# Research Article



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

MARCUS ELFSTRÖM, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432, Ås, Norway

ANDREAS ZEDROSSER, Department of Environmental and Health Studies, Telemark University College, NO-3800, Bø i Telemark, Norway; and Institute of Wildlife Biology and Game Management, Department of Integrative Biology and Biodiversity Research, University of Natural Resources and Applied Life Sciences, Gregor-Mendel-Str. 33, A-1180, Vienna, Austria

KLEMEN JERINA, Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Večna pot 83 SI-1000, Ljubljana, Slovenia

OLE-GUNNAR STØEN, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432, Ås, Norway

JONAS KINDBERG, Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83, Umeå, Sweden

LARA BUDIC, Faculty of Forestry and Environmental Sciences, University of Freiburg, Tennenbacherstr. 4 DE-79106, Freiburg, Germany; and Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432, Ås, Norway

MARKO JONOZOVIČ, Slovenia Forest Service, Večna pot 2 SI-1000, Ljubljana, Slovenia

JON E. SWENSON, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, NO-1432, Ås, Norway; and Norwegian Institute for Nature Research, NO-7485, Trondheim, Norway

ABSTRACT Bears foraging near human developments are often presumed to be responding to food shortage, but this explanation ignores social factors, in particular despotism in 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 (i.e., problem bears; n = 149), in self-defense (n = 51), or were hunter-killed nonproblem bears (n = 1,896) during 1990–2010. We compared patterns between areas with (Slovenia) and without supplemental feeding (Sweden) of bears relative to 2 hypotheses. The food-search/food-competition hypothesis predicts that problem bears should 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, that BCI and human density should have a positive correlation, and problem bear occurrence and seasonal mean BCI of nonproblem bears should have a negative correlation (i.e., more problem bears during years of low food availability). Food competition among bears additionally predicts an inverse relationship between BCI and bear density. The safety-search/naivety hypothesis (i.e., avoiding other bears or lack of human experience) predicts no relationship between BCI and human density, provided no dietary differences due to spatiotemporal habitat use among bears, no relationship between problem bear occurrence and seasonal mean BCI of nonproblem bears, and does not necessarily predict a difference between BCI for problem/nonproblem bears. 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 or nonproblem bear status, or between age and human density. We found no difference in BCI or its variability 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 fall hyperphagia). Problem bears were younger than nonproblem bears, and both problem and nonproblem bears were younger in areas of 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, suggested safety-search and naïve dispersal to be the primary mechanisms responsible for bear occurrence near settlements. Younger bears are less competitive, more vulnerable to intraspecific predation, and lack human experience, compared to adults. Body condition was inversely related to the bear density index in Sweden, whereas we found no correlation in Slovenia, suggesting that supplemental feeding may have reduced 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 explained why most bears were involved in encounters with people or viewed as problematic near settlements

Received: 17 April 2013; Accepted: 4 April 2014

Published: 17 June 2014

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made. 

1E-mail: marcus.elfstrom@nmbu.no

in our study. © 2014 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

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

Because of successful conservation efforts, populations of large carnivores have increased in numbers and geographic range in many areas around the world (Linnell et al. 2001, Enserink and Vogel 2006). This increase has occurred even in areas with high human densities in Europe (Linnell et al. 2001). However, the occurrence of large carnivores near human settlements is often viewed as problematic, because these animals can damage property, and people fear them (Røskaft et al. 2003).

Bears (*Ursidae*) may approach human settlements in search of food, which can result in food conditioning (McCullough 1982, Gunther et al. 2004, Rogers 2011). Several studies have reported a negative correlation between the 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 explanation, 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 lethal removal (Beckmann et al. 2004, Spencer et al. 2007).

Although bears generally avoid human activity and settlements (Mace and Waller 1996, Jerina et al. 2003, Nellemann et al. 2007), some do use areas close to people or settlements, even when food attractants 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*a*).

Dominant bears may use more remote areas and, therefore, predation-vulnerable conspecifics may select habitats closer to people to avoid being killed by these dominant bears (i.e., a despotic effect; Stevaert et al. 2013a, Elfström et al. 2014). Spatial or temporal segregation based on sex, age, and reproductive class occurs in bears (Mattson et al. 1987, Wielgus and Bunnell 1994, Ben-David et al. 2004, Steyaert et al. 2013a), and social hierarchies occur at aggregation sites for feeding (Craighead et al. 1995). Because older bears may kill younger conspecifics (McLellan 1994, Swenson et al. 2001), subadults and females with dependent offspring are most vulnerable (Mattson 1990, Swenson et al. 2001, McLellan 2005). Females with young of the year often come closer to settlements than solitary adult females and adult males (Steyaert et al. 2013a). 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).

Our objective was to test 2 hypotheses that emerged from a review of the literature by Elfström et al. (2014): foodsearch/food-competition and safety-search/naivety to determine the potential mechanisms underlying the phenomenon of brown bear (*Ursus arctos*) occurrence near settlements. We used data from Slovenia and Sweden, 2 countries that differ in regards to supplemental feeding, bait hunting, and harvest selectivity (Bischof et al. 2008, Krofel et al. 2012, Kavčič et al. 2013). We analyzed the abundance, location, age distribution, and body condition of removed problem bears and bears killed during regular hunting (hereafter, nonproblem bears), in relation to densities of bears and people. Problem bears were bears 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 body condition, either higher or lower in problem bears compared to nonproblem bears (Table 1). High body condition in problem bears near people may result from exploitation of easily accessible and highly nutritious foods (Hobson et al. 2000, Robbins et al. 2004) in combination with reduced intraspecific competition in areas with concentrated settlements. Low body condition in problem bears may result from failure to find food in remote areas in combination with high food competition (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 problem bears exploit crops or other human-derived foods regularly. The effects of food competition among bears, independently of problem bear status, predict 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 natural food availability (Mattson et al. 1992, Schwartz et al. 2006), and during times of the year with lower natural food availability (e.g., early spring after den emergence, fall hyperphagia when mast availability is poor; Gunther et al. 2004). We expected the age distribution to be equal between problem and nonproblem bears if bears primarily search for food near settlements. However, if interference competition occurs among bears, food shortage may affect smaller bears more, 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 should

**Table 1.** Predictions and results of testing hypotheses separating food search and social organization to explain the occurrence of management-killed problem brown bears near settlements and hunter-killed nonproblem brown bears in Slovenia and Sweden between 1990 and 2010. Results are based on the most parsimonious linear mixed models and generalized linear models using Akaike's Information Criterion, when analyzing body condition index (BCI), age, annual frequency of problem bear incidences, and reported time-of-the-year of problem bear incidences.

	Hypothe		
Variables or interactions	Food search/food competition	Safety search/naivety	Results
BCI of problem versus nonproblem bears	Lower or higher	No difference <sup>a</sup>	No difference
Variation in BCI of problem versus nonproblem bears	Lower in problem bears	No difference	No difference
BCI versus human density	Positive relationship	No relationship	No relationship
BCI versus bear density	Negative if competing for food	No relationship <sup>a</sup>	No relationship in Slovenia, negative relationship in Sweden
Age of problem versus nonproblem bears	Same or older <sup>b</sup> but younger if competing for food	Younger problem bears	Younger problem bears
Age versus human density	No relationship <sup>b</sup> but negative if competing for food	Negative relationship	Negative relationship
Time-of-the-year of problem bear incidences <sup>c</sup>	Early spring or fall <sup>d</sup> (pre-/post mating season)	Spring and early summer (mating season)	Spring and early summer (mating season)
Frequency of problem bears versus mean BCI of nonproblem bears	Negative relationship	No relationship	No relationship

<sup>&</sup>lt;sup>a</sup> Provided no dietary effects from different spatiotemporal use among bears.

be younger in areas with higher human density. Alternatively, because of 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 could be older.

The safety-search/naivety hypothesis predicts no difference in body condition, and low variability, between problem and nonproblem bears (Table 1). We would expect no correlation between problem bear occurrence and general food availability if avoidance of predation is more important than food competition. The frequency of bear problems was expected to be higher during the breeding season, when more aggression is shown towards subadults (Swenson et al. 2001), 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. 2014).

If bears shot in self-defense have experienced food shortage, we expected them to be in poorer body condition compared to nonproblem bears. Younger bears may be more likely than older ones to leave their diurnal resting sites when approached by people (Moen et al. 2012). Therefore, we expected that, independently of body condition, bears shot in self-defense should be older than nonproblem bears.

#### **STUDY AREA**

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, established in 1966, which is 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 2,970-3,670 animals in 2008, distributed over the northern 66% of the country (Kindberg et al. 2009, 2011). Human density in the Swedish bear range is low, although more populated areas occur at the edge of the bear distribution along the eastern coast (Kindberg et al. 2011). Body masses of bears are similar between Slovenia and Sweden, but they show different patterns and trends among seasons (Swenson et al. 2007). Swedish bears are characterized by a greater loss of body mass 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 lose body mass in spring, whereas Swedish bears gain weight, perhaps because of higher use of protein-rich meat and insects during spring in Sweden compared to Slovenia (Swenson et al. 2007).

### **METHODS**

### **Hunting and Supplemental Feeding**

In Slovenia, bears have access to supplemental food throughout the year; these feeding sites are used to attract bears, red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*) for hunting purposes. Supplemental feeding sites are not allowed within 2 km of human settlements, have a density of 1/400–700 ha, and all hunting occurs from elevated stands (Jerina 2012, Krofel et al. 2012). The Slovenian brown bear hunting season is from 1 October to 30 April, and the quota is prescribed based on 3 body mass categories; <100 kg (min. of 75% of quota), 100–150 kg (max. 15% of quota), and

<sup>&</sup>lt;sup>b</sup> Provided no density-dependent effects among bears.

<sup>&</sup>lt;sup>c</sup> Descriptive only.

<sup>&</sup>lt;sup>d</sup> Provided major mast failures in fall.

>150 kg (max. 10% of quota; Krofel et al. 2012). The bear harvest in Slovenia has increased significantly during the last 10 years, because of an increasing trend in bear damage (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 increased threefold during the last 10 years (Bischof et al. 2009a), and the quota was 322 animals in 2010, corresponding to a harvest rate of approximately 10%. In Sweden, hunting bears at bait sites and supplemental or diversionary feeding is illegal. The hunting season is from 21 August to 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 because of harvest regulations (Krofel et al. 2012). In Sweden, no hunter selectivity, in terms of sex and age distribution, seems to occur (Bischof et al. 2008, 2009a). The protection of females with cubs from hunting in both countries may underestimate their occurrence in the population when analyzing shot bears. Managers also may be more reluctant to kill problem females with offspring than solitary adult females (i.e., 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 are not suitable for explicitly testing for differences in sex or female reproductive status between problem and nonproblem bears.

#### **Data Collection**

We categorized a bear as a problem bear if 1) it had caused enough problems or incidents with people within 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. We considered bears reported to be shot in self-defense during hunting mostly other game species than bears to be a separate category, and such data were only available for Sweden.

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

#### Densities of Humans and Bears

We extracted human population densities within a 10-km radius around the kill position for every bear in Sweden and Slovenia using ArcGIS 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA). We calculated an index of bear density in Sweden from 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 indexed observations of bears are highly correlated (adjusted  $R^2 = 0.60-0.88$ ) with independent density estimates based on DNA in scats and capturemark-recapture methods and, thus, correctly reflect the true bear density (Kindberg et al. 2009). The mean ( $\pm$ SD) size of LMUs where bears were shot was  $2,208 \pm 1,576 \,\mathrm{km^2}$ , 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, when the observations started, and 2006 (we excluded 495 bears shot outside this period from analyses that included bear densities). We estimated Slovenian bear densities by combining 4 types of data with high correlation (r=0.75-0.80): 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). We extracted number of bears using an area of 120 km<sup>2</sup> 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). We calculated the BCI of bears according to Equation (1), where n is number of shot bears,  $e_{\rm st}$  is standardized residual, BM is body mass (kg), PW is front paw width (cm), and d is Julian date:

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

We extracted standardized residuals separately for subadults and adults because resource allocation may differ among age classes. The age of sexual maturity and of first litters in Slovenia is 4 years (Svigelj 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 old as subadults and bears ≥4 years as adults. We also extracted residuals separately for season (spring-summer and fall-winter) and country. We defined spring-summer as 1 March–15 July. This period started with the onset of spring hunting season in Slovenia (Krofel et al. 2012), although Swedish bears had not yet emerged from their winter dens (Friebe et al. 2001, Manchi and Swenson 2005), and ended with the termination of the mating season in both Slovenia (Krofel et al. 2010) and Sweden (Dahle and Swenson 2003a). We defined fall-winter as 1 August-15 February. This period started after the onset of the hyperphagia period and ended 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 hunting 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. The capturing of the bears were approved by the Swedish Environmental Protection Agency (permit Dnr 412-7327-09 Nv). We used the front paw width as a body size index, because it is likely not influenced by interannual fluctuations in body mass. Others have used body length as an index of body size when calculating body condition index (BCI) values (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 of overall size in bears (and better than total body length). A high BCI indicates high nutritional status and a low BCI indicates low nutritional status. To determine 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 obtained by bioelectrical impedance analysis (Farley and Robbins 1994).

# Comparing Age and Body Condition among Bears

We constructed linear mixed models (LMM) to model log-transformed age using the following fixed factors: sex, bear status (problem, nonproblem, or shot in self-defense), density index of bears, density of people, and country. We included year killed as a random effect. We modeled logtransformed body mass/paw width with an LMM, using the proportion of fat as a log-transformed fixed factor to compare BCI of captured bears. We included year as a random effect in this analysis. We modeled BCI using an 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. We included year killed 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. We standardized the bear density index, and included it only as an interaction with country, because it was calculated differently in Sweden and Slovenia, and because we were interested in separate inferences of the effects of bear density in each country.

We indexed the predictability of food resources via variability in BCI, and compared this variability between problem and nonproblem bears. We used a random subsample of nonproblem bears to generate equal sample sizes of problem and nonproblem bears. We expressed the variability in BCI as absolute values of BCI subtracted by mean BCI. We formally tested for equal variability in BCI between problem bears and nonproblem bears using an LMM, with a square-root transformed response; we treated

bear status (problem or nonproblem) as a fixed factor and included year killed as a random effect.

# Frequency of Problem Bears and Seasonal Body Condition

We used generalized linear models (GLM) to test if annual frequencies of shot problem bears could be explained by seasonal mean BCI. We used only nonproblem bears to calculate the mean BCI for a specific period, with residuals extracted separately for adults and subadults and country. We used 4 alternative periods to calculate seasonal mean BCI relative to frequencies of killed problem bears. We used seasonal mean BCI as a fixed factor, estimated for the fallwinter of the previous year, fall-winter in the current year, fall-winter of the previous year combined with springsummer of the current year, and spring-summer combined with fall-winter in the current year, to test for any lagged 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. We used the annual population size estimates as a fixed factor to control for increasing bear populations in relation to annual numbers of killed problem bears.

### Model Selection and Validation

We constructed all candidate models 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 Criterion, adjusted for small sample sizes (AIC<sub>c</sub>) and AIC<sub>c</sub> weights (w<sub>i</sub>; Akaike 1973, Burnham and Anderson 2002). We analyzed the number of problem bears in relation to seasonal mean BCI assuming a Poisson distribution, and we controlled for potential overdispersion in our GLMs by using quasi-likelihood theory for AIC model selection (qAIC; Richards 2008). We conducted all analyses using R.2.14.1 (R Development Core Team 2011). We used the package lme4 (Bates and Maechler 2010) for statistical modeling and generated parameter estimates (B) and 95% highest posterior density intervals (HPDs) 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). We considered effects as influential when the HPD around  $\beta$  did not include 0 in parsimonious models. We controlled for outliers by using Cleveland dotplots, and multicollinearity by using variance inflation factors (Zuur et al. 2009).

## **RESULTS**

The ratio between body mass and paw width was positively related to the proportion of fat in the same bear ( $\beta = 0.31 \pm 0.11$  SE) based on measurements from 61 bears. This relationship ( $w_i = 0.67$ ) was ranked as more parsimonious than an intercept-only model  $\Delta AIC_c = 1.38$ ; Appendices 1 and 2 available online at www.onlinelibrary.wiley.com).

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

The median density of bears in Slovenia was 110 (1st and 3rd quartiles: 67–156) bears per 1,000 km² where 726 nonproblem bears were shot and 123 (1st and 3rd quartiles: 105–139) bears per 1,000 km² where 117 problem bears were shot during 1996–2010. The median density index of bears in Sweden was 0.70 (1st and 3rd quartiles: 0.40–1.12) bears per 1,000 observation hours where 553 nonproblem bears were shot, 0.85 (1st and 3rd quartiles: 0.69–1.39) bears per 1,000 observation hours where 7 problem bears were shot, and 0.68 (1st and 3rd quartiles: 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 and Nonproblem Bears

In Slovenia, the median age was 2 (1st and 3rd quartiles: 2–4) years for 877 hunter-killed nonproblem bears and 2 (1st and 3rd quartiles: 1–3) years for 134 shot problem bears during 1996–2010. In Sweden, the median age was 3 (1st and 3rd quartiles: 2–7) years for 1,021 hunter-killed nonproblem bears, 3 (1st and 3rd quartiles: 2–10) years for 15 shot problem bears, and 7 (1st and 3rd quartiles: 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 age of killed Slovenian and Swedish bears ( $w_i = 0.94$ , 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  $\Delta AIC_c = 12.82$ ,  $w_i < 0.00$  (Appendix 3 available online at www.onlinelibrary.wiley.com). Therefore, we excluded the bear density index parameter and reran our candidate model set, thus

**Table 2.** Model selection based on corrected Akaike's Information Criterion (AIC<sub>c</sub>) values (K= number of parameters,  $w_i$ = AIC<sub>c</sub> weights, and  $w_i$  cum. = cumulative weights) finding the most parsimonious linear mixed model when fitting age of 2,096 brown bears shot in Slovenia and Sweden (1990–2010) with year shot as a random effect and excluding bear density (response is log transformed). Status categorizes bears as nonproblem, problem, or shot in self-defense, human density is log transformed, and ":" represents an interaction term without main effects.

Candidate models	K	$AIC_c$	$\Delta AIC_c$	$w_i$	$w_{i \text{ cum}}$ .
Sex + status + human density:country	8	5,063.86	0.00	0.98	0.98
Sex + status:human density + country	8	5,072.14	8.29	0.02	1.00
Sex + country	5	5,099.09	35.23	0.00	1.00
Intercept only	3	5,188.71	124.86	0.00	1.00

increasing our sample size by 495 bears. Bear status and human density were again included in the most parsimonious LMM ( $w_i$ =0.98, Table 2). Problem bears were 1.6  $\pm$  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 3, Fig. 1). Bears shot in self-defense in Sweden were 4.2  $\pm$  1.3 (SE) years older than nonproblem bears (log-transformed:  $\beta$ =0.619  $\pm$ 0.116 SE; Table 3).

# Body Condition of Problem and 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  $\Delta AIC_c = 5.14$ ,  $w_i = 0.05$  (i.e., an evidence ratio 12.8 times less likely than the most parsimonious LMM; Table 4). Bear density was included in 1 of the 2 LMMs with highest support ( $w_i = 0.64$ ; Table 4). Body condition indices 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 to bear density ( $\beta$ /SE < 0.5, and HPD interval of  $\beta$  included 0; Table 5, Fig. 2).

# Frequency of Problem Bears 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 (mode: Jun, median: 26 May [1st and 3rd quartiles: 20 Apr-20 Jun], n=75) and the second peak during late autumn (mode: Oct, median: 10 Oct [1st and 3rd quartiles: 5 Sep-3 Nov], n=59). The distribution of dates when problem bears were killed in Sweden (n=15) was unimodal with a mode of June and median of 15 June (1st and 3rd quartiles: 29 May-28 Aug). The distribution of dates when 51 Swedish bears were shot in self-defense was unimodal with a mode of September and median of 17 September (1st and 3rd quartiles: 2 Aug-25 Oct).

The frequency of problem bears killed annually was not related to seasonal mean BCI in either Slovenia (1999–2010) or Sweden (1997–2008) using any of our 4 alternative periods (entire current year, current fall, previous fall, and previous fall combined with current spring), nor with annual population size, because our intercept-only model was ranked as most parsimonious ( $w_i$ =0.99; Table 6). Variability in BCI was not different between problem and nonproblem bears, because our intercept-only LMM was ranked as most parsimonious ( $w_i$ =0.97; Table 7).

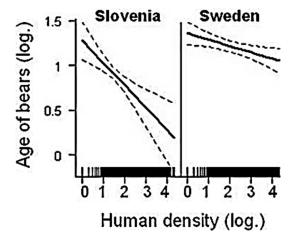
#### **DISCUSSION**

We found age differences between problem and nonproblem bears in both Slovenia and Sweden. Problem bears were 1.6 years  $\pm$  1.2 (SE) younger than nonproblem bears in both countries combined. In general, bears killed in areas with

Table 3. Log-transformed age among shot bears in Slovenia and Sweden between 1990 and 2010, in relation to bear status (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 log-transformed density of people, with year as a random effect. Variances of random effects are 0.0045 for year and 0.6406 for residuals, based on the most parsimonious linear mixed model. We provide Markov Chain Monte Carlo-simulated parameter estimates ( $\beta_{MCMC}$ ) and 95% highest posterior density intervals (HPD) with  $\beta$  and standard errors (SE) based on a *t*-distribution.

Model parameters	β	SE	$\beta_{ m MCMC}$	HPD lower	HPD upper
(Intercept)	1.359	0.059	1.362	1.250	1.480
Male	-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
Density people(log) × Slovenia	-0.125	0.016	-0.125	-0.154	-0.091
Density people(log) × Sweden	-0.027	0.010	-0.028	-0.049	-0.010

higher human density were younger, suggesting that younger bears have a higher likelihood of occurring closer to settlements than older conspecifics. 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, especially in Sweden where age selectivity in the harvest does not occur (Bischof et al. 2008, 2009a). Therefore, food competition, in combination with predation avoidance, could explain the greater number of young bears killed in areas with a higher human density (Elfström et al. 2014). 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



**Figure 1.** Separate effects, and 95% confidence intervals, on age in relation to human density among shot brown bears in Slovenia and Sweden between 1990 and 2010 based on the linear mixed model with highest support ( $w_i$ = 0.98). The data consisted of 149 (134 Slovenian, 15 Swedish) problem bears, 47 Swedish bears shot in self-defense, and 1,896 (877 Slovenian, 1,019 Swedish) nonproblem bears. Variables are log transformed (log.).

conspecifics (i.e., a despotic distribution; Støen et al. 2006, Zedrosser et al. 2007, Elfström et al. 2014). The Slovenian hunting quotas target bears with lower body weight and more males than females (because females with offspring are protected), and, consequently, more young and male bears are killed by hunters (49% of hunting quota is <4-year-old males; Krofel et al. 2012). This indicates 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).

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 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 concentrated in or near any potential expansion fronts in either Slovenia or Sweden. Total mortality from bear hunting may be greater 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 mortality rates have been reported to be greater in areas with lower bear density (Jerina et al. 2013), indicating 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, at least partially, 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 to separate the effects of human-induced mortality and adult avoidance of settlements on the observed spatial pattern of age distribution. Hunting success and sex and age composition of harvested black bears (Ursus americanus) may change in relation to natural food availability, with more and older females harvested when food availability is low (Noyce and Garshelis 1997). However, no harvest selectivity in terms of the bears' sex and age occurs in Sweden (Bischof et al. 2008, 2009a) and European brown bears experience generally higher food productivity than those in North America (Bojarska and Selva 2012), indicating that variation in food availability may be generally lower in Europe.

**Table 4.** Model selection based on corrected Akaike's Information Criterion (AIC<sub>c</sub>) values (K= number of parameters,  $w_i$ = AIC<sub>c</sub> weights, and  $w_i$  cum. = cumulative weights) finding the most parsimonious linear mixed model when fitting body condition index (BCI) of 1,433 brown bears shot in Slovenia and Sweden (1996–2010), with year 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. Age is log-transformed; status categorizes bears as nonproblem, problem, or shot in self-defense; human density is log-transformed; bear density is standardized, and ":" represents an interaction term without main effects.

Candidate models	K	$AIC_c$	$\Delta AIC_c$	$w_i$	$w_{i \text{ cum}}$ .
Sex × age + country + bear density:country	9	3,852.92	0.00	0.64	0.64
$Sex \times age + country$	7	3,854.96	2.04	0.23	0.88
$Sex \times age + country + status + human density:country + bear density:country$	13	3,858.06	5.14	0.05	0.92
$Sex \times age + country + status + human density:country$	11	3,858.84	5.92	0.03	0.96
$Sex \times age + country + status:human density$	10	3,859.38	6.45	0.03	0.98
$Sex \times age + country + status:human density + bear density:country$	12	3,860.24	7.32	0.02	1.00
Intercept only	3	4,152.23	299.31	0.00	1.00

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); thus, the fact that mostly young bears were killed 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 females with offspring occur more often near settlements than adult males (Steyaert et al. 2013a) or the lower diet quality of females with dependent young compared to other bear categories (Elfström 2013, Steyaert et al. 2013b), if a despotic distribution is not considered (Elfström et al. 2014).

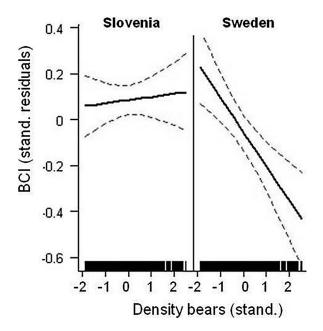
Reports of bears eating garbage and other human-derived foods close to settlements (Gunther et al. 2004, Greenleaf et al. 2009, Hopkins et al. 2012) suggest that these food items are attractive and that bears may approach settlements in search of food. However, we found no differences in BCI between 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., eating 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. The 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. Elfström (2013) reported that neither diet composition nor diet quality differed for Swedish brown bears when near settlements compared to when the same GPS-collared bears used remote terrain, based on DNA metabarcoding and near-infrared spectroscopy of feces. These results are consistent with the lack of differences in BCI between problem and nonproblem bears that we documented, suggesting other reasons than searching for food or food shortage to explain why most European brown bears approach settlements.

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 and thus approach people, as suggested by Yamanaka et al. (2009).

**Table 5.** Body condition index (BCI) of brown bears shot in Slovenia and Sweden between 1996 and 2010, in relation to standardized density of bears, sex, and age, and with year as a random effect. The factors human density and bear status are not included. We analyzed records of 124 (117 Slovenian, 7 Swedish) problem bears, 30 Swedish bears shot in self-defense, and 1,279 (726 Slovenian, 553 Swedish) nonproblem bears. Variances for random effects for year and residuals, respectively, are <0.0000 and 0.8356, and <0.0000 and 0.8437, from the 2 most parsimonious linear mixed models based on differences in corrected Akaike's Information Criterion ( $\Delta$ AIC<sub>c</sub>) values and AIC<sub>c</sub> weights ( $w_i$ ). We provide Markov Chain Monte Carlo-simulated parameter estimates (β<sub>MCMC</sub>) and 95% highest posterior density intervals (HPD) with β and standard errors (SE) based on a *t*-distribution. Age is log-transformed (log) and density of bears is standardized (stand).

Model parameters	β	SE	$\beta_{MCMC}$	<b>HPD</b> lower	HPD upper
Model 1: $\Delta AIC_c = 0.00; \ w_i = 0.64$					
(Intercept)	-0.434	0.060	-0.433	-0.549	-0.321
Male	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
$Male \times age(log)$	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
Model 2: $\Delta AIC_c = 2.04$ ; $w_i = 0.23$					
(Intercept)	-0.444	0.060	-0.445	-0.562	-0.324
Male	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
$Male \times age(log)$	0.410	0.062	0.410	0.287	0.524



**Figure 2.** Separate effects, and 95% confidence intervals, on BCI distribution in relation to standardized (stand.) density of bears among shot brown bears in Slovenia and Sweden between 1996 and 2010 based on the linear mixed model with highest support ( $w_i$ =0.64). The data consisted of 124 (117 Slovenian, 7 Swedish) problem bears, 30 Swedish bears shot in self-defense, and 1,279 (726 Slovenian, 553 Swedish) nonproblem bears. We calculated density of bears differently between Slovenia and Sweden.

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 that 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 ate human-derived foods near settlements, but were shot before they had gained body mass (i.e., increased 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.

**Table 7.** Model selection based on corrected Akaike's Information Criterion (AIC<sub>c</sub>) values (K= number of parameters,  $w_i$ = AIC<sub>c</sub> weights, and  $w_i$  cum. = cumulative 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 BCI was square-root transformed.

Candidate models	K	$AIC_c$	$\Delta AIC_c$	$w_i$	$w_{i \text{ cum}}$ .
Intercept only	3	-0.61	0.00	0.97	0.97
Problem versus nonproblem bears	4	6.55	7.15	0.03	1.00

The body mass/paw width ratio was positively related to the proportion of fat in the same bear; thus our BCI reflected variation in body condition. This is supported by other studies in Scandinavia; body condition fluctuates annually and is related to bear vital rates. Cub survival in primiparous females and body size of female bears were both positively related to a similar annual index of food condition (based on yearling body mass; Zedrosser et al. 2006, 2009).

Body condition index was negatively related to the bear density index for Swedish bears, indicating competition among bears for food. Zedrosser et al. (2006) documented that size of female Scandinavian brown bears was positively related to food conditions and negatively related to bear density, which also indicated food competition among bears. Another explanation for the negative relation between BCI and bear density index for 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 generally are located in more productive areas. However, negative effects of human disturbance (Martin et al. 2010, Ordiz et al. 2011) probably constrain improvements in body condition. In contrast to Sweden where bears forage on berries, a relatively evenly dispersed resource, we found no relation between BCI and bear density for Slovenian bears. This may be because the use of supplemental feeding in Slovenia reduces food competition, in combination with the high (20%) harvest of bears (Krofel et al. 2012). Supplemental feeding may reduce the seasonal variability in natural food availability. Alternatively, a despotic distribution may be amplified if dominant bears limit the access of predationvulnerable conspecifics to these feeding sites. If so, this would

**Table 6.** Model selection based on quasi-likelihood corrected Akaike's Information Criterion (qAIC<sub>c</sub>) values (K= number of parameters,  $w_i$ = qAIC<sub>c</sub> weights, and  $w_i$  cum. = cumulative weights) finding the most parsimonious generalized linear model when fitting averaged body condition index 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, and ":" represents an interaction term without main effects.

Candidate models	K	$qAIC_c$	$\Delta$ q $AIC_c$	$w_i$	$w_{i \text{ cum}}$ .
Intercept only	3	6.29	0.00	0.99	0.99
Population size:country	5	14.87	8.59	0.01	1.00
Fall <sub>previous</sub> spring <sub>current</sub> × country + population size:country	8	26.53	20.24	0.00	1.00
Spring <sub>current</sub> fall <sub>current</sub> × country + population size:country	8	26.74	20.45	0.00	1.00
Fall <sub>current</sub> × country + population size:country	8	26.81	20.52	0.00	1.00
$Fall_{previous} \times country + population size:country$	8	27.41	21.13	0.00	1.00

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 the different relationships between BCI and bear density in Slovenia and Sweden may be the different methods and areas used when estimating relative bear densities.

Studies reporting a negative correlation between abundance of naturally occurring bear food and occurrence of incidents of bears damaging human property (Garshelis 1989, Mattson et al. 1992, Oka et al. 2004, Schwartz et al. 2006) indicate that food shortage causes bears to search for food close to settlements. However, we found no relationship between problem bear occurrences and seasonal mean BCI in our study, which suggests that bears in general did not experience acute food shortage in either Slovenia or Sweden during our study period which spanned 1999–2010 in Slovenia and 1997-2008 in Sweden. Our study period probably best reflected conditions during periods of low variability or normal natural food availability. However, food shortages may be more common in other areas, causing bears there to approach settlements more often in search of food (Mattson et al. 1992, Oka et al. 2004).

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-human incidences 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 variability in BCI between problem and nonproblem bears. This indicates that reasons other than food-search or food competition might explain why some bears approach settlements, independently of food availability and predictability. The age difference in relation to human density and lack of difference in BCI between problem and nonproblem bears that we documented indicate safety-search and naïve dispersal to be the primary mechanisms behind bear occurrence near settlements.

In summary, all predictions based on the safety-search/ naivety hypothesis were supported (Table 1). Thus, our results provide support for the behavioral mechanism that young bears approach settlements ultimately in search of safety from other bears, perhaps in combination with being naïve, but no support for food competition to explain problem bear incidences in Slovenia and Sweden. We found limited support for the food-search/food-competition hypothesis; however, the results did not support food search to explain problem bear incidences near settlements. The difference in age between problem and nonproblem bears and the negative relationship between age and human density suggested either food-competition and/or safety-search/naivety behind problem bear incidences (Table 1). The negative relationship between body condition and bear

density in Sweden suggested density-dependent food competition but was not associated with problem bear incidences. Based on a literature review, Elfström et al. (2014) concluded that despotic behavior is the ultimate mechanism to explain the type of bears occurring near settlements, which may secondarily result in these bears searching for food near settlements. However, our results indicate that searching for food because of malnutrition is not a common cause behind brown bear occurrence near settlements in Europe.

Bears shot in self-defense were  $4.2 \pm 1.3$  (SE) years older than nonproblem bears. This may be because these incidents occurred mostly during hunting away from settlements, where older bears are more common (Nellemann et al. 2007), and older bears more often remain in their daybed when approached by people than younger bears (Moen et al. 2012). 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, because 18 hunters injured by bears in Sweden 1976–2012 first saw the bear at an average distance of 14 m and shot at the bear at an average of 9 m (Sahlén 2013). Shooting bears in self-defense may be more common in areas where hunters lack experience with them, or these shootings may have 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. Thus, managers in these countries must also consider factors other than food to explain bear problems (or incidences) near settlements. Bear deterrence programs may be required independently of food availability to reduce bear problems near settlements. The safety-search/naivety hypothesis was supported by the following results: younger bears with increasing human density when controlling for problem bear status, younger problem than nonproblem bears, similarities in BCI between problem and nonproblem bears, lack of correlation between BCI and human density, and no correlation between frequency of problem bears and seasonal mean BCI. We suggest that younger bears primarily become problem bears because they occur closer to settlements as a result of dispersal and avoidance of intraspecific predation or aggression, rather than because of food search or food competition. However, other mechanisms may operate if failure of natural foods occurs. The BCI of Swedish bears was negatively related to bear density indices, with no supplemental feeding, whereas we found no correlation among Slovenian bear densities, where supplemental feeding is a common practice. This indicates that supplementary feeding, in combination with high harvest rates, may reduce potential competition for food among bears. However, we are not aware of any documentation to support the practice of supplementary feeding to prevent the occurrence of problem bears near settlements and therefore do not recommend this as a management practice. This practice may even unintentionally alter behavior and life-history traits of bears (Craighead et al. 1995).

#### ACKNOWLEDGMENTS

We thank D. Garshelis for critical comments on an earlier draft. We thank A. Söderberg at the Swedish National Veterinary Institute for providing body measurements of killed bears in Sweden. We thank the Swedish Environmental Protection Agency for financial support. This is scientific publication number 162 from the Scandinavian Brown Bear Research Project.

# LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.
- 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.
- Bates, D. M., and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes R package version 0. 999375-37. <a href="http://CRAN.R-project.org/package=lme4:29">http://CRAN.R-project.org/package=lme4:29</a>. Accessed 16 Sep 2013.
- 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.
- 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.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- 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. 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. Pages 19–26 in M. Bromley, editor. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest

- Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Elfström, M. 2013. Patterns and mechanisms behind the occurrence of bears close to human settlements. Dissertation, Norwegian University of Life Sciences, Ås, Norway.
- Elfström, M., A. Zedrosser, O.-G. Støen, and J. E. Swenson. 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. Mammal Review 44:5–18.
- 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. Pages 169–180 *in* M. Bromley, editor. Bear–people conflicts: proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.
- Gilbert, B. 1989. Behavioural plasticity and bear-human conflicts. Pages 1–8 in M. Bromley, editor. Bear-people conflicts: proceedings of a symposium on management strategies. 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. 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., 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., 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., M. Jonozovič, M. Krofel, and T. Skrbinšek. 2013. Range and local population densities of brown bear *Ursus arctos* in Slovenia. European Journal of Wildlife Research 59:459–467.
- 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, Slovenia.
- 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.
- Kavčič, I., M. Adamič, P. Kaczensky, M. Krofel, and K. Jerina. 2013. Supplemental feeding with carrion is not reducing brown bear depredations on sheep in Slovenia. Ursus 24:111–119.
- 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. 2006. Populationsberäkning av björnstammen i Sverige 2005 [Estimate of the bear population in Sweden in 2005] Report No. 2006-2 of the Scandinavian Brown Bear Research Project to the Swedish Environmental Protection Agency Stockholm, Sweden. [In Swedish.]
- 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. 2010-5 of the Scandinavian Brown Bear Research Project to the Swedish Environmental Protection Agency Stockholm, Sweden [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. Jonozovič, 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. Pages 126–153 in B. Kryštufek, B. Flajšman and H. I. Griffiths, editors. Living with bears, a large European carnivore in a shrinking world. Ecological Forum of the Liberal Democracy of Slovenia, Ljubljana, Slovenia.
- 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., 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.
- 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.
- McCullough, D. R. 1982. Behavior, bears, and humans. Wildlife Society Bulletin 10:27–33.
- McLellan, B. 1994. Density-dependent population regulation of brown bears. Pages 15–24 in M. Taylor, editor. Density-dependent population regulation of black, brown, and polar bears. Ursus Monograph Series 3. Washington, D.C. USA. International Association for Bear Research and Management.
- 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.
- 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.
- 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:e31699.

- 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. Pages 44–47 *in* T. Oi, N. Ohnishi, T. Koizumi and I. Okochi, editors. FFPRI Scientific Meeting Report 4 Biology of Bear Intrusions. Forestry and Forest Products Research Institute, Ibaraki, Japan.
- 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.
- 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., 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.
- Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. Oecologia 128:62–71.
- 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.
- Sahlén, V. 2013. Encounters between brown bears and humans in Scandinavia—contributing factors, bear behavior and management perspectives. Dissertation, Norwegian University of Life Sciences, As, Norway.
- 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. 2013a. Male reproductive strategy explains spatiotemporal segregation in brown bears. Journal of Animal Ecology 82:836–845.
- Steyaert, S. M. J. G., C. Reusch, S. Brunberg, J. E. Swenson, K. Hackländer, and A. Zedrosser. 2013b. Infanticide as a male reproductive strategy has a nutritive risk effect in brown bears. Biology Letters 9:1–4.

- 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., M. Adamič, D. Huber, and S. Stokke. 2007. Brown bear body mass and growth in northern and southern Europe. Oecologia 153:37–47.
- Swenson, J. E., B. Dahle, and F. Sandegren. 2001. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. Ursus 12:81–91.
- 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.
- Tremblay, A. 2011. A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. <a href="http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html">http://cran.r-project.org/web/packages/LMERConvenienceFunctions/index.html</a>. Accessed 16 Sep 2013.
- 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. 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? Pages 48–51 in T. Oi, N. Ohnishi, T. Koizumi,

- and I. Okochi, editors. FFPRI Scientific Meeting Report 4 Biology of Bear Intrusions. Forestry and Forest Products Research Institute, Ibaraki, Japan.
- 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.
- 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., 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.
- 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, New York, USA.

Associate Editor: Scott McCorquodale.

#### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.