments at the species level into a single representative grouping. We then created a concatenated fecal sample versus dietary item matrix from all the samples from which all seven markers were successfully amplified and sequenced. The matrix was then rarified to an even sequencing depth of 75,000 reads per sample, and converted to presence-absence data, as differences in primer efficiencies and PCR bias render abundances noncomparable among the different markers.

Diet quality analysis

We quantified the nutritive quality of fecal remains using NIRS, which has been widely used to analyze the chemical content and composition of analytes (Foley et al. 1998, Cen and He 2007), and has been reported as an accurate technique to evaluate diet based on fecal remains for omnivorous species, i.e. the brown bear (Steyaert et al. 2012). Commonly used indices for dietary quality include the fecal constituents of nitrogen, crude fiber, acid detergent lignin (ADL), neutral detergent fiber (NDF), and dry matter (DM) (Pritchard and Robbins 1990, Dixon and Coates 2009). Unknown sample concentrations can be predicted with NIRS, by linking spectral signatures with that from a calibration set (Næs et al. 2001). We used standard lab procedures (Kjeldahl, Weender and detergent fiber analysis) to obtain measures of fecal nutritive content from each of 174 reference samples (Nehring 1960, Naumann and Bassler 1976, van Soest et al. 1991). We analyzed five fecal constituents for our reference set: crude fat (CFA), crude protein (CP), ADL, and NDF, measured relative to the fecal DM content (% of DM). The spectroscopy was performed with a MPA Multi Purpose FT – NIR spectrometer (Bruker Optik GmbH). NIRS analyses and preprocessing optimization functions were performed using the Opus 6.5 SP2 software from Bruker Optics (Bruker Optik GmbH), and followed the descriptions in Steyaert et al. (2012). We used partial least square regression (PLSR) for multivariate calibration on the 3600-12,500 cm^{-1} spectral range (Conzen 2006), and created calibration methods for each of the components analyzed with wet-chemistry. We used the cross validation with one leave-out sample to examine the R^2 and the Root Mean Square Error of Cross Validation (RMSECV) to assess the quality of the calibration methods.

Statistical analyses

Diet composition; model selection and validation

We compared the occurrence of each of the dietary items identified in $\geq 25\%$ of all fecal remains in relation to habitat type (prior to settlement, settlement, and remote) and bear

category (SUB, FC, FY, AM, LF), by separate generalized linear mixed-effect models (GLMM) with binomial distribution using the package ‘lme4’ (Bates and Maechler 2010). We constructed 2 *a priori* candidate GLMMs for each diet item, one intercept-only and one with habitat type and bear category as fixed factors, with bear identity included as a random effect. We evaluated the most parsimonious GLMM to explain the occurrence of diet items, based on AIC_c and AIC_{cw} (Akaike 1973, Burnham and Anderson 2002). We inferred GLMMs only if the intercept-only model was not supported.

Diet quality; model selection and validation

We constructed three identical candidate sets, with each containing 11 *a priori* linear mixed-effect models (LMM), to explain the variation in fecal CFA, CP, and ADL/NDF separately. We used the following fixed factors: habitat type (prior to settlement, settlement, and remote), human presence (yes, no, and unknown), settlement duration (in minutes), bear category (SUB, FC, FY, AM, LF), field exposure time (in minutes), Julian date, and included bear identity as a random effect. We evaluated the most parsimonious LMM to explain variation in each fecal nutritive constitute, based on Akaike’s Information Criteria scores for small sample sizes (AIC_c) and AIC_c weights (AIC_{cw}) (Akaike 1973, Burnham and Anderson 2002). All statistical analyses were carried out in R 2.15.0 (R Development Core Team 2011). We used the package ‘lme4’ (Bates and Maechler 2010) for statistical modeling and generated β and its 95 % highest posterior density interval (HPD) for the fixed effects of the LMM with a Markov Chain Monte Carlo (MCMC) algorithm using 1,000 simulations, using the package ‘LMERConvenienceFunctions’ (Tremblay 2011). We controlled for outliers by using Cleveland dotplots, and multicollinearity by using variance inflation factors (Zuur et al. 2009).

Diet composition and quality combined; model selection and validation

Global Nonmetric Multidimensional Scaling (GNMDS) (Kruskal 1964b;a, Minchin 1987) and Detrended Correspondence Analysis (DCA) (Hill 1979, Hill and Gauch Jr 1980) ordinations were conducted in parallel on a presence-absence matrix of fecal samples versus diet items using the *vegan* package implemented in R (Oksanen et al. 2011, R Development Core Team 2011). GNMDS was run with the following options [following recommendations by T. Økland (1996b) and Liu et al. (2008)]: distance measure = Bray-Curtis distance, dimensions = 2 or 3, initial configurations = 100, maximum iterations = 200, convergence ratio for stress = 0.9999999. We used the default options in DCA analyses. We inspected both ordinations for outliers and known artefacts, like the arch effect (in GNMDS) and the tongue effect (in DCA) (Økland 1990, Økland and Eilertsen 1993). The nonparametric Kendall's rank correlation coefficient τ was used to calculate correlations between DCA and GNMDS axes. We interpreted similar results from the two methods (Table S1) and absence of visual artefacts as a strong indication that a reliable gradient structure had been found (Økland 1996a). The *envfit* function in *vegan* was used to fit Julian date, visit duration (i.e. time elapsed between first and last GPS relocation inside the settlement area), CFA, ADL/NDF and CP as vectors to each DCA ordination, as well as bear identity, bear category, and habitat type (prior to settlement, settlement, and remote) as factors, using 999 random permutations. We used partial canonical correspondence analysis (CCA) (ter Braak 1986) to further investigate the effect of settlement visits. The hypothesis that settlement visits did not explain significant variation in the data set was tested against the one-tailed alternative (greater than) by conducting 999 permutations of the habitat variable (i.e. prior to settlement, settlement, and remote), and examining the variation in the dataset remaining after the effects of bear identity and Julian date had been partialled out.

Results

We analyzed 120 fecal samples for diet quality after 36 approaches close to settlements; 28 prior-to-visit-to-a-settlement fecal samples, 51 near-settlement samples, and 41 remote samples. These samples were derived from 21 individuals (33 fecal samples from 5 AM-adult males, 14 from 3 FC-females with cubs-of-the-year, 11 from 3 FY-females with yearlings, 37 from 2 FL-lone adult females, and 25 from 9 SUB-subadult males and females). One female accompanied with cubs-of-the-year lost her offspring and was therefore included also as a lone parous female. Of females accompanied with offspring >0.5 years of age, there were 8 fecal samples from females with 1-year-old offspring and 3 from females with 2-year-old offspring. For the diet composition analysis, we recovered a complete dietary profile for 106 fecal samples. The median number of feces per bed site was 1 (1st and 3rd quartiles: 1 and 2). Median (1st and 3rd quartiles) duration of a bear visit near settlements was 30 (10 and 230) minutes.

Diet composition

We detected 228 dietary items in the analyzed fecal samples, of which 140 were plants, 62 were invertebrates, and 26 were vertebrates (Table S2). Common, expected dietary items were detected in high frequencies, including berries (*Vaccinium myrtillus*, *V. uliginosum*, *V. microcarpum*, *V. vitis-idaea*, *Empetrum nigrum*, *Rubus idaeus*), mammalian prey (*Alces alces*), and insect food sources (*Formica* and *Camponotus* ant species). In addition, a number of presumed settlement-associated items were detected, including a variety of cereals (*Avena* sp., *Hordeum vulgare*, *Triticum aestivum*, *Malus* sp.), domesticated animals (*Bos* sp., *Ovis* sp., *Sus scrofa*) and nonnative plant species (*Musineon vaginatum*, *Areca triandra*, *Cannabis sativa*). We also identified species known as endemic to places outside of Sweden, but with a genus commonly occurring within the country and study area. These identifications may have been identified incorrectly, or may represent horticultural specimens specifically associated

with settlement areas. By including nonnative species that may be incorrectly identified, we avoided removing potential differences in our analyses of diet among habitat types (prior to visit to a settlement, settlement, and remote areas).

The most parsimonious GLMM included the intercept-only model for all dietary items, except for the presence of *S. scrofa* and one unknown species of Poeae (intercept-only GLMM: $\Delta AIC_c = 12.87$, $AIC_{cw} = 0.00$, and $\Delta AIC_c = 8.68$, $AIC_{cw} = 0.01$, respectively, Table 1). Thus, GLMMs that included habitat type (prior to visit to a settlement, settlement, and remote areas) and bear category were not more parsimonious than intercept-only models to capture the presences of dietary items of the bears, with the exceptions of *S. scrofa* and one unknown species of Poeae. Bears had a higher frequency of *S. scrofa* in their feces prior to settlement visits than when in remote areas ($\beta = 1.5$, $SE = 0.6$, $z = 2.5$, $p = 0.011$), whereas the frequencies were similar between settlements and remote areas. We also tested the dietary presence of *S. scrofa*, with samples prior to settlement visits as reference level instead of remote area for this GLMM, and found that settlement samples had lower occurrence of *S. scrofa* than samples prior to settlement visits ($\beta = -1.6$, $SE = 0.6$, $z = -2.8$, $p = 0.006$). Females with cubs-of-the-year and lone adult females had higher fecal frequency of one unknown species of Poeae than adult males ($\beta = 3.6$, $SE = 1.0$, $z = 3.7$, $p < 0.000$, and $\beta = 1.4$, $SE = 0.7$, $z = 2.1$, $p = 0.038$, respectively). We found no other significant differences in dietary items in relation to settlements among sex, age and reproductive bear categories (Table 1). However, when separating females with young (i.e. females with cubs-of-the-year combined with females with yearlings) from other bears, and thus increasing the sample sizes among bear categories, we found that females with young had lower fecal frequency of *S. scrofa* than other bear categories ($\beta = -1.8$, $SE = 0.7$, $z = -2.5$, $p = 0.012$). The intercept-only GLMM was not supported regarding fecal presence of *S. scrofa*, when ranked against

candidate GLMM with only one fixed factor; separating bears into groups with and without the company of young; $\Delta AIC_c = 6.84$, $AIC_{cw} = 0.03$.

Diet quality

Bear category (SUB, FC, FY, AM, LF) was included in the LMM with highest support to explain variation in fecal CP among bears ($\Delta AIC_c = 0.00$, $AIC_{cw} = 0.97$, Table 2). Females with yearlings had $\beta = -5.05 \pm 2.89$ (SE) % lower fecal CP than adult males ($p = 0.024$), whereas no other differences were found among bear categories (Table 3). Fecal CP decreased during the season (i.e. Julian day $\beta = -0.08 \pm 0.01$ (SE) %, $p = 0.001$, Table 3). Habitat type (prior to visit to a settlement, settlement, or remote areas) and presence of human activity were not included in the LMM with the highest support to explain variation in fecal CP among bears (Table 2). Our models were not successful in capturing variation in fecal CFA and ADL/NDF, because the intercept models were ranked as the most parsimonious LMMs, ($\Delta AIC_c = 0.00$, $AIC_{cw} = 0.92$, and $\Delta AIC_c = 0.00$, $AIC_{cw} = 1.00$, Tables 4 and 5, respectively). Descriptive fecal estimates for CP, CFA and ADL/NDF are represented in relation to habitat types (prior to visit to a settlement, settlement, and remote areas) and in relation to bear categories in Fig 1.

Diet composition and quality combined

Bear diet, as reconstructed from genetic barcoding of fecal remains, was significantly structured by time of year (Julian date), fecal CFA and CP, and by bear category, and bear identity (Fig. 2, Table 6). The samples distributed along DCA axis 1 largely according to date and fecal CP, where low DCA axis 1 scores represented early season collections with high protein content. Samples were distributed along DCA axis 2 somewhat according to fecal CFA, with low DCA axis 2 scores representing higher fecal CFA. The species optima of common dietary items (occurring in >25% of fecal remains) were assorted along DCA axis 1 with common insect items (*Formica* sp., *Camponotus herculeanus*, *Lasius* sp.) associated

with low DCA axis 1 scores, and berries (*Vaccinium* sp., *Rubus idaeus*, *Empetrum* sp.) associated with the later part of the DCA axis 1 gradient. We found no significant differences between dietary composition and visitation of settlements based on DCA ordinations (correlation vector (r^2) = 0.02, p = 0.349). When the effects of date, bear category, and bear identity were removed (accounting for 26.6 % of total variation in diet composition) in a CCA ordination, only 1.9 % of the remaining total variability in diet composition was significantly explained by prior-to-visit-to-a-settlement, settlement, or remote-area effects, corresponding to p = 0.001 (r^2 = 0.40) for the test of the null hypothesis of no relationship. The fecal nutritive measures were, however, still not different in relation to settlements (CP: r^2 < 0.00, p = 0.799, CFA: r^2 = 0.03, p = 0.226, ADL/NDF: r^2 = 0.01, p = 0.713).

Discussion

The dietary composition of individual bears was not different prior to settlement visits, when they were near settlements, or when in remote areas, based on GLMMs. We found no differences in fecal CFA, CP and ADL/NDF in relation to prior to a settlement visit, during a settlement visit, or when bears used remote areas based on model selection of *a priori* defined LMMs. The only variables related with fecal CP were time of the year (date) and bear category, whereas no other variation in fecal nutritive measurements was captured in the LMMs. Similarly, DCA ordination suggested that the bears' diet composition was primarily structured by time of year, bear category, and individual dietary preferences, and was not strongly influenced by settlement visits. Variation in fecal CFA and CP were significantly correlated with dietary composition and similarly reflected the effects of time of year and bear categories, not settlement visits. Ordination structure primarily reflected a shift from a protein-rich, early-season diet that included a variety of ant species at high frequency, to a less protein-rich diet late in the season, with berry species occurring at high frequency. Although CCA ordination, in which the effects of date, bear category, and individual were

partialled out of the analysis, identified a significant effect of settlement visits on diet composition, this accounted for only 1.9 % of the remaining variation in diet composition. Because this structure did not correlate with CFA, CP, or ADL/NDF, and accounted for a small proportion of the variation in diet, we considered the effects of settlement visits to be negligible in the overall determination of diet composition and quality. Thus, we found no support for a substantially different diet with higher nutritive quality near settlements, i.e. the food-search hypothesis. This contrasts with reports from North America and Asia, where bears often seem to utilize human-related foods near settlements (Gunther et al. 2004, Sato et al. 2005, Greenleaf et al. 2009, Hopkins et al. 2012). Higher food quality near settlements may explain why some bears occur in areas with a higher potential for human disturbance. Others have reported a negative correlation between abundance of naturally occurring bear foods and occurrence of “problem” bears and their use of human-related foods (Rogers 1987, Mattson et al. 1992, Schwartz et al. 2006), but, based on body condition indices, no such relation has been found for Swedish bears (Elfström 2013) or Asiatic black bears, *Ursus thibetanus* in Japan (Yamanaka et al. 2009). Our results suggest that reasons other than food availability or nutritive quality prompt bears to approach settlements in south-central Sweden.

Although avoidance of settlements by bears (Mace and Waller 1996, Nellemann et al. 2007) suggests that human activity is associated with costs to bears, such as disturbance (Martin et al. 2010, Ordiz et al. 2011), it is plausible that especially dispersing subadults approach settlements because of no experience of such costs (i.e. naivety) (Elfström et al. 2013b). Thus, no dietary advantages would be required to explain the occurrence of naïve (young) bears near settlements. In contrast, bears could also approach settlements without having any dietary advantages, because they are human habituated (McCullough 1982). Alternatively, if settlements in fact are not associated with any costs to the bears, there is no reason to expect a trade-off between bears’ diet quality and distance to settlements.

Bears more often ingested *Sus scrofa* within 48 hours prior to a settlement visit and while occurring >150 m from any settlements than compared to when using settlement or remote areas. Thus, bears in areas between settlement and remote areas seem to exploit *S. scrofa* more often than in other areas. The *S. scrofa* probably originated from illegal dumps of domestic pigs slaughter remains, because wild boars are not common in the study area (Kindberg et al. 2008), and because depredation on pigs by bears has not been documented in Sweden (Karlsson et al. 2013).

We detected no fecal nutritive differences between subadults or females with cubs-of-the-year in comparison with adult males, suggesting no effects from interference competition. But females with yearlings had lower fecal CP than adult males, which lends support for some form of a despotic distribution among bears, where predation-vulnerable individuals less frequently exploit important foods (e.g. protein-rich items), because of avoidance of dominant conspecifics (Elfström et al. 2013b). However, females with cubs-of-the-year showed no significant differences in dietary composition or quality compared to adult males, except for a higher use of one unknown species of Poaceae, compared to adult males. Also lone adult females ingested this same species more often than adult males. Thus, we found no support for a despotic distribution from the dietary composition among various reproductive categories of females compared to adult males. The sample sizes within bear categories were generally small, which elevated the risk of committing a type II error and, thus, we may have underestimated dietary differences among bear categories. When combining all females accompanied by offspring (i.e. females with cubs-of-the-year and females with yearlings), we found fecal remains of pigs (*S. scrofa*) less often among females with offspring (i.e. predation-vulnerable) compared to other (i.e. more predation-tolerant) bear categories. Predation avoidance may result in predation-vulnerable individuals utilizing habitats with lower diet quality (Nevin and Gilbert 2005, Rode et al. 2006b). Our results indicated only

weak support for a despotic distribution among bears in terms of diet, however, spatiotemporal differences in habitat use among sex, age and reproductive categories of bears could still be present (Steyaert et al. 2013).

We identified berries (*Vaccinium vitis idaea*, *V. myrtillus*, *Empetrum* spp.), ants (*Camponotus* spp, *Formica* spp.), and moose (*Alces alces*) among the most common food items of Scandinavian bears, which confirms results from earlier studies of diet from central Sweden and our study area (Dahle et al. 1998, Swenson et al. 1999, Rauset et al. 2012). Diet items with presumed association with settlements included oats (*Avena* sp.), which was relatively commonly identified in the bear fecal samples, and oat fields occurred not only near settlements but also in remote areas in our study area. Apples (*Malus* sp.) are also a settlement-associated item, although it was less commonly identified in bears' feces. In addition, we identified other, less commonly ingested species, some of which are nonnative; e.g. hemp (*Cannabis sativa*) which requires permission to be cultivated and its documented production was small and did not occur in most of the study area during 2010 (pers. comm. Martin Henriksson and Berit Löfgren, 2013, County Administrative Boards of Dalarna and Gävleborg, respectively), but the seeds are commonly used as birdseed (Stenberg 2003).

We analyzed exploited food items by using fecal remains from bears, thus our study represents an objective comparison of foraging behavior among habitats and bear categories. The DNA metabarcoding approach allowed us to identify dietary items without relying on visually identifiable remains after digestion. Stable carbon and nitrogen isotope analysis derived for example from hair samples, has been used for diet studies of 'problem' bears (Hobson et al. 2000, Hopkins et al. 2012), but cannot provide the fine-scale data we required in this study. We analyzed only fecal remains found at resting sites, to ensure sampling from the correct individual, and, thus, defecations made by bears elsewhere were excluded. Although fecal NIRS has been reported to have very high ($r^2 \geq 0.9$) validation for fecal

nitrogen and NDF in brown bears (Steyaert et al. 2012), there are disadvantages of using proximate nutrient analysis based on NIRS of fecal remains. Fecal CFA content may be overestimated when bears feed on berries or seeds, because of a high proportion of undigested oil-rich seeds and waxes in fecal remains. Fecal CP content may also be overestimated, because non-protein nitrogen, e.g. nucleic acids, is falsely recovered as protein. A drawback of the fiber analysis was that the fiber content may be elevated when bears' diet is comprised of ants (*Formica* spp., *Camponotus* spp.), because the chitin in ants cannot be distinguished from other fiber components, such as cell walls of plants (Naumann and Bassler 1976). However, by combining nutritive data based on fecal NIRS with dietary items based on DNA metabarcoding, we could account for any differences in dietary constituents when comparing bears' diet in relation to settlements and age, sex and reproductive bear categories.

Conclusions

The dietary composition and quality of brown bears, based on their fecal remains, were similar near settlements compared to when the same individuals were in remote areas and, thus, we found no support for a food-search hypothesis. However, females with yearlings had lower fecal CP than adult males, and females with cubs-of-the-year combined with females with yearlings less often utilized slaughter remains from pigs (*S. scrofa*) than other bear categories, suggesting that predation-vulnerable bears were affected to some degree by the despotic behavior of dominant bears.

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Literature cited

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. B. Petrov, and F. Caski, eds. Proceeding of the Second International Symposium on Information Theory:267-281.
- Arnemo, J. M., A. Evans, Å. Fahlman, P. Ahlqvist, H. Andrén, S. Brunberg, O. Liberg, J. D. C. Linnell, J. Odden, P. Persson, H. Sand, P. Segerström, K. Sköld, T. H. Strømseth, O.-G. Støen, J. E. Swenson, and P. Wabakken. 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway:14.
- Baamrane, M. A. A., W. Shehzad, A. Ouhammou, A. Abbad, M. Naimi, E. Coissac, P. Taberlet, and M. Znari. 2012. Assessment of the Food Habits of the Moroccan Dorcas Gazelle in M'Sabih Talaa, West Central Morocco, Using the trnL Approach Plos One 7.
- Bates, D. M., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes R package version 0.999375-37. <http://CRAN.R-project.org/package=lme4>:29.
- Bellemain, E., J. E. Swenson, O. Tallmon, S. Brunberg, and P. Taberlet. 2005. Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears. Conservation Biology 19:150-161.

- Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465-474.
- Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78:656-665.
- Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. *Biological Conservation* 58:41-67.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. New York, Springer-Verlag.
- Cen, H. Y., and Y. He. 2007. Theory and application of near infrared reflectance spectroscopy in determination of food quality. *Trends in Food Science & Technology* 18:72-83.
- Ciarniello, L. M., M. S. Boyce, D. C. Heard, and D. R. Seip. 2007. Components of Grizzly Bear Habitat Selection: Density, Habitats, Roads, and Mortality Risk. *Journal of Wildlife Management* 71:1446-1457.
- Coissac, E., T. Riaz, and N. Puillandre. 2012. Bioinformatic challenges for DNA metabarcoding of plants and animals. *Molecular Ecology* 21:1834-1847.
- Conzen, J. P. 2006. Multivariate calibration a practical guide for the method development in the analytical chemistry. Second English edition. Bruker Optik GmbH.
- Dahle, B., O. Sørensen, J., E. Wedul, H., J. E. Swenson, and F. Sandegren. 1998. The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. *Wildlife Biology* 4:147-158.

- Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* 260:329-335.
- Dixon, R., and D. Coates. 2009. Review: Near infrared spectroscopy of faeces to evaluate the nutrition and physiology of herbivores. *Journal of Near Infrared Spectroscopy* 17:1-31.
- Elfström, M., J. E. Swenson, and J. P. Ball. 2008. Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* 14:176-187.
- Elfström, M., and J. E. Swenson. 2009. Effects of sex and age on den site use by Scandinavian brown bears. *Ursus* 20:85-93.
- Elfström, M. 2013. Patterns and mechanisms behind the occurrence of bears close to human settlements. Doctoral thesis. 2013:47. Norwegian University of Life Sciences. ISBN 978-82-575-1147-0.
- Elfström, M., O.-G. Støen, A. Zedrosser, I. Warrington, and J. E. Swenson. 2013a. Gut retention time in captive brown bears *Ursus arctos*. *Wildlife Biology* 19:1-8.
- Elfström, M., A. Zedrosser, O.-G. Støen, and J. E. Swenson. 2013b. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. *Mammal Review* in press.
- Ficetola, G. F., E. Coissac, S. Zundel, T. Riaz, W. Shehzad, J. Bessiere, P. Taberlet, and F. Pompanon. 2010. An In silico approach for the evaluation of DNA barcodes. *Bmc Genomics* 11.
- Foley, W. J., A. McIlwee, I. Lawler, L. Aragones, A. P. Woolnough, and N. Berding. 1998. Ecological applications of near infrared reflectance spectroscopy a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. *Oecologia* 116:293-305.

- Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6:16.
- Gibeau, M. L., A. P. Clevenger, S. Herrero, and J. Wierzchowski. 2002. Grizzly bear response to human development and activities in the Bow River Watershed, Alberta, Canada. *Biological Conservation* 103:227-236.
- Greenleaf, S. S., S. M. Matthews, R. G. Wright, J. J. Beecham, and H. M. Leithead. 2009. Food habits of American black bears as a metric for direct management of human–bear conflict in Yosemite Valley, Yosemite National Park, California. *Ursus* 20:94-101.
- Gunther, K. A., M. A. Haroldson, K. Frey, S. L. Cain, J. Copeland, and C. C. Schwartz. 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992-2000. *Ursus* 15:10-22.
- Hill, M. O. 1979. DECORANA – A FORTRAN program for detrended correspondence analysis and reciprocal averaging. New York, USA: Cornell University.
- Hill, M. O., and H. G. Gauch Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47-58.
- Hobson, K. A., B. N. McLellan, and J. G. Woods. 2000. Using stable carbon ($\delta C-13$) and nitrogen ($\delta N-15$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River basin, British Columbia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78:1332-1339.
- Hopkins, J. B., P. L. Koch, C. C. Schwartz, J. M. Ferguson, S. S. Greenleaf, and S. T. Kalinowski. 2012. Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. *Journal of Wildlife Management* 76:703-713.

- Hristienko, H., and J. E. McDonald. 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* 18:72-88.
- Johansson, M., M. Sjöström, J. Karlsson, and R. Brannlund. 2012. Is Human Fear Affecting Public Willingness to Pay for the Management and Conservation of Large Carnivores? *Society & Natural Resources* 25:610-620.
- Kaczensky, P., D. Huber, F. Knauer, H. Roth, A. Wagner, and J. Kusak. 2006. Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. *Journal of Zoology* 269:474-485.
- Karlsson, J., J. Danell, J. Månsson, L. Svensson, and R. Hellberg. 2013. Viltskadestatistik 2012 - Skador av fredat vilt på tamdjur, hundar och gröda. Rapport från Viltskadecenter [Report from Grimsö Wildlife Damage Center] Report No. 2013-1 [In Swedish].
- Kindberg, J., N. Holmqvist, and G. Bergqvist. 2008. Årsrapport Viltövervakningen 2006/2007 [In Swedish]. Svenska Jägareförbundet. Viltforum 2/2008 26pp.
- Kruskal, J. B. 1964a. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115-129.
- Kruskal, J. B. 1964b. Multidimensional scaling optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1-27.
- Linnell, J. D., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4:345-349.
- Liu, H. Y., T. Økland, R. Halvorsen, J. X. Gao, Q. R. Liu, O. Eilertsen, and H. Bratli. 2008. Gradient analyses of forests ground vegetation and its relationships to environmental variables in five subtropical forest areas, S and SW China. *Sommerfeltia* 32:1-196.

- Mace, R. D., and J. S. Waller. 1996. Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. *Wildlife Society Bulletin* 24:461-467.
- Martin, J., M. Basille, B. Van Moorter, J. Kindberg, D. Allaine, and J. E. Swenson. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology* 88:875-883.
- Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Ursus* 7:259-273.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management* 56:432-442.
- McCullough, D. R. 1982. Behavior, bears, and humans. *Wildlife Society Bulletin* 10:27-33.
- McLoughlin, P. D., R. L. Case, R. J. Gau, H. D. Cluff, R. Mulders, and F. Messier. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132:102-108.
- Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89-107.
- Moe, T. F., J. Kindberg, I. Jansson, and J. E. Swenson. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* 85:518-525.
- Næs, T., T. Isaksson, T. Fearn, and T. Davies. 2001. A userfriendly guide to multivariate calibration and classification. - NIRS publications, Chichester, UK:344 pp.
- Naumann, C., and R. Bassler. 1976. VDLUFA-Methodenbuch III. Die chemische Untersuchung von Futtermitteln. Loose leaflet collection with supplements from 1983, 1988 and 1993. Darmstadt, Verband Deutscher Landwirtschaftlicher

- Untersuchungs- und Forschungsanstalten. VDLUFA-Verlag, Melsungen, Neumann-Neudamm, Germany. (In German).
- Nehring, K. 1960. Agrikulturchemische Untersuchungsmethoden für Dünge- und Futtermittel, Böden und Milch. . P. Parey, Hamburg, Germany, 310 pp. (In German).
- Nellemann, C., O. Støen, J. Kindberg, J. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157-165.
- Nevin, O. T., and B. K. Gilbert. 2005. Measuring the cost of risk avoidance in brown bears: Further evidence of positive impacts of ecotourism. *Biological Conservation* 123:453-460.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package. R package version 2.0-0. <http://CRAN.R-project.org/package=vegan>.
- Ordiz, A., O.-G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears *Oecologia* 166:59-67.
- Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 68:1645-1651.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.Version.

- Rauset, G. R., J. Kindberg, and J. E. Swenson. 2012. Modeling female brown bear kill rates on moose calves using global positioning satellite data. *Journal of Wildlife Management* 76:1597-1606.
- Riaz, T., W. Shehzad, A. Viari, F. Pompanon, P. Taberlet, and E. Coissac. 2011. ecoPrimers: inference of new DNA barcode markers from whole genome sequence analysis. *Nucleic Acids Research* 39.
- Robbins, C. T., C. C. Schwartz, and L. A. Felicetti. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15:161-171.
- Rode, K., S. Farley, and C. Robbins. 2006a. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation* 133:70-80.
- Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128:62-71.
- Rode, K. D., S. D. Farley, and C. T. Robbins. 2006b. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636-2646.
- Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008. Grizzly bears and forestry - II: Grizzly bear habitat selection and conflicts with road placement. *Forest Ecology and Management* 256:1262-1269.
- Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population dynamics of black bears in northeastern Minnesota. *Wildlife Monographs* 97:1-72.
- Røskoft, E., T. Bjerke, B. Kaltenborn, J. D. C. Linnell, and R. Andersen. 2003. Patterns of self-reported fear towards large carnivores among the Norwegian public. *Evolution and Human Behavior* 24:184-198.

- Sato, Y., T. Mano, and S. Takatsuki. 2005. Stomach contents of brown bears *Ursus arctos* in Hokkaido, Japan. *Wildlife Biology* 11:133-144.
- Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1-68.
- Stelmock, J. J., and F. C. Dean. 1986. Brown bear activity and habitat use, Denali National Park: 1980. *Ursus* 6:155-167.
- Stenberg, L. 2003. Den nya nordiska floran. Wahlström and Widstrand, Tangen, Norge [In Swedish] 928pp.
- Steyaert, S. M. J. G., F. J. Hütter, M. Elfström, A. Zedrosser, K. Hackländer, M. H. Lê, W. Windisch, J. Swenson, and T. Isaksson. 2012. Fecal spectroscopy: a practical tool to assess diet quality in an opportunistic omnivore. *Wildlife Biology* 18:431-438.
- Steyaert, S. M. J. G., J. Kindberg, J. Swenson, and A. Zedrosser. 2013. Male reproductive strategy explains spatiotemporal segregation in brown bears. *Journal of Animal Ecology* 82:836-845.
- Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 77:551-561.
- Taberlet, P., E. Coissac, F. Pompanon, L. Gielly, C. Miquel, A. Valentini, T. Vermet, G. Corthier, C. Brochmann, and E. Willerslev. 2007. Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. *Nucleic Acids Research* 35.
- Taberlet, P., E. Coissac, F. Pompanon, C. Brochmann, and E. Willerslev. 2012. Towards next-generation biodiversity assessment using DNA metabarcoding. *Molecular Ecology* 21:2045-2050.

- ter Braak, C. F. J. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.
- Tremblay, A. 2011. A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. <http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html>.
- Valentini, A., C. Miquel, M. A. Nawaz, E. V. A. Bellemain, E. Coissac, F. Pompanon, L. Gielly, C. Cruaud, G. Nascetti, P. Wincker, J. E. Swenson, and P. Taberlet. 2009. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the trnL approach. *Molecular Ecology Resources* 9:51-60.
- van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* 74:3583-3597.
- Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. *Ecology* 78:1105-1119.
- Wielgus, R. B., and F. L. Bunnell. 1994. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405-413.
- Wielgus, R. B., and F. L. Bunnell. 1995. Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59:552-560.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126-2128.
- Yamanaka, A., M. Asano, M. Suzuki, T. Mizoguchi, M. Shimozuru, and T. Tsubota. 2009. Is there any relationship between the number of nuisance-killed Japanese black bears (*Ursus thibetanus japonicus*) and their nutritional condition? . In T. Oi, N. Ohnishi, T. Koizumi, I. Okochi eds. FFPRI Scientific Meeting Report 4 "Biology of Bear Intrusions". Forestry and Forest Products Research Institute, Ibaraki, Japan:48-51.

- Zedrosser, A., O. Støen, S. Sæbø, and J. Swenson. 2007. Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour* 74:369-376.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York 1st edition:532-536.
- Økland, R. H. 1990. *Vegetation ecology: theory, methods and applications with reference to Fennoscandia*. *Sommerfeltia* Supplementary: S1-S233.
- Økland, R. H., and O. Eilertsen. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. *Sommerfeltia* 16:1-254.
- Økland, R. H. 1996a. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *Journal of Vegetation Science* 7:289-292.
- Økland, T. 1996b. Vegetation-environment relationships of boreal spruce forest in ten monitoring reference areas in Norway. *Sommerfeltia* 22:1-349.

Table 1. Dietary composition in relation to settlements by sex, age, and reproductive categories of brown bears for all dietary items with $\geq 25\%$ frequency of occurrence among 106 fecal remains in south-central Sweden in 2010, identified by DNA metabarcoding and ranked in decreasing frequency from the top. Dietary composition was based on separate generalized linear mixed-effect models (GLMM) with a binomial distribution for each food item, using habitat and bear category as fixed factors and bear identity as a random effect. AIC_c values (w_i = AIC_c weights) are given for the intercept-only GLMM, when ranked against one alternative candidate GLMM (with habitat type + bear category). Remote areas are reference level for prior to visit to a settlement and settlement areas. Adult males are reference level for females with cubs of the year (FC), females with yearlings (FY), lone parous females (FL), subadult males and females (SUB).

OTU Name ^a	Taxon ID	ΔAIC_c	w_i	Prior settl.	Settl.	FC	FY	FL	SUB	Frequency (%)
gh_00001	<i>Vaccinium vitis-idaea</i>	0.00	0.71							85.8
mav_00001	<i>Formica</i> sp.	0.00	0.95							82.1
ast_00001	<i>Tussilago farfara</i>	0.00	0.98							81.1
ast_00003	<i>Taraxacum</i>	0.00	0.99							79.2
v05_00002	<i>Alces alces</i>	3.9	0.12							78.3
ast_00002	<i>Cirsium palustre</i>	0.00	0.92							74.5
poa_00003	<i>Avenella flexuosa</i>	0.00	0.98							64.2
ros_00001	<i>Rubus idaeus</i>	0.00	0.93							62.3
poa_00004	<i>Deschampsia</i> sp.	0.00	1.00							55.7
summed6	<i>Cicerbita alpina</i>	0.00	0.99							55.7
gh_00003	<i>Vaccinium myrtillus</i>	0.00	0.98							50.9
mav_00002	<i>Oliarces clara</i>	0.00	0.97							50.0
v05_00010	<i>Bos</i> sp.	0.00	0.98							50.0
ast_00012	<i>Hieracium</i> sp.	0.00	0.90							49.1
poa_00001	<i>Avena</i> sp.	0.00	0.95							48.1
v05_00003	<i>Sus scrofa</i>	12.87	0.00	+						47.2
poa_00002	Poeae	1.12	0.36							40.6
cyp_00002	<i>Carex</i> sp. 1	0.00	0.88							39.6
poa_00008	Poeae	0.00	0.99							38.7
summed7	<i>Crepis paludosa</i>	0.00	0.75							37.7
mav_00004	<i>Camponotus herculeanus</i>	0.00	0.99							36.8
ast_00010	<i>Cirsium</i> sp.	0.00	0.62							34.9
gh_00002	Asterales	0.00	0.55							34.9
gh_00007	Poeae	8.68	0.01			+++		+		31.1
gh_00005	<i>Empetrum</i> sp.	0.00	0.91							24.5

^a OTU-Operational taxonomic unit.

Positive (+) or negative (-) relationships within a factor are indicated based on the following significance $p_{z(>z)}$ values *** = 0.001, ** = 0.01, * = 0.05, (*) = 0.10, and empty cells = 1.

Plant species are indicated on light-gray, insects on dark-gray, and vertebrates on white background.

Table 2. Model selection based on AIC_c values (w_i = AIC_c weights) finding the most parsimonious linear mixed-effect model when fitting 120 samples of fecal crude protein (CP) of brown bears in relation to sex, age and reproductive categories and habitat types (prior to visit to settlements, settlements, and remote areas), and human presence and bear duration at settlements, in south-central Sweden between May and September 2010.

A variable on gray background and strikethrough represents its exclusion. BC=bear category, Fe=field exposure, d=Julian date, HP=human presence, Sd=settlement duration, SR= prior to visit to a settlement, settlement, and remote areas

Candidate models	K	AIC _c	ΔAIC _c	w_i	$w_{i \text{ cum.}}$
mod 10 BC + SR + Fe + Sd + d	8	681.77	0.00	0.97	0.97
mod 9 BC + HP + Fe + Sd + d	6	689.70	7.93	0.02	0.98
mod 8 BC + SR + Fe + Sd + d	6	690.07	8.30	0.02	1.00
mod 7 BC + SR + Fe + Sd + d	5	707.49	25.71	0.00	1.00
mod 11 Intercept only	3	708.12	26.35	0.00	1.00
mod 3 BC + SR + Fe + Sd + d	10	710.79	29.01	0.00	1.00
mod 2 BC + HP + Fe + Sd + d	12	711.20	29.43	0.00	1.00
mod 1 BC + SR + Fe + Sd + d	12	711.72	29.95	0.00	1.00
mod 6 BC + SR + Fe + Sd + d	6	718.91	37.13	0.00	1.00
mod 5 BC + HP + Fe + Sd + d	8	719.27	37.50	0.00	1.00
mod 4 BC + SR + Fe + Sd + d	8	719.76	37.99	0.00	1.00

Table 3. Fecal crude protein (CP) among categories of brown bears during May – September 2010, based on the most parsimonious linear mixed-effect model with bear identity as random effect (Table 2). Markov Chain Monte Carlo (MCMC)-simulated β and its 95 % highest posterior density interval (HPD) and P-values are given with β and standard errors (SE) based on a t -distribution. Variances of random effects are 11.06 for bear identity and 12.04 for residuals for highest ranked model. Adult males are reference level within the bear category factor.

$\Delta\text{AIC}_c = 0.00, w = 0.97$	β	SE	β_{MCMC}	HPD 95 % lower	HPD 95 % upper	P_{MCMC}
(Intercept)	30.772	3.013	29.547	24.147	35.112	0.001
Females w cubs of the year	-1.573	2.379	-1.930	-5.707	1.996	0.294
Females with yearlings	-5.045	2.888	-4.556	-9.008	-0.181	0.024
Lone adult females	-0.293	1.991	-0.239	-3.455	2.612	0.904
Subadult females and males	-0.057	1.987	-0.061	-2.982	2.976	0.972
Julian date	-0.081	0.014	-0.074	-0.098	-0.045	0.001

Table 4. Model selection based on AIC_c values (w_i = AIC_c weights) finding the most parsimonious linear mixed-effect model when fitting 120 samples of fecal crude fat (CFA) of brown bears in relation to sex, age and reproductive categories and habitat types (prior to visit to settlements, settlements, and remote areas), and human presence and bear duration at settlements, in south-central Sweden between May and September 2010. A variable on gray background and strikethrough represents its exclusion. BC=bear category, Fe=field exposure, d=Julian date, HP=human presence, Sd=settlement duration, SR= prior to visit to a settlement, settlement, and remote areas

Candidate models	K	AIC _c	Δ AIC _c	w_i	$w_{i \text{ cum.}}$
mod 11 Intercept only	3	488.59	0.00	0.92	0.92
mod 10 BC + SR + Fe + Sd + d	8	493.75	5.15	0.07	0.99
mod 8 BC + SR + Fe + Sd + d	6	498.15	9.55	0.01	1.00
mod 9 BC + HP + Fe + Sd + d	6	500.01	11.41	0.00	1.00
mod 7 BC + SR + Fe + Sd + d	5	518.16	29.57	0.00	1.00
mod 1 BC + SR + Fe + Sd + d	12	526.60	38.01	0.00	1.00
mod 3 BC + SR + Fe + Sd + d	10	527.42	38.83	0.00	1.00
mod 2 BC + HP + Fe + Sd + d	12	529.31	40.72	0.00	1.00
mod 4 BC + SR + Fe + Sd + d	8	531.25	42.66	0.00	1.00
mod 6 BC + SR + Fe + Sd + d	6	531.70	43.11	0.00	1.00
mod 5 BC + HP + Fe + Sd + d	8	533.73	45.13	0.00	1.00

Table 5. Model selection based on AIC_c values (w_i = AIC_c weights) finding the most parsimonious linear mixed-effect model when fitting 120 samples of fecal crude acid detergent lignin/neutral detergent fiber (ADL/NDF) of brown bears in relation to sex, age and reproductive categories and habitat types (prior to visit to settlements, settlements, and remote areas), and human presence and bear duration at settlements, in south-central Sweden between May and September 2010. A variable on gray background and strikethrough represents its exclusion. BC=bear category, Fe=field exposure, d=Julian date, HP=human presence, Sd=settlement duration, SR= prior to visit to a settlement, settlement, and remote areas

Candidate models	K	AIC _c	Δ AIC _c	w_i	$w_{i \text{ cum.}}$
mod 11 Intercept only	3	36.91	0.00	1.00	1.00
mod 9 BC + HP + Fe + Sd + d	6	55.14	18.23	0.00	1.00
mod 8 BC + SR + Fe + Sd + d	6	58.57	21.66	0.00	1.00
mod 10 BC + SR + Fe + Sd + d	8	64.65	27.74	0.00	1.00
mod 7 BC + SR + Fe + Sd + d	5	70.54	33.63	0.00	1.00
mod 6 BC + SR + Fe + Sd + d	6	86.55	49.64	0.00	1.00
mod 5 BC + HP + Fe + Sd + d	8	93.89	56.98	0.00	1.00
mod 4 BC + SR + Fe + Sd + d	8	96.53	59.63	0.00	1.00
mod 3 BC + SR + Fe + Sd + d	10	102.97	66.06	0.00	1.00
mod 2 BC + HP + Fe + Sd + d	12	111.52	74.61	0.00	1.00
mod 1 BC + SR + Fe + Sd + d	12	112.68	75.78	0.00	1.00

Table 6. Correlation and significance of factors and vectors fitted to the detrended correspondence analysis (DCA) ordination for dietary composition of brown bears in south-central Sweden.

Significant factors and vectors are indicated in bold. P-values are based on 999 random permutations.

Factor	r²	P_{r(>r)}
Visit	0.7454	0.001
Settlement distance	0.0229	0.349
Bear identity	0.5215	0.001
Sex, age, repr. category	0.0904	0.021
Date	0.5350	0.001
Fat (% feces)	0.0805	0.014
ADL/NDF (% feces)	0.0028	0.856
Protein (% feces)	0.3443	0.001
Visit duration	0.0253	0.283
Field exposure	0.0827	0.140

r² – the maximized correlation vector.

ADL/NDF – acid detergent lignin/neutral detergent fiber

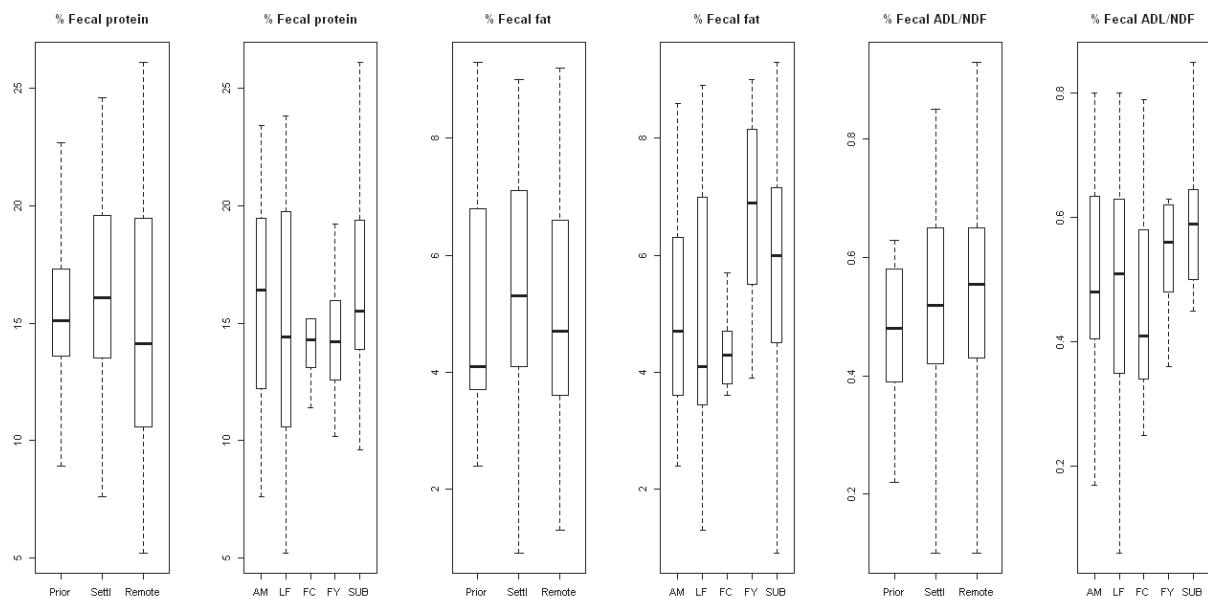


Figure 1. Boxplots (i.e. median, 1st and 3rd quartiles and range) of fecal nutritive content for sex, age and reproductive categories of brown bears (AM-adult males, LF-lone parous females, FC-females with cubs of the year, FY-females with yearlings, SUB-subadult males and females) and in relation to before visit to settlements (Prior), at settlements (Settl), and in remote areas, during May-September 2010. Nutritive parameters are measured relative to the dry matter content (in %), based on near-infrared spectroscopy (ADL-acid detergent lignin, NDF-neutral detergent fiber).

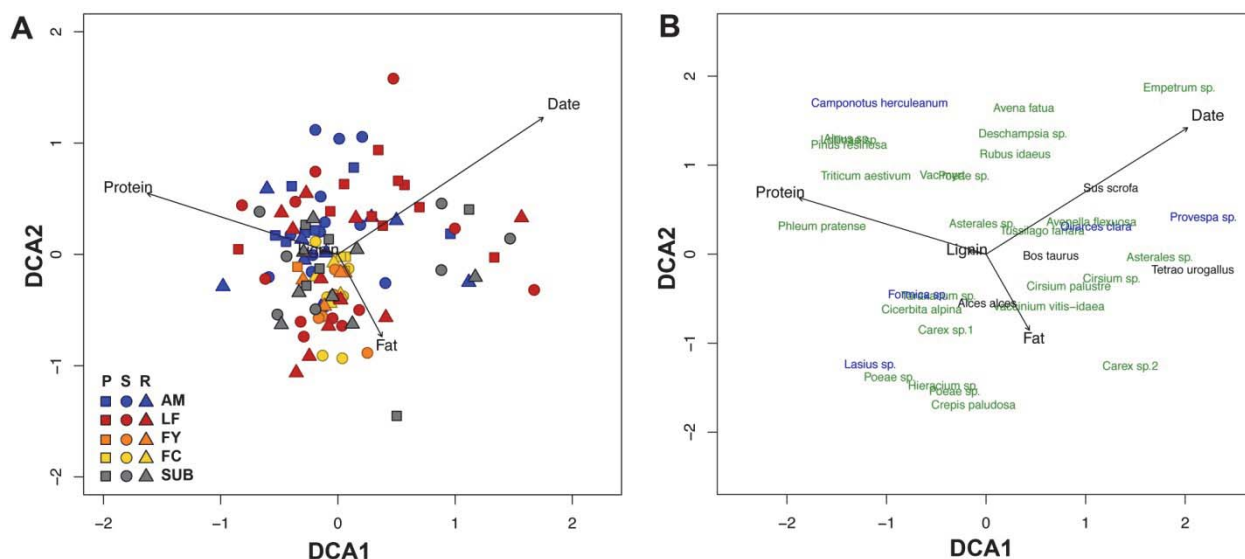


Figure 2. Detrended correspondence analysis of diet composition and quality based on 106 fecal samples from brown bears of different sex, age and reproductive categories before or when they occurred near settlements, or used remote areas in south-central Sweden 2010. Dietary composition A) shown in relation to settlements and sex, age and reproductive bear categories, and B) shown in relation to common food items. Nutritive quality is based on near infrared spectroscopy and species identification of diet is based on the DNA metabarcoding approach. Categories are defined as follows: P-prior to settlement visits, S-settlements, R-remote areas, AM-adult males, LF-lone parous females, FY-females with yearlings, FC-females with cubs, SUB-subadult females and males.

Appendix

Table S1. Kendall's Tau correlation tests of Scandinavian brown bears' diet between detrended correspondence analysis (DCA) and global nonmetric multidimensional scaling (GNMDS) axes for GNMDS ordinations run in two dimensions. Significant correlation between axes ($p < 0.05$) is indicated by bold font.

	<u>GMDS 1</u>		<u>GNMDS 2</u>	
	Kendall's tau	$P \tau_{(\tau)}$	Kendall's tau	$P \tau_{(\tau)}$
DCA1	0.309	<0.001	-0.401	<0.001
DCA2	0.565	<0.001	0.343	<0.001

Table S2. Frequency and identity of 228 diet items recovered from analysis based on DNA metabarcoding of 106 fecal remains of brown bears in south-central Sweden 2010. Plant species are indicated on light-gray, insects on dark-gray, and vertebrates on white background.

OTU Name ^a	Kingdom/Phylum	Species	Frequency	Reads	Best identity
gh_00001	Plantae	<i>Vaccinium vitis-idaea</i>	91	4034929	1.00
mav_00001	Arthropoda	<i>Formica</i> sp.	87	2572392	1.00
ast_00001	Plantae	<i>Tussilago farfara</i>	86	1067530	1.00
ast_00003	Plantae	<i>Taraxacum</i>	84	533355	1.00
v05_00002	Chordata	<i>Alces alces</i>	83	241930	1.00
ast_00002	Plantae	<i>Cirsium palustre</i>	79	927587	1.00
poa_00003	Plantae	<i>Avenella flexuosa</i>	68	310499	1.00
ros_00001	Plantae	<i>Rubus idaeus</i>	66	282754	1.00
poa_00004	Plantae	<i>Deschampsia</i> sp.	59	209737	1.00
summed6	Plantae	<i>Cicerbita alpina</i>	59	345647	1.00
gh_00003	Plantae	<i>Vaccinium myrtillus</i>	54	1429792	0.98
mav_00002	Arthropoda	<i>Oliarces clara</i>	53	1767672	0.97
v05_00010	Chordata	<i>Bos</i> sp.	53	30189	1.00
ast_00012	Plantae	<i>Hieracium</i> sp.	52	83706	1.00
poa_00001	Plantae	<i>Avena</i> sp.	51	404048	1.00
v05_00003	Chordata	<i>Sus scrofa</i>	50	78161	1.00
poa_00002	Plantae	Poeae	43	355698	1.00
cyp_00002	Plantae	<i>Carex</i> sp. 1	42	51055	1.00
poa_00008	Plantae	Poeae	41	81144	1.00
summed7	Plantae	<i>Crepis paludosa</i>	40	235110	0.97
mav_00004	Arthropoda	<i>Camponotus herculeanus</i>	39	1453732	1.00
ast_00010	Plantae	<i>Cirsium</i> sp.	37	91064	1.00
gh_00002	Plantae	Asterales	37	1540008	0.98
gh_00007	Plantae	Poeae	33	540600	0.98
gh_00005	Plantae	<i>Empetrum</i> sp.	26	1166872	0.94
gh_00016	Plantae	Asterales sp.	23	279616	0.98
mav_00007	Arthropoda	<i>Lasius</i> sp.	23	337584	1.00
gh_00036	Plantae	<i>Pinus resinosa</i>	21	64671	0.98
poa_00010	Plantae	<i>Triticum aestivum</i>	21	43586	1.00
summed11	Plantae	<i>Phleum pratense</i>	21	27849	1.00
cyp_00004	Plantae	<i>Carex</i> sp. 2	20	32019	1.00
mav_00005	Arthropoda	<i>Provespa barthelemyi</i>	20	1198307	0.97
poa_00031	Plantae	Loliinae	20	10376	1.00
summed14	Plantae	<i>Alnus</i> sp.	20	54561	1.00
v05_00007	Chordata	<i>Tetrao urogallus</i>	20	46519	1.00
ros_00011	Plantae	<i>Potentilla anglica</i>	19	11185	1.00
poa_00005	Plantae	Agrostidinae	18	105960	1.00

ast_00019	Plantae	<i>Hieracium</i> sp.	17	19194	1.00
cyp_00025	Plantae	<i>Carex</i> sp. 3	17	5385	1.00
cyp_00003	Plantae	<i>Carex</i> sp. 4	16	44303	1.00
gh_00008	Plantae	Salicaceae	16	400681	0.98
gh_00017	Plantae	<i>Musineon vaginatum</i>	16	247771	0.98
poa_00023	Plantae	Triticeae	15	15192	1.00
v05_00004	Chordata	<i>Oryctolagus cuniculus</i>	15	76285	1.00
v05_00009	Chordata	Anatidae	15	33497	1.00
v05_00035	Chordata	<i>Gallus</i> sp.	15	4165	1.00
summed2	Plantae	<i>Ambrosia artemisiifolia</i>	14	9198	0.99
mav_00009	Arthropoda	Vespoidea	13	158702	0.97
summed5	Plantae	<i>Chamerion angustifolium</i>	13	192289	1.00
v05_00016	Chordata	<i>Ovis</i> sp.	13	14080	1.00
gh_00038	Plantae	<i>Picea breweriana</i>	12	57292	0.98
poa_00019	Plantae	Poeae	12	19278	1.00
poa_00024	Plantae	Triticeae	12	12742	1.00
ros_00005	Plantae	<i>Rubus arcticus</i>	12	26093	1.00
summed1	Plantae	<i>Carex vaginata</i>	12	6712	0.99
summed13	Plantae	<i>Poa trivialis</i>	12	4581	1.00
ast_00032	Plantae	Asteracea	11	8739	1.00
ros_00003	Plantae	<i>Potentilla</i> sp.	11	67184	1.00
v05_00011	Chordata	<i>Tetrao</i> sp.	11	25117	1.00
v05_00405	Chordata	<i>Cervus elaphus</i>	11	149	1.00
ast_00022	Plantae	<i>Hieracium</i> sp.	10	6736	0.99
ast_00030	Plantae	<i>Cirsium</i> sp.	10	10712	0.99
gh_00032	Plantae	<i>Rumex hastatulus</i>	9	79844	0.97
gh_00039	Plantae	<i>Calluna vulgaris</i>	9	44191	1.00
mav_00057	Arthropoda	<i>Eriesthis</i> cf. 'rhodesiana'	9	13059	1.00
poa_00057	Plantae	<i>Hordeum vulgare</i>	9	3805	1.00
ros_00032	Plantae	<i>Alchemilla</i> sp.	9	1359	1.00
gh_00042	Plantae	<i>Lathyrus pratensis</i>	8	42330	1.00
gh_00046	Plantae	<i>Vaccinium uliginosum</i>	8	29965	1.00
mav_00033	Arthropoda	Protostomia	8	27815	0.97
poa_00007	Plantae	Agrostidinae	8	59721	1.00
ros_00193	Plantae	<i>Sorbus</i> sp.	8	375	1.00
summed15	Plantae	<i>Vaccinium microcarpum</i>	8	63599	0.98
ast_00017	Plantae	Tussilaginatae	7	14876	0.99
mav_00013	Arthropoda	<i>Bombus</i> sp.	7	93199	1.00
poa_00012	Plantae	<i>Triticum</i> sp.	7	9840	1.00
summed9	Plantae	<i>Malus</i> sp.	7	70	1.00
v05_00059	Chordata	<i>Sylvia crassirostris</i>	7	3796	1.00
v05_00693	Chordata	<i>Erinaceus concolor</i>	7	111	1.00
ast_00356	Plantae	<i>Tragopogon</i> sp.	6	927	1.00

cyp_00007	Plantae	<i>Carex</i> sp. 5	6	22570	0.99
mav_00027	Arthropoda	Mycetophilidae	6	33444	1.00
ros_00014	Plantae	<i>Comarum palustre</i>	6	6775	1.00
v05_00558	Chordata	<i>Felis catus</i>	6	131	1.00
ast_00027	Plantae	Gnaphalieae	5	12468	0.95
ast_00498	Plantae	Cichorieae	5	656	1.00
cyp_00045	Plantae	<i>Carex</i> sp. 6	5	3378	0.97
mav_00014	Arthropoda	Protostomia	5	92869	0.97
mav_00028	Arthropoda	<i>Pyrobombus</i> sp.	5	33332	1.00
mav_00046	Arthropoda	<i>Argulus americanus</i>	5	17976	0.97
ros_00600	Plantae	<i>Prunus</i> sp.	5	61	1.00
v05_00037	Chordata	<i>Lepus</i> sp.	5	5018	1.00
ast_00011	Plantae	<i>Lactuca</i> sp.	4	82117	1.00
mav_00032	Arthropoda	<i>Sylvicola fenestralis</i>	4	29681	1.00
poa_00048	Plantae	Loliinae	4	5730	1.00
poa_00081	Plantae	Poeae	4	2248	0.97
ros_00052	Plantae	<i>Prunus</i> sp.	4	1463	1.00
v05_00113	Chordata	<i>Actitis hypoleucos</i>	4	2174	1.00
ast_00047	Plantae	Cichorieae	3	3108	0.99
ast_01398	Plantae	<i>Prenanthes purpurea</i>	3	86	1.00
cyp_00052	Plantae	<i>Carex</i> sp. 7	3	2363	1.00
gh_00056	Plantae	<i>Luzula pilosa</i>	3	18877	1.00
gh_00095	Plantae	<i>Melampyrum sylvaticum</i>	3	5178	1.00
mav_00044	Arthropoda	<i>Symydobius kabae</i>	3	17348	1.00
mav_00064	Arthropoda	Pancrustacea	3	10493	0.97
mav_00065	Arthropoda	Ditrysia	3	10021	0.97
poa_00054	Plantae	<i>Milium effusum</i> subsp. <i>effusum</i>	3	3783	1.00
poa_00077	Plantae	Poeae	3	2792	1.00
ros_00042	Plantae	<i>Alchemilla</i> sp.	3	2714	1.00
ros_00377	Plantae	<i>Rubus</i> sp.	3	11	1.00
v05_00066	Chordata	<i>Sylvaemus</i> sp.	3	3605	1.00
v05_00577	Chordata	<i>Canis</i> sp.	3	62	1.00
cyp_00010	Plantae	<i>Carex</i> sp. 8	2	32	1.00
cyp_00170	Plantae	<i>Carex</i> sp. 9	2	493	1.00
gh_00018	Plantae	<i>Cannabis sativa</i>	2	241885	1.00
gh_00047	Plantae	<i>Areca triandra</i>	2	27985	0.98
gh_00052	Plantae	Brassicaceae	2	15432	0.97
gh_00065	Plantae	<i>Melampyrum pratense</i>	2	11255	1.00
gh_00115	Plantae	<i>Lotus japonicus</i>	2	5716	0.98
gh_00117	Plantae	<i>Polygonum cognatum</i>	2	6509	0.96
gh_00125	Plantae	Hypnales	2	4842	0.96
gh_00137	Plantae	<i>Geranium</i> sp.	2	4885	0.96
gh_00174	Plantae	<i>Viola bulbosa</i> subsp. <i>tuberifera</i>	2	1055	0.98
gh_00259	Plantae	<i>Sphagnum</i> sp.	2	2697	0.96

mav_00019	Arthropoda	<i>Bombus sporadicus</i>	2	55845	1.00
mav_00036	Arthropoda	<i>Cosmophasis micarioides</i>	2	25046	0.97
mav_00048	Arthropoda	<i>Bombus</i> sp.	2	17569	0.97
mav_00126	Arthropoda	Athetini	2	4427	1.00
mav_00143	Arthropoda	Caeciliusidae	2	3838	1.00
mav_00164	Arthropoda	Pancrustacea	2	3286	0.97
mav_00177	Arthropoda	<i>Stemonyphantes</i> sp.	2	2635	1.00
mav_00193	Arthropoda	<i>Bombus</i> sp.	2	3015	1.00
mav_00228	Arthropoda	<i>Evarcha</i> sp.	2	1946	1.00
mav_00270	Arthropoda	Pancrustacea	2	2001	0.97
poa_00039	Plantae	<i>Alopecurus japonicus</i>	2	7616	1.00
poa_00055	Plantae	Pooideae	2	758	0.99
poa_00060	Plantae	<i>Oryza</i> sp.	2	4304	1.00
poa_00072	Plantae	<i>Vahlodea atropurpurea</i>	2	1599	0.99
poa_00086	Plantae	Poeae	2	2134	0.97
poa_00140	Plantae	<i>Dactylis glomerata</i>	2	1047	1.00
poa_00152	Plantae	<i>Holcus lanatus</i>	2	855	1.00
ros_00077	Plantae	<i>Rubus</i> sp.	2	729	1.00
summed10	Plantae	<i>Molinia caerulea</i>	2	8994	0.99
ast_00075	Plantae	<i>Cirsium</i> sp.	1	2528	0.99
ast_00078	Plantae	Cichorieae	1	2417	0.99
ast_00125	Plantae	<i>Cirsium arvense</i>	1	2065	1.00
ast_01047	Plantae	<i>Cirsium</i> sp.	1	20	0.99
ast_01267	Plantae	<i>Leontodon hispidus</i>	1	133	1.00
ast_01693	Plantae	Tussilagininae	1	19	0.98
cyp_00099	Plantae	<i>Carex</i> sp. 10	1	917	1.00
cyp_00112	Plantae	<i>Carex</i> sp. 11	1	205	1.00
cyp_00173	Plantae	<i>Carex</i> sp. 12	1	533	0.96
cyp_00223	Plantae	<i>Carex</i> sp. 13	1	361	1.00
cyp_00254	Plantae	<i>Carex</i> sp. 14	1	344	1.00
cyp_00469	Plantae	<i>Carex</i> sp. 15	1	142	1.00
cyp_00634	Plantae	<i>Carex</i> sp. 16	1	58	1.00
gh_00006	Plantae	<i>Vaccinium ovalifolium</i>	1	2028	1.00
gh_00105	Plantae	<i>Teucrium</i> sp.	1	4779	0.98
gh_00106	Plantae	<i>Morella diversifolia</i>	1	7598	0.96
gh_00138	Plantae	<i>Trifolium gymnocarpon</i>	1	5259	0.98
gh_00157	Plantae	<i>Musa rosea</i>	1	1705	0.98
gh_00160	Plantae	<i>Trifolium</i> sp.	1	4100	0.98
gh_00179	Plantae	<i>Ptilium crista-castrensis</i>	1	3667	1.00
gh_00198	Plantae	<i>Trientalis europaea</i>	1	1941	1.00
gh_00261	Plantae	<i>Leucothoe</i> sp.	1	2532	0.98
gh_00340	Plantae	<i>Allium</i> sp.	1	1140	0.98
gh_00366	Plantae	<i>Vicia cracca</i>	1	1798	1.00

gh_00484	Plantae	Arecaceae	1	1192	0.96
gh_01045	Plantae	<i>Tumamoca macdougalii</i>	1	354	0.96
gh_01574	Plantae	<i>Juncus balticus</i>	1	241	0.98
gh_02455	Plantae	<i>Asparagus</i> sp.	1	148	0.98
mav_00018	Arthropoda	<i>Bombus campestris</i>	1	66625	1.00
mav_00026	Arthropoda	Aphidomorpha	1	34608	0.97
mav_00061	Arthropoda	Pancrustacea	1	11508	0.97
mav_00078	Arthropoda	<i>Prosarthria teretirostris</i>	1	8368	0.97
mav_00083	Arthropoda	Pancrustacea	1	7388	0.97
mav_00159	Arthropoda	Schizophora	1	3398	0.97
mav_00230	Arthropoda	Pancrustacea	1	2538	0.97
mav_00239	Arthropoda	Scarabaeidae	1	1405	1.00
mav_00240	Arthropoda	Obtectomera	1	1928	0.97
mav_00243	Arthropoda	Pancrustacea	1	1818	0.97
mav_00276	Arthropoda	<i>Metoeus</i> sp.	1	1855	1.00
mav_00283	Arthropoda	Mandibulata	1	1776	0.97
mav_00290	Arthropoda	Cicadellidae	1	1436	0.97
mav_00293	Arthropoda	<i>Deroceras reticulatum</i>	1	1873	1.00
mav_00299	Arthropoda	<i>Macrosteles fascifrons</i>	1	1787	1.00
mav_00300	Arthropoda	Lycosidae	1	1807	0.97
mav_00360	Arthropoda	Pancrustacea	1	1197	0.97
mav_00371	Arthropoda	Polyphaga	1	1322	0.97
mav_00377	Arthropoda	Nicrophorinae	1	1306	0.97
mav_00387	Arthropoda	Protostomia	1	1282	0.97
mav_00411	Arthropoda	Aleocharinae	1	587	1.00
mav_00437	Arthropoda	Miridae	1	1054	1.00
mav_00458	Arthropoda	<i>Evarcha</i> sp.	1	348	0.97
mav_00472	Arthropoda	<i>Pardosa</i> sp.	1	650	1.00
mav_00480	Arthropoda	<i>Thrips flavidulus</i>	1	678	0.97
mav_00492	Arthropoda	<i>Syneta adamsi</i>	1	886	1.00
mav_00530	Arthropoda	<i>Bolitochara pulchra</i>	1	778	1.00
mav_00587	Arthropoda	<i>Isotoma viridis</i>	1	541	0.97
mav_00722	Arthropoda	Polyphaga	1	433	0.97
mav_00754	Arthropoda	<i>Paralamyctes</i> sp.	1	382	1.00
mav_01252	Arthropoda	Endopterygota	1	146	0.97
mav_01374	Arthropoda	Mandibulata	1	165	0.97
mav_01381	Arthropoda	<i>Ampedus</i> sp.	1	156	1.00
poa_00062	Plantae	Agrostidinae	1	444	0.99
poa_00074	Plantae	<i>Poa</i> sp.	1	158	1.00
poa_00098	Plantae	Triticeae	1	285	1.00
poa_00132	Plantae	Poeae	1	807	0.99
poa_00182	Plantae	Poeae	1	808	0.96
poa_00197	Plantae	Loliinae	1	872	0.99
poa_00298	Plantae	Poeae	1	388	0.99

poa_00385	Plantae	<i>Melica picta</i>	1	295	1.00
poa_00530	Plantae	Poeae	1	113	0.97
poa_00689	Plantae	Poeae	1	239	0.97
ros_00053	Plantae	<i>Potentilla reptans</i>	1	57	1.00
ros_00073	Plantae	<i>Fragaria</i> sp.	1	21	1.00
ros_00468	Plantae	<i>Rosa</i> sp.	1	52	1.00
summed3	Arthropoda	<i>Apis mellifera</i>	1	201	1.00
summed4	Arthropoda	<i>Bradysia amoena</i>	1	557	0.97
v05_00114	Chordata	<i>Meleagris gallopavo</i>	1	163	1.00
v05_00130	Chordata	<i>Dama dama</i>	1	1516	1.00
v05_00184	Chordata	<i>Tetrastes bonasia</i>	1	108	1.00
v05_00192	Chordata	<i>Sorex araneus</i>	1	731	1.00
v05_00216	Chordata	<i>Anas</i> sp.	1	647	1.00
v05_00269	Chordata	<i>Turdus philomelos</i>	1	74	1.00
v05_00356	Chordata	<i>Rana temporaria</i>	1	195	1.00
v05_00516	Chordata	<i>Lutra lutra</i>	1	201	1.00
v05_00821	Chordata	<i>Canis lupus familiaris</i>	1	38	1.00

^a OTU-Operational taxonomic unit

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