Brown bears in northern and southern Europe: are they seeking food or avoiding dominant bears?

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ABSTRACT

Large carnivore populations have successfully recovered in many areas of Europe and other parts of the world as a consequence of conservation-based management, which has resulted in their increased appearing close to human settlements as well. They are perceived as a threat to human property and safety and must be managed properly to prevent unpleasant consequences that could halt the conservation efforts. I have studied this problem in brown bears (*Ursus arctos*). Many believe that the only reason brown bears approach people is to obtain food. In this thesis, I tested an alternative social-organization hypothesis, which predicts that problem bears are subdominant individuals forced to use lower-quality habitat near human settlements, in order to avoid dominant adult bears. The study included brown bears from northern (Sweden and Finland) and southern (Slovenia and Croatia) European populations. My results suggest that problem bears occur near humans as a consequence from a combination of factors involving both social constraints and food availability. Problem bears were mostly subadults of both sexes characterized by a lower body condition index than nonproblem killed bears. They appeared mostly during the "high-aggression" period (May-July), and their numbers could be influenced by extremely poor natural food abundance. Supplemental feeding does not seem to completely solve this problem, and might even promote an increase in number of problem bears, particulary of subadults. Supplemental feeding alone is therefore not enough to reduce the occurrence of bears near humans, but it could be used in combination with other management strategies, which should be developed without focusing only on food availability, but rather considering also social interactions and behavioral ecology.

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INTRODUCTION

Europeans coexisted with large carnivores for 30,000 years. With the arrival of industrialization in human society their attitudes towards large carnivores changed and modern weapons gave them the power to effectively control their numbers (Schwartz et al. 2003). A centuries-long history of large carnivore persecution in Europe followed, from the Middle Ages to the early 20th century. They were seen as a threat to life and property, particularly livestock, so encouragements and bounties were given to professional hunters to kill carnivores by any means, and at the same time habitat destruction and elimination of native herbivores contributed to their extermination in Europe (Schwartz et al. 2003). This lasted until 1960-70s, when the public attitude and policy objectives shifted towards conservation and many species were included in protected and endangered species lists (Linnell et al. 2001; Enserink & Vogel 2006). It is only after predators were largely exterminated throughout Europe that this dramatic change of public attitude occurred. Conservation-based management has proved to be effective and has allowed populations of carnivores, including bears, to increase in numbers and return to their original habitats in many parts of the world (Linnell et al. 2001; Enserink & Vogel 2006), even in areas with high human densities when correct and effective management is applied (Linnell et al. 2001). Reintroductions and expansion of carnivores throughout Europe inevitably cause opposing reactions and tensions. This charismatic species often comes in conflict situations with humans, competing for space, ungulate game, depredating on livestock, and although it is an extremely rare event, they can be perceived as a threat to human safety (Enserink & Vogel 2006; Katajisto 2006). This makes the management of large carnivores such as brown bears (*Ursus arctos*) an extremely ambitious task.

In many areas large carnivores have become accustomed to human presence, they are coming close to human habitation, causing damage while searching for food. This paradigm that the large carnivores, and among them bears, come close to human settlements primarily to obtain food, is commonly accepted and believed by many to be the major reason why they approach people. I will refer to this as the "food-search hypothesis".

In order to solve this problem, managers often relocate bears, scare them with dogs, shoot them with rubber bullets (Beckmann et al. 2004), and human garbage is secured by bear-proof containers (Spencer et al. 2007). However, even though food sources are removed, some large carnivores still come close to humans and, then, lethal control seems to be the only way of removing them. But the actual reason behind this behavior is still unknown, so these individuals are considered to be showing “unnatural behavior” and management techniques are based on this assumption. However, some previous studies have shown that bears generally avoid areas close to people (Mace & Waller 1996; Gibeau et al. 2002; Nellemann et al. 2007), and a new study showed that a majority of the bears coming close to human-dominated areas were subadults of both sexes (Nellemann et al. 2007). This could suggest that their behavior in relation to humans lies in their social organization. I propose a “social-organization hypothesis” which suggests that subdominate large carnivores come close to human habitation primarily to avoid dominant members of the same species, and may secondarily find food there. In this thesis, I test these two hypotheses in an effort to determine the mechanisms underlying the phenomenon of large carnivores occurring near people, using brown bears in Northern and southern Europe as a model species.

Classification of bears

Problem bears are defined as all those bears occurring near village, and were further separated into “nuisance”, bears which occurred in villages, close to people and/or showed no fear or searched for food in garbage, but did not cause any other damage, and “depredators”, which were depredating on livestock, hens, beehives, fields or caused other damage in villages.

Nonproblem bears refers to hunted bears, those which died in accidents or due to sickness, poaching or unknown causes, and bears captured for research or management purposes.

Predictions:

According to the food-search hypothesis, there should not be any sex difference between problem and nonproblem bears. Age categories are expected to be similar, or with somewhat higher proportion of adult bears who would occupy the resource-rich areas near settlements. The periods with most problem bears should be those with less natural food presence and in times of major energy demand: early spring after the emergence from the den or in autumn during the “hyperphagia” period. Food should always be present near human settlements and natural food availability should play a major role in problem bear occurrences. According to this hypothesis, all problem bears are expected to have lower body condition index (BCI) i.e. lower than average body mass in relation to their size, as they are supposed to be undernourished individuals in search for additional food. All bears are expected to be "depredators" because their primary reason for being in human proximity is acquiring food (Table 1).

According to the social-organization hypothesis, problem bears are expected to be subdominant, smaller and/or younger individuals, and mostly male bears (females live together in matriarchal groups), or females with cubs that are avoiding males who might kill the cubs which are not their own offspring (Swenson et al. 1997; Bellemain et al. 2006). However, we do expect some subadult females as well, as a natal dispersal study in Scandinavia reported 32% and 46% of juvenile females dispersing in the north and south respectively (Støen et al. 2006a). Dispersing subadult females were found to be smaller in relation to non-dispersing females (Zedrosser et al. 2007), therefore we expect to find a lower BCI among problem than nonproblem subadult females. According to this hypothesis, problem bears are supposed to be mostly "nuisance" bears i.e. only present near villages but not depredating on livestock or other food resources. In addition, the occurrence of problem bears is expected to be higher in the period when more aggression is shown towards subadults (Swenson et al. 2001), or during the dispersal period when they meet unfamiliar bears (Støen et al. 2006a): both of these periods occur during the breeding season from May to July in northern (Dahle & Swenson 2003), and from April to June in southern populations (Skrbinsek et al. 2008). Food is not necessarily present near human settlements and natural food availability should not have a significant impact on problem bear occurrences. I expect to see some differences in BCI (Body Condition Index: live mass/paw width) between problem and nonproblem bears. According to social-organization hypothesis problem bears are subdominant or younger individuals, and are therefore expected to have a lower BCI than nonproblem bears, or same as the other subadult nonproblem bears.

There is a substantial overlap among some of the predictions of the two hypotheses, due to the nature of the phenomenon being studied.

Table 1 Predictions of different variables of problem brown bears in relation to nonproblem bears, according to the food-search and social-organization hypotheses

Variable: problem bears in relation to nonproblem bears		Food-search hypothesis	Social-organization hypothesis
Age	Subadults	To a lesser extent	Predominately
	Adults	Predominately	To a lesser extent
Sex	Females	Equal proportion	Mostly females with cubs
	Males	Equal proportion	Predominately
Problem bear category	Depredators	Predominate	To a lesser extent
	Nuisance	Few	Most common
Timing of problem		Den-emergence Hyperphagia	"Aggression period"
Food presence		Yes	Not necessarily
Influence of natural food availability		High	Little or none
Body condition index		Lower	Lower or no difference

If the predictions of the social-organization hypothesis are upheld, it could cause a paradigm shift in our seeing of the phenomenon of problem bears. Until now, the reasons behind the behavior of problem bears are still not clear. Understanding and knowing what are the causes is of utmost importance and absolutely necessary in order to deal with this problem correctly and apply appropriate measures in management of problem bears. For example it might be useful to observe how adult bears signal their presence and apply this knowledge to increase the avoidance of human inhabited areas.

Study area

Southern Europe; Slovenia and Croatia

Slovenian and Croatian bears belong to the Alps-Dinaric-Pindos population which extends from eastern Alps in Austria and Italy through Slovenia, Croatia, Bosnia & Herzegovina, Macedonia, Serbia, Albania to the Pindos Mountains in Greece and is estimated to 2,800 bears (Swenson et al. 2000). Bears have no obstacles in crossing the border between Croatia and Slovenia, studies have shown they are genetically identical (Huber et al. 2008a).

Brown bear habitat is spread on 5,500 km^2 over the southern and a part of central Slovenia with bears living mainly in region covered by Dinaric Mountains (Krofel et al. 2010). These large forested areas are dominated by Norway spruce (*Picea abies*), beech (*Fagus sylvatica*) and fir (*Abies alba*), and extend to Gorski Kotar in Croatia, forming an interconnected bear habitat (Kobler & Adamic 1999). Slovenia is the most forested country in Europe, after the Scandinavian countries, with 57% of the territory being covered by forests, and is characterized by three distinct climates: continental, alpine and submediterranean (Kobler & Adamic 1999). The Core Bear Protective Area, which covers 3,480 km^2, was established in 1966 (Fig 1). Hunting was strictly regulated inside this area and it contained most of the population, which was then reported to be only 160 bears (Svigelj 1961 cited in Jerina & Adamič 2009; Krofel et al. 2010). From 1992 the brown bear was protected also outside the Core Area, and as a consequence the population expanded significantly to the neighboring regions, reaching 25% of the today's total numbers. Bears have spread to the west, north and northeast, but mainly to the Alps. Most of the bears outside the Core Area are subadult males, the most active dispersers, female presence declines sharply with distance from the core area due to their less frequent dispersal and shorter home ranges. Since in the period 1994-2002 bears in alpine and subalpine regions (less than 5% of the total population) were responsible for 67% of the damage in all Slovenia, hunting has significantly increased in the last years, which has stopped the expansion towards these areas (Jerina & Adamič 2009), even though it constitutes a crucial link for the expansion of brown bears to the Alps (Kobler & Adamic 1999).

The population is estimated by counting bears on feeding sites and is approximated to 450-550 bears (Ministry of Environment and spatial Planning, Slovenia, 2002), but a recent modelling approach in estimating the Slovenian population revealed a somewhat lower number: 375-425 bears in the year 2000 (Jerina et al. 2003).

Feeding stations in Slovenia are located only in the core area of the bear habitat, one every 6.000-10.000 ha, and are regularly supplied. They must be at least 2 km from human settlements and 1 km from agricultural lands. (Ministry of Environment and spatial Planning, Slovenia, 2003).

The hunting season in Slovenia lasts from 1 October to 30 April, and bears can only be killed at feeding sites.

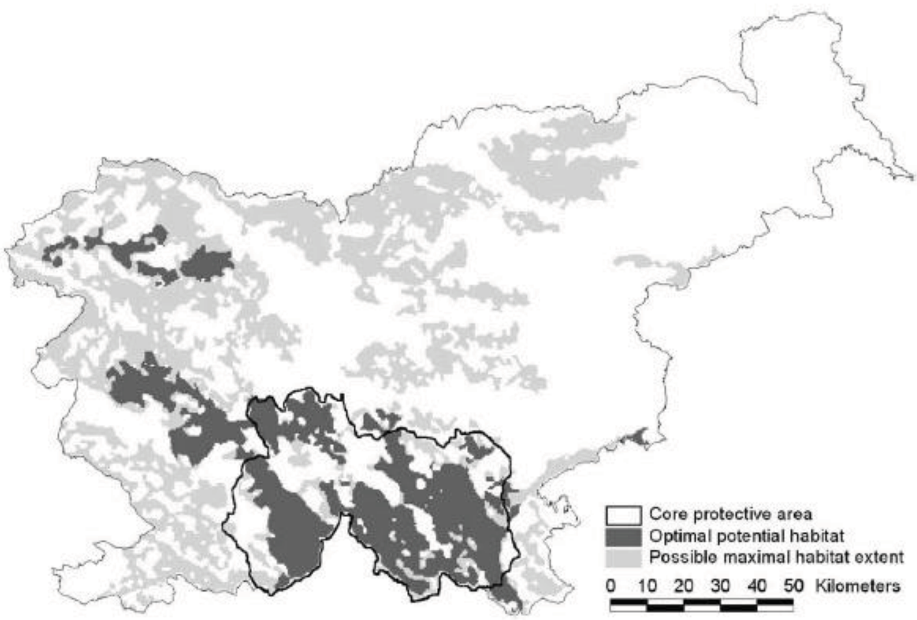

Fig 1 The present core protective area and optimal and possible maximal habitat for brown bears in Slovenia, as modelled by Jerina et al (2003)

The permanent brown bear distribution in Croatia extends over the Dinaric region in Gorski Kotar and Lika, to the south and west of Karlovac County, and part of Istria, with elevations varying from the sea level to 1,831 m (Fig 2). Undesirable areas include island of Krk and the coastal zones. The core area covers 9,253 km^2 and occasional presence area includes additional 2,570 km^2, with brown bear densities ranging from 0.5 to 2 bears per 10 km^2 (Huber et al. 2008a). The bear habitat is situated in the Central European climate zone with Mediterranean climate influence. Around 70% of the habitat is covered by forests, the most present community is (Abieti-Fagetum dinaricum) with highest prevalence of beech being an important food source, fir, Norway spruce and other species depending on elevation and exposure of the terrain (Huber et al. 2008b).

The bear is a game species in Croatia. Quotas are set annually, with the hunting season lasting from 2 March to 30 April, and from 1 October to 15 December. Hunting is only allowed at feeding sites (Huber et al. 2008a). The size of the Croatian population is uncertain and estimated at 600-1000 bears, the lower limit being a maximum estimate in 1999 and upper limit (1000) given by viewing, tracking and counting bears (850) combined with bears in national parks (50) and those from non-hunting areas (100) (Huber et al. 2008a). Newer genetic studies involving analysis of fecal DNA in the period 2003-2008 indicated the upper limit of 1000 bears is quite probable (Huber 2008c). In Croatia supplemental feeding is performed at a minimum distance of 2 km from human habitation in November, February, March and April (Huber et al. 2008a).

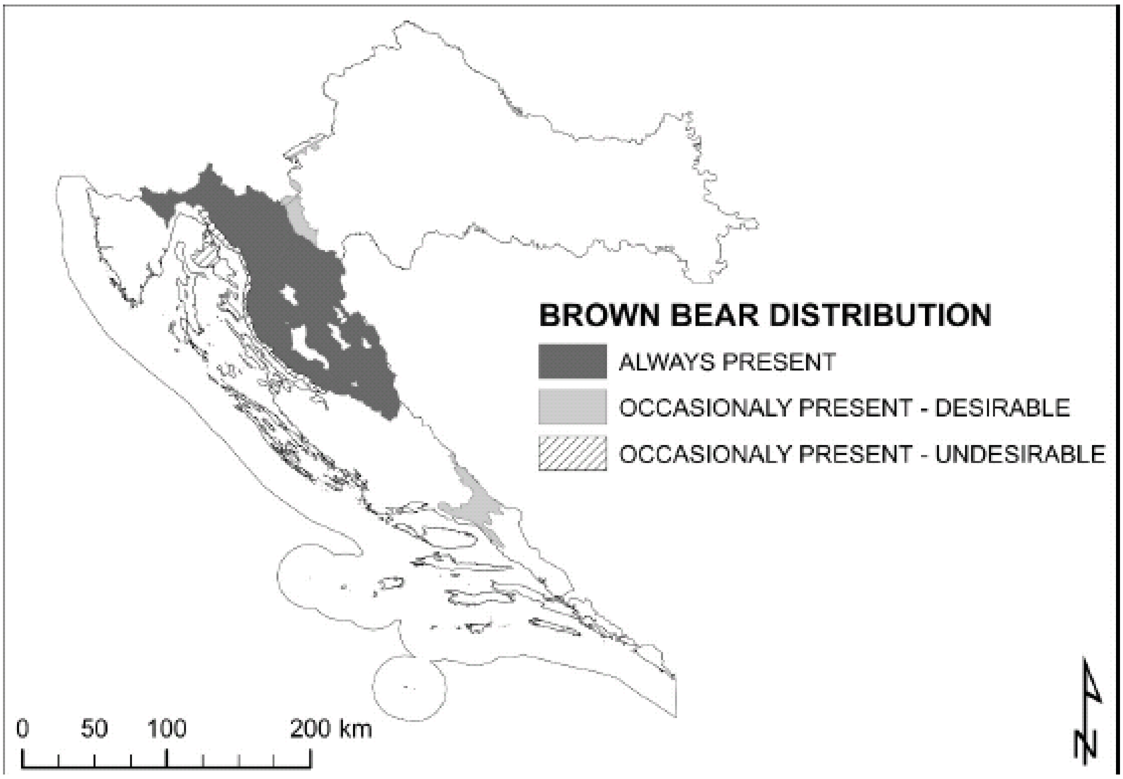

Fig 2 Brown bear distribution in Croatia (Huber et al 2008), the figure is from (Decak et al. 2005)

Northern Europe; Sweden and Finland

Swedish bears make up almost the entire Scandinavian population as 95% of bears occur in Sweden and only 5% in Norway. The population size in Scandinavia varied greatly in the past, from 4000-5000 brown bears in 1850, to a bottleneck in 1930 when only about 130 bears remained (Swenson et al. 1994). Since then the population recovered and is currently estimated to 2,950-3,490 brown bears in Sweden in 2008, with a distribution that covers the northern two-thirds of the country (Kindberg et al. 2009). Brown bear habitat in central Sweden is characterized by intensively managed boreal forest with the prevailing vegetation species being Scots pine (*Pinus sylvestris*) and Norway spruce, and vegetation period lasting 150-180 days from mid May to late October. Elevations vary from 200 m in the southeast to 1,000 m in the west. The north of Sweden is characterized by deep valleys dominated by mountain birch, Scots pine and Norway spruce, glaciers and plateaus reaching up to 2,000 m with the tree line limit at 600 m. Vegetation period is somewhat shorter and last 110-130 days (Zedrosser et al. 2006), and references therein). The spatial distribution of bears in Sweden covers four female Core Areas, with males dispersing in between. However there are only three genetic sub-populations. A study involving phylogenetic analysis (Manel et al. 2004), showed that the two northernmost sub-populations are not genetically distinct (Fig 3).

The hunting season is in autumn with quotas decided separately for every county by the responsible authorities. It starts on 21 August and lasts until the quota is filled, but no later than 31 October (15 October in the north). Hunters are requested to report all bears that were killed or wounded (Katajisto 2006). Location, sex, body measurements and samples are taken and documented by management officials.

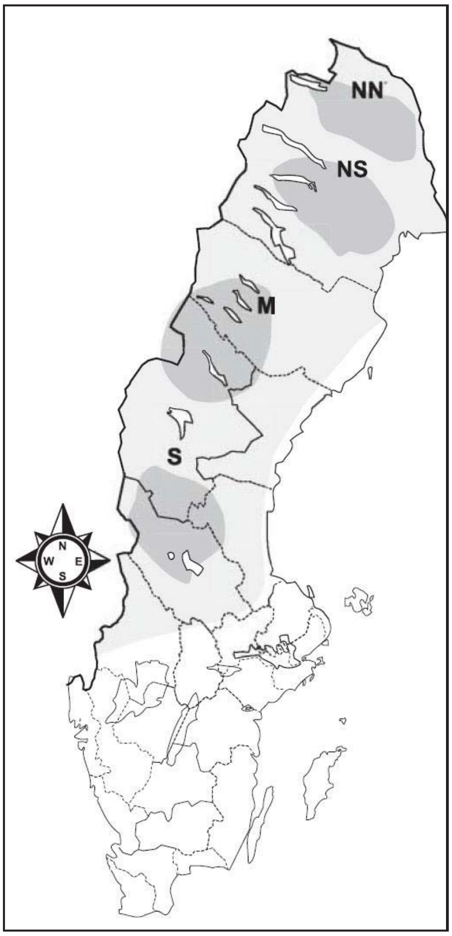

Figure 3 The Core Areas with female brown bears (dark areas) and all bears (ligher areas) in Sweden Showing the three subpopulations: S, M, and NS/NN (Manel et al. 2004).

Finnish brown bears belong to the Northeastern European population. With the total of 37,500 bears this is the most extensive population in Europe and is spread from the Ural

Mountains in the east to the west coast of Finland. They are distributed all over the Finnish territory, with highest densities in the southeast and the lowest in the north and southwest parts of the country (Swenson et al. 2000).

After being nearly extinguished around 1920, brown bears in Finland recovered and today the population is estimated to be about 800-900 bears. They are partly connected to the Scandinavian population, and the high density Russian population which is the source of a substantial number of dispersing bears (Swenson et al. 2000, Finnish Large Carnivore Research Project web page).

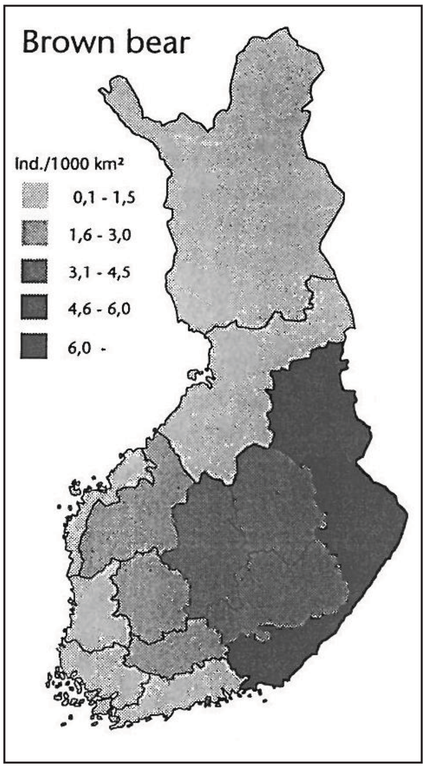

Fig 4 Minimum density of brown bear in different management districts in Finland in 1995 (Finnish Game and Fisheries Research Institute). The figure is from (Pulliainen et al. 1996).

Comparison of northern and southern brown bears

The body mass of brown bears varies during the year and among geographical areas with highest values before denning in autumn and lowest in the spring. According to von Bertalanffy growth curves, northern and southern populations in Europe do not have different body masses, but they show different patterns and trends between seasons. In the south, mean adult female weight varies from 115 kg in spring to 141 kg in autumn, whereas adult males weigh on average 248 kg and 243 kg in spring and autumn respectively. Northern populations are characterized by a greater body mass variation from autumn to spring due to longer denning period of 6.9-7.5 months, compared to 2.9 months in the south (Swenson et al. 2007). Northern females weight 96 kg and 158 kg, and males 201 kg and 273 kg in spring and autumn respectively (Swenson et al. 2007).

Brown bear diet varies between seasons and consists mainly of vegetarian food (green vegetation, soft fruits, beechnuts), only 5% of their nutrition includes animal food (mostly invertebrates and carcasses of larger animals (Huber et al. 2008a). Although their digestive tract is almost entirely a carnivore tract, they are able to digest most protein, starch and sugars from plants. There can be again some differences between different regions, with northern European populations having in general more protein-rich food available as ants, moose (*Alces alces*) and insects, particularly in spring (Swenson et al. 2007).

MATERIALS AND METHODS

My dataset consists of all known bears killed by humans in Slovenia and Croatia during January 1996 – June 2009 and January 2005 – June 2009, respectively. The Croatian data were obtained from official "brown bear forms", which were filled in by hunters or managers who are requested to report detailed information about every bear that has been killed or died for other reasons. This includes date, hunting district, feeding station, food baits, the hunter's personal data and details about each bear: sex, estimated age, live and dressed weight, front and back foot width, head length, body length and other measurements, as well as a list of samples that were taken. If a bear had been killed as problem bear by an intervention team, this is reported under "special condition of the kill" and is usually accompanied by additional documents submitted by the local hunting unit with reported damages and reasons justifying their intervention killing request. The documents were obtained from the Croatian Ministry of Regional Development, Forestry and Water Management, Directorate for Hunting, and from the Faculty of Veterinary Medicine, University of Zagreb. Slovenian data were obtained in digital format from the Slovenia Forest Service. Information about every killed bear included date of the kill, hunting district, coordinates, live and dressed weight, sex, age (estimated and in some years documented by tooth sectioning), front paw width, and the bear category: regular hunt, intervention killing, poaching, accident, sickness, capture and other. Bears killed as problem bears had additional details explaining the reasons for intervention.

Bears shot in Sweden are measured and documented by management officials. All data has been collected and provided at a national level by the National Veterinary Institute. Data for bears shot in Finland have been collected and provided by Finnish Game and Fisheries Research Institute.

In the analysis, I excluded cubs-of-the-year (COY), due to dependency on their mother. The true age for most Croatian and Slovenian bears was unknown, but there were 8 Slovenian COY killed in autumn in the dataset, and their mean weight was 37 kg. From the quartiles of Swedish weights of COY calculated from10 bears in spring (<181 Julian days, 30 June) and 41 in autumn (>182 Julian days, 1 July), it appears that Slovenian COY are somewhat heavier and their weights fall between the 75% and 100% quantile of Swedish COY (Table 2). Mean body mass of 1-year-old bears in were also found. In spring (<181 Julian days) they were calculated from 26 bears and autumn (>182 Julian days) from 256 bears. To ensure that all

COY were excluded, I discarded all the bears with weights that fell under the 25% percentile of Swedish 1-year-olds; i.e. all bears with a live body mass lower than 21.6 kg in spring, and 50.0 kg in autumn. I felt that it was justified to use Swedish weights to classify Croatian and Slovenian bears, because the growth in body weight was similar for all these brown bears in spring (Swenson et al. 2007).

Table 2 Live body masses of Swedish brown bear cubs-of-the-year and yearlings in spring (<182 Julian days) and autumn (>182 Julian days), expressed in quartiles.

		0%	25%	50%	75%	100%	Mean
Spring	COY	1.3	2.2	3.6	5.7	10.3	4.19
	1 year old	12.9	**21.6**	26.8	32.5	91	29.19
Autumn	COY	5.6	23.3	26.0	34.4	89	31.07
	1 year old	25.0	**50.0**	56.5	70.0	145.0	60.77

The remaining bears were then categorised into "subadults" and "adults". The earliest primiparity among European brown bears has been found to be at 3 years; in Austria (Zedrosser et al. 2004), and Croatia (Frkovic et al. 2001). The age of sexual maturity and of first litters in Slovenia is reported to be 4-5 (Švigelj, 1961 cited in Jerina et al. 2003). Therefore, when the true age was known, bears up to 3.9 years were classified as subadults, and bears above the age of 4 as adults. Given that the true age was not always known, we referred to Swenson et al. (2007), where individual growth curves were generated using the von Bertalanffy equation (Von Bertalanffy 1938; Kingsley et al. 1988) for bears in southern and northern Europe. I separated subadults from adults according to the estimated masses for 3- and 4-year-old males and females in spring and autumn (Table 3), based on their equations. Only the bears whose weight fell within the limits of estimated mass for a given season, sex and age category were included. This means that bears below the estimated mass for 3-year olds were labelled "subadults" and bears above the estimated mass for 4-year olds as "adults", and those with a weight in between, and therefore uncertain which category they belong, were discarded.

Table 3 Estimated mass of 3- and 4-year-old brown bears in southern Europe, based on equations in Swenson et al. (2007).

	Age	Season	Estimated mass (kg)
M	3	Spring	111.35
	3	Autumn	133.28
	4	Spring	133.09
	4	Autumn	152.46
F	3	Spring	87.74
	3	Autumn	93.71
	4	Spring	94.69
	4	Autumn	107.37

There was a total of 1,060 sampled bears from the southern population: 224 from Croatia and 836 from Slovenia, of which 120 were problem bears (54 nuisance and 66 depredators) and 940 nonproblem bears (Table 7). The database from the northern population consisted of 1,568 bears: 541 from Finland and 1027 from Sweden, of which only 17 were problem bears; 57 were killed in self defence and the rest were killed for other reasons (Table 11).

A recent study in Sweden reported that the ages of primiparity vary from the south to the north of the country, and averaged 4.71 and 5.29 years respectively (Zedrosser et al. 2009). However, there is substantial evidence that they could be sexually mature even earlier. Females living in matrilinear assemblages were found to give birth at a later age than dispersing females, which indicates they have a delayed primiparity due to socially induced reproductive suppression (Støen et al. 2006b). In the northern European population all bears are aged using tooth sectioning, and they were categorized in the same manner; up to the age of 3.9 years as subadults and above 4 years as adults.

Body Condition Index (BCI)

From the available body measures, I wanted to create an index that represented the body condition of each bear, i.e. that would indicate whether a bear has a lower or higher than average body mass in relation to its body size.

Seven commonly used morphometric measurements have been found to significantly explain variation in body size: neck and head circumference, chest girth, body height, body length, front foot width, and back foot width (Bischof et al. 2009). Because any of these is a reliable measurement for overall size, I selected the front paw width for my analysis. My Body Condition Index (BCI) was calculated for each bear as live mass/front paw width (kg/cm).

Body mass alone is not a reliable measure of body condition if the body size is not known. Paw width reflects body size of a bear and it is not dependent on body mass, which means bears of the same size will have similar paw width regardless of their weight, since fat tissue do not accumulate on paws.

Therefore fatter bears with a large body mass but a relatively small size (and therefore small paw width) will have a very high BCI. In contrast, thinner bears with disproportionally small body mass compared to their size and paw width will be characterized by a low BCI.

Statistical analysis

In the final database the records for each bear included in the analysis consisted of: age category (adult or subadult), population, Julian day of killing, live weight, paw width, bear category (problem or nonproblem bear), and BCI (live mass/paw width). The records with missing values were excluded from the analysis.

Some of the initial comparisons of BCI, total weight, and sex and age categories between Croatia and Slovenia in the south, and between Sweden and Finland in the north, were conducted only with nonproblem bears.

The same datasets, but including all bears were used when running linear models (LM). The BCI was fitted with a linear model (LM) in order to see which of the variables (Julian date, bear category, country, age) significantly explained the variation in BCI. Because different sex and age frequencies were found between problem and nonproblem bears in the southern population, the models were run separately for each category. This was necessary because males and females as well as adults and subadults, differ in body size, and therefore their BCI may be different as well. Two models were developed for each class; at first the predictors included were sex, age, Julian date, country, and bear category. Secondly, we also tested BCI by separating problem bears into nuisance (i.e. showing no fear, but not causing damage) and depredators (i.e. causing damage in the village). For the southern population, LM could not be conducted for adult male bears, because the number of problem bears in this category was too small (n=7).

Akaike's Information Criterion (AIC) values were calculated and variables were selected with forward selection and forward/backward stepwise regression (i.e. both selection and elimination), retaining those significant at $\alpha=0.10$. A best subset selection was performed as well, choosing best model according to the lowest Mallow's Cp value (Kobayashi & Sakata 1990). Seven models were developed for the southern population: 2 for all bears, 3 for females and 2 for male bears (Table 12).

The same procedure was performed for the northern population. There were only 17 problem bears and no difference was found in sex and age distribution between problem and non-problem bears, therefore it was not necessary to run separate models for males and females, nor for adults and subadults. Another bear category in the northern population was represented by bears shot in self defence. A total of 57 individuals were in this category and they were also analysed using LM. As for other categories the first step consisted in performing chi-square tests to search for differences in age/sex distribution between bears shot in self defence and nonproblem bears, and according to the results of this first step, LM were subsequently developed. More adults were killed in self-defence than among nonproblem bears, therefore the model was run separately for age categories. Three models were developed for the northern population: 1 for all the bears, 1 for adults and 1 for subadults (Table 13).

Effect of natural food conditions on occurrence of problem bears

An effect of natural food abundance on the occurrence of problem bears has been found among grizzly bears in the Yellowstone area in the USA, as they appeared more frequently near human habitation in years with low food availability (Mattson et al. 1992). I wanted to test whether a similar relation exists in northern and southern populations in Europe. My assumption was that a year with poor food availability in autumn will be reflected by a lower mean BCI in the same time period, and during the next spring. If more problem bears appear after a year with poorer food availability, and therefore, lower mean BCI, this finding would give support to the food-search hypothesis, suggesting that bears occur closer to human-habitat as a consequence of a lack of sufficient natural food resources.

The Croatian and Slovenian data had to be separated for this analysis for two reasons: data records for Slovenian bears covered 1996 to 2009, whereas those from Croatia 2005 to 2009. Therefore the number of problem bears would appear disproportionally high in the last 4 years, compared to 1996-2004 period, when we have only Slovenian bears. The second reason is a much higher BCI among Croatian bears, which would influence the results. There were only 8 problem bears in Croatia, therefore this analysis was conducted just for Slovenian brown bears.

Swedish and Finnish data were also separated. There was a significant difference in BCI values between the two countries as well, and data records started at different times; from 1990 in Sweden and 1996 in Finland. Because there were only 3 problem brown bears in 13 years in Finland, the correlation analysis was performed only for Swedish bears.

In the southern population, the dataset was divided into two periods according to the calendar year: spring period from (1January-15 July), which corresponds to < 196 Julian days, and autumn period from (16 July-31 December), which is >197 Julian days. This was necessary because BCI values showed different trends between the two seasons, and it might have been useful to determine if and which period influences the occurrence of problem bears to a greater extent. In the northern population, except rare exceptions, bears were killed only in autumn during the hunting season. Therefore I used only the autumn period for the calculation. The dataset was the same as for the other analyses, but because there was a significant difference in BCI between bears belonging to different categories (problem and nonproblem bears), only nonproblem bears' were included to find the mean BCI. To correct for date, standardized residuals were extracted by regressing BCI on Julian date as a predictor. The mean of the standardized residuals was then calculated for each season and year, and was correlated to the number of problem bear occurrences in the following time periods.

RESULTS

Differences between nonproblem bears by country

Southern population (Slovenia and Croatia):

There was a significant difference in BCI values between Croatian and Slovenian nonproblem bears (ANOVA: F=191.03, P=0.000). The Slovenian sample size consisted of 724 bears (mean BCI ± SD; 8.340 ± 3.020) and the Croatian of 216 individuals (11.681 ± 3.428). To search for a possible cause; I compared the mean Julian dates of killing in the two countries. There was no significant difference in mean killing date in spring between Croatia (96.81 ± 22.85) and Slovenia (95.76 ± 29.76), with sample size of 109 and 408 bears respectively (ANOVA, F=0.12, P=0.733). In contrast, mean Julian date for the autumn period was significantly different: (305.28 ± 29.91), 1 November for Croatia and (294.52 ± 29.85), 21 October for Slovenia, with sample sizes of 107 and 316 bears respectively (ANOVA, F=10.38, P=0.001).

According to Swenson et al (2007), brown bears in the south decrease their weight in spring, and increase in autumn. This could indicate that the possible reason for different BCI is a later killing date in Croatia, which could have caused a higher body mass of the killed bears, and hence a higher condition index. But interestingly, both the mean body mass and mean condition index for Croatian bears were lower in autumn than in spring, exactly the opposite of that was found for Slovenian bears. (Table 4)

Table 4 Mean body condition index (BCI) and body mass of nonproblem brown bears in Croatia and Slovenia (2005-2009, 1996-2009 respectively

	SPRING		AUTUMN	
	Croatia ±SD	Slovenia ±SD	Croatia ±SD	Slovenia ±SD
Mean body mass (kg)	173.59 ± 58.41	97.79 ± 49.44	141.59 ± 58.90	106.72 ± 48.50
Mean BCI (kg/cm)	12.43 ± 3.29	8.05 ± 3.05	10.92 ± 3.40	8.72 ± 3.57
N	109	408	107	316

The difference in body mass and BCI are most likely due to different proportions of age and sex classes among killed bears in the two countries. A Chi-square test showed there was a significant difference in frequency of adults and subadults in two countries (χ^2=104.428, d.f.=1, p<0.001). In Slovenia 72% of all killed bears were subadults, in contrast to only 34% among Croatian bears (Table 5). Because subadults have a generally lower body mass and therefore, a potentially lower BCI, this seems to be a plausible explanation for the differences seen among the two countries.

In both countries there was a larger proportion of male bears killed compared to female bears (Table 6). However, this divergence was more pronounced in Croatia than Slovenia (χ^2=10.667, d.f.=1, p=0.001), with as much as 75% of killed bears being males (Table 6). This could be the result of selective hunting, with avoidance of females with cubs and selection for bigger trophies in Croatia (Huber et al. 2008b).

Table 5Age distribution of killed nonproblem Croatian and Slovenian brown bears 2005-2009 and 1996-2009 respectively

	Subadults	**Adults**	**Total**
Slo	524	200	724
%	72	28	100
Cro	74	142	216
%	34	66	100

Table 6 Sex distribution of killed nonproblem Croatian and Slovenian brown bears 2005-2009 and 1996-2009 respectively

Females	**Males**	**Total**
268	456	724
37	63	100
54	162	216
25	75	100

Northern population (Sweden and Finland):

Swedish and Finnish nonproblem bears had a significantly different body condition index (ANOVA: F=443.25, P=0.000), with Swedish brown bears having lower values (9.442 ± 3.366) than Finnish (12.666 ± 1.422) (Table 7).

Table 7 Mean body condition index (BCI) and body mass of nonproblem brown bears in Sweden (1990-2008) and Finland (1996-2008)

	Sweden ± SD	Finland ± SD
Mean body mass (kg)	123.9 ± 59.38	159.7 ± 23.73
Mean BCI (kg/cm)	9.44 ± 3.36	12.67 ± 1.42
N	963	531

In contrast to the southern population, there was an almost equal age distribution of bears killed in Sweden and Finland, with 49% and 54 % subadults in the two countries respectively (χ^2=3.15, d.f.=1, p=0.076), (Table 8). Male bears were killed more frequently than females in both countries, but this trend was significantly more pronounced in Finland, with 64 % of males, compared to Sweden, with 56 % (χ^2=10.42, d.f.=1, p=0.001) (Table 9).

There was also a small but significant difference in median killing date, with Swedish bears being killed 4 days earlier than the Finnish (W=260267.5, p=0.024).

Table 8 Age distribution of nonproblem brown bears from 1996-2008 and 1990-2008, respectively

	Subadults	**Adults**	**Total**
Swe	505	528	1033
%	49	51	100
Fin	291	252	543
%	54	47	100

Table 9 Sex distribution of nonproblem brown bears from 1996-2008 and 1990-2008, respectively

Females	**Males**	**Total**
460	573	1033
44.5	55.5	100
196	347	543
36	64	100

Differences between problem and nonproblem bears

Southern population:

There was a different sex and age distribution between problem and nonproblem bears. Problem bears had an equal distribution of females and males: 48 % and 52 % respectively, whereas nonproblem bears consisted of 34 % females and 66 % males (χ^2=13.964, d.f.=1, P=0.000). The distribution of adults and subadults was different as well, with problem bears having a higher proportion of subadults; 76 %, than nonproblem bears; 64 % (χ^2=9.038, d.f. =1, P=0.003), (Table 10).

Table 10 Age and sex distribution of problem and nonproblem brown bears killed in Slovenia and Croatia

		Sex		Age		Country		
		Female	Male	Adult	Subadult	Croatia	Slovenia	Total
Counts	Nonproblem	322	618	342	598	216	724	940
	Problem	62	58	27	93	8	112	120
Proportion	Nonproblem	34	66	36	64	23	77	100
	Problem	52	48	22.5	77.5	8	92	100

Among problem bears, a significant difference was found for the proportions of subadults and adults for each sex category (χ^2=7.005, d.f. =1, P=0.008). Only 7 bears out of 58 males were adults (12%), whereas there were 20 adult females of 62, (32 %).

Northern population:

There was suggestively more subadults and males among problem than among nonproblem bears (χ^2=3.641, d.f.=1, p=0.056), (χ^2=3.256, d.f.=1, p=0.071) respectively (two problem bears with missing Julian date were included).

In contrast, bears shot in self-defence were mostly adults (82 %), and therefore have a significantly different age distribution than nonproblem bears (χ^2=25.53, d.f.=1, p=0.000), although no difference was found in sex distribution (χ^2=1.9431, d.f.=1, p=0.1633) (Table 11).

Table 11 Age and sex distribution of problem and nonproblem brown bears in Sweden and Finland, 1990-2008 and 1996-2008, respectively. The value in brackets refer to 2 problem males with unknown Julian date.

		Sex		Age		Country		
		Female	Male	Adult	Subadult	Sweden	Finland	Total
Counts	Nonproblem	621	873	722	772	963	531	1494
	Problem	4	13(15)	5	12(14)	14(16)	3	17(19)
	Self defence	29	28	47	10	50	7	57
Proportion	Nonproblem	41.6	58.4	48.3	51.7	64.5	35.5	100
	Problem	20.0	80.0	30.0	70.0	82.4	17.6	100
	Self defence	50.9	49.1	82.5	17.5	87.7	12.3	100

Time periods of problem bear occurrences

A study in Scandinavia examining intraspecific predation among brown bears showed that 86% of 14 intraspecific predations occurred in May-July, which corresponds to the breeding season (Swenson et al. 2001). In Slovenia the breeding season starts somewhat earlier, in April-June (Skrbinsek et al. 2008), therefore I expected a higher aggression and intraspecific predation in that period.

There were almost no problem bears from January to March in Slovenia, which corresponds to denning time and emergence from the den (Fig. 5). Most problem bears, and particularly nuisance bears, occurred in the “aggression” period, April-June, with 54% of all nuisance bears occurring in those three months. A somewhat lower presence of problem bears occurred during late summer (August-September), followed by another peak in autumn, particularly in October during the “hyperphagy” period. In Slovenia a problem bear is generally killed within two weeks after appearing in the village, causing damage, or other problems (Jonozovic M, Slovenian Hunters Association, personal communication). Therefore I assumed that dates of kill in Slovenia corresponded to periods of major problems. I examined the data from Croatia separately, because the killing date there does not always reliably represent the period when a particular bear started causing problems. This was evident from the documents accompanying the intervention killing request, as some problem bears were reported months before the actual killing date. However, nuisance bears occurred only in the spring/summer and depredating bears only during the late hyperphagy period (Fig 6).

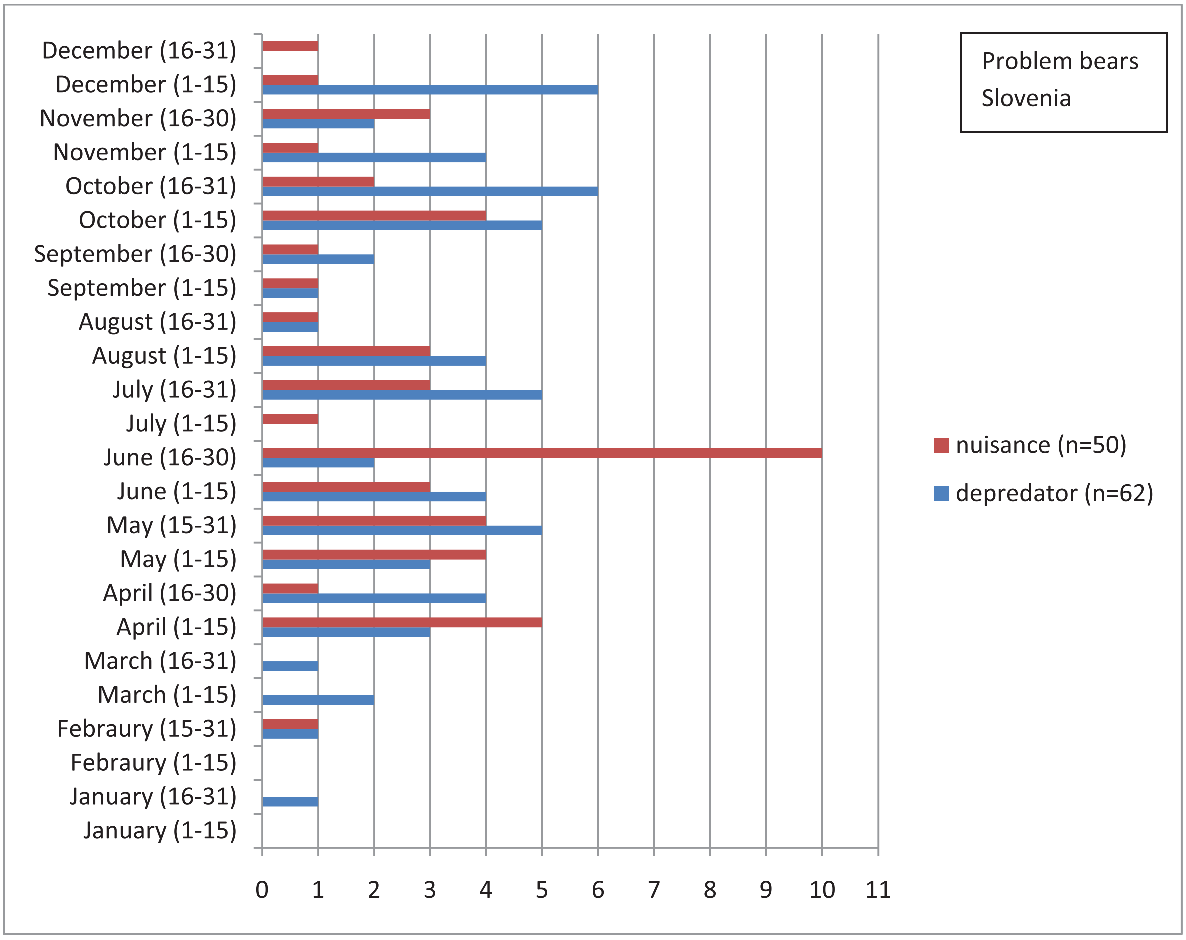

Fig. 5 Occurrence of problem brown bears at different times of the year in Slovenia, (1996-2009)

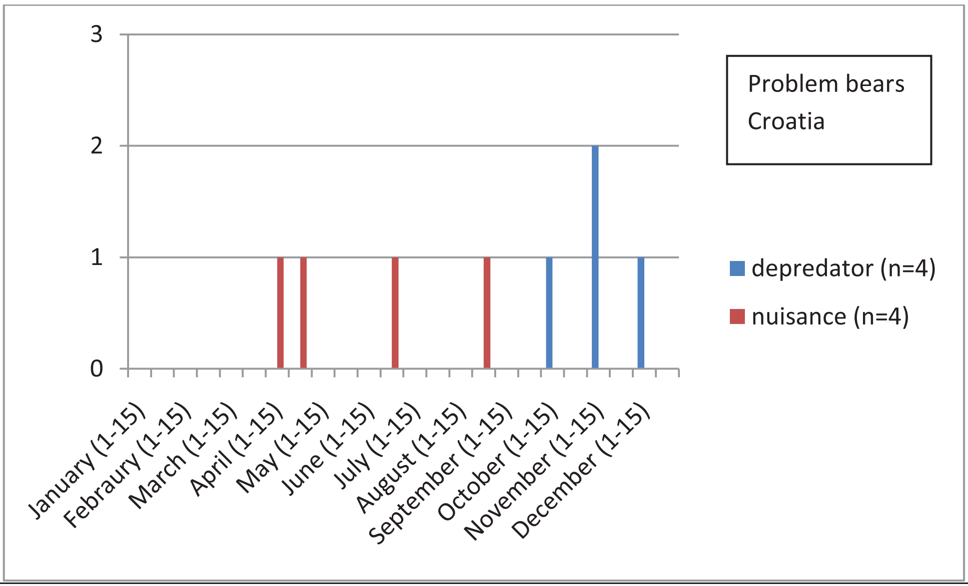

Figure 6 Occurrence of problem brown bears at different times of the year in Croatia, (2005-2009)

Northern population:

Nuisance bears in the northern population occurred from April to mid-November, with a peak during 30 days in late May to mid-June (35 %). Bears shot in self defence were killed mostly in the autumn period from September to November (77 %), (Fig. 7).

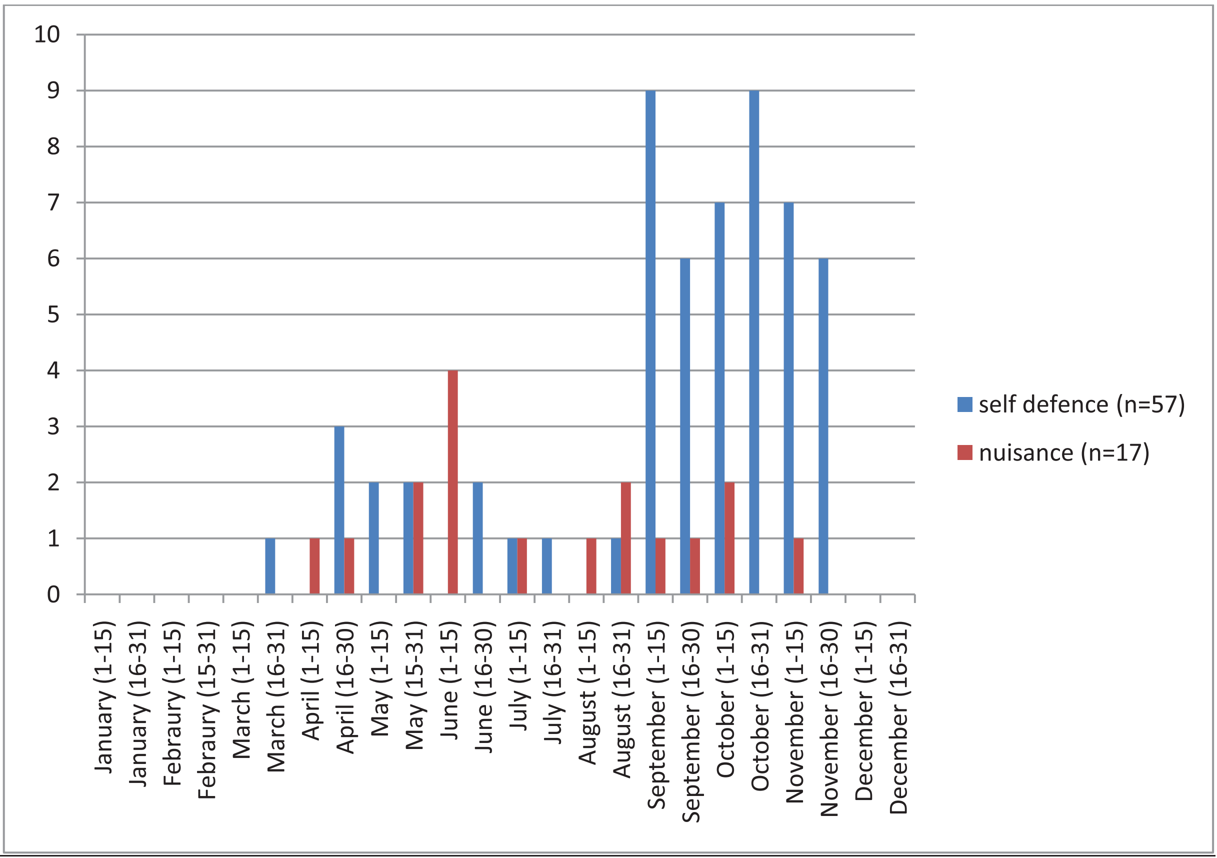

Fig. 7 Occurrence of nuisance brown bears and bears shot in self defence in Finland and Sweden, 1996-2008 and 1990-2008 respectively

Factors explaining variation in the body condition index (Linear Models)

Linear models were developed to test which variables best explained the differences in the bears' BCI, and in particular to see the contribution of the different bear categories (bears killed as problem and nonproblem bears).

Southern population:

Because I found a different sex and age distribution between nonproblem (i.e. hunter-killed bears) and problem bears, it was necessary to develop separate models for each category.

Females

In the best model with all bears together, the bear category (problem or nonproblem bear) was selected by forward selection and stepwise forward/backward regression analyses and significantly explained variation in the response variable (variation in standardized BCI). Problem bears had on average -0.147 kg/cm lower BCI (when all other predictors were held constant) ($P<0.000$) than other bears; the model explained 61% of the variation. The same pattern was found in the model when problem bears were separated into nuisance and depredators; they had -0.179 kg/cm and -0.122 kg/cm lower body condition, respectively, than nonproblem bears. Both factors were included in the best model, which explained 61 % of the variation in BCI.

The model with only adult females did not include problem bears, nor nuisance and depredators, as significant factors. This could be due to small sample size of 20 problem bears.

In contrast, the model with subadult females, which explained 10% of variation, included the category of problem bears $P=0.001$, which had -0.804 kg/cm lower BCI than nonproblem bears. After further separation, nuisance bears showed a significantly lower BCI: -0.768 kg/cm, $P=0.015$, as did depredators: -0.854 kg/cm, $P=0.019$ and were included in the model.

Males

It was not possible to run the models with adult males alone, due to the small sample size of problem bears (n=7). Among subadult males, problem bears contributed significantly in explaining the difference in BCI, (P=0.001, R^2=10%). Separation into nuisance and depredators showed that nuisance bears had a significantly lower BCI of -0.072 kg/cm than nonproblem bears, (P=0.001), and depredators were significant at α=0.10 with -0.018 kg/cm lower BCI (R^2=10 %).

Country was always a significant predictor in all models, with P<0.001, and for subadult females at P<0.10. Furthermore, regardless of sex it was possible to observe a generally lower condition index among subadult bears and bears from Slovenia.

Northern population (Sweden and Finland)

There were only 17 problem bears in Sweden and Finland and there was no difference in BCI between problem and nonproblem bears (p=0.87).

In addition to problem bears, I decided also to analyse bears shot in self defence. The sample size was 57 bears, and because more adults were shot in self-defence than nonproblem bears, each age category was analyzed separately. No difference in BCI was found between adult bears shot in self defence and nonproblem bears (p=0.97) and the model explained 16% of the variation (Table 13). Among subadults, bears shot in self defence had 1.386 kg/cm higher BCI than nonproblem bears, P=0.01, R^2=67%, but the sample size was low (10 bears).

Table 12 Best models for different age/sex categories explaining differences in BCI between problem brown bears (nuisance and depredators) and nonproblem bears in Croatia and Slovenia

Model description	Variables	*t* value	SE	Estimated difference	*p* value	Forward and forward/backward selection RSS	AIC	F	Pr (F)	R^2	Best subsets R^2adj	Cp
(1) All bears (no sex/age separation)	Intercept	90.146	0.037	3.321	0.000					0.612	0.610	6.000
	Sex (Male)	11.994	0.022	0.269	0.000	138.67	-2146.9	153.067	0.000			
	Subadults	-32.561	0.024	-0.772	0.000	158.77	-2005.6	1101.882	0.000			
	Julian day	5.443	0.000	0.001	0.000	128.10	-2226.9	26.405	0.000			
	Country (Slo)	-6.835	0.028	-0.191	0.000	131.31	-2202.7	59.170	0.000			
	Category (Problem)	-4.323	0.034	-0.147	0.000	125.86	-2243.5	18.686	0.000			
(2) All bears, (no sex/age Separation)	Intercept	90.083	0.037	3.323	0.000					0.612	0.610	7.000
	Subadults	5.390	0.024	-0.771	0.000	158.77	-2005.6	1101.882	0.000			
	Julian day	5.390	0.000	0.001	0.000	128.10	-2226.9	26.405	0.000			
	Country (Slo)	-6.858	0.028	-0.192	0.000	131.31	-2202.7	59.170	0.000			
	Category(Nuisance)	-3.658	0.049	-0.179	0.000	125.77	-2242.4	9.749	0.000			
	(Depredators)	-2.736	0.044	-0.122	0.006							
(3) Females, (adults)	Intercept	21.712	0.408	8.866	0.000					0.349	0.614	5.000
	Julian day	6.754	0.001	0.002	0.000	871.81	320.85	51.145	0.000			
	Country (Slo)	-2.764	0.299	-0.825	0.006	838.35	307.83	15.163	0.000			
	Category (Problem)	-0.440	0.356	-0.157	0.661	819.19	300.95	8.866	0.003			
(4) Females, (subadults)	Intercept	17.268	0.374	6.450	0.000					0.106	0.095	4.000
	Julian day	3.828	0.001	0.004	0.000	557.87	203.85	13.338	0.000			
	Country (Slo)	-1.935	0.321	-0.622	0.054	525.39	192.61	3.745	0.054			
	Category (Problem)	-3.242	0.025	-0.804	0.001	533.26	194.39	11.583	0.001			
(5) Females, (subadults)	Intercept	17.104	0.377	6.442	0.000					0.106	0.091	5.000
	Julian day	3.817	0.001	0.004	0.000	557.87	203.85	13.338	0.000			
	Country (Slo)	-1.912	0.323	-0.617	0.057	525.32	194.57	3.655	0.057			
	Category(Nuisance)	-2.452	0.313	-0.768	0.015	533.03	196.27	5.827	0.003			
	(Depredators)	-2.346	0.364	-0.854	0.020							

Table continued

Model description	Variables	t value	SE	Estimated difference	p value	Forward and forward/backward selection RSS	AIC	F	Pr (F)	R^2	Best subsets R^2adj	Cp
(6) Males,	Intercept	23.555	0.349	8.224	0.000					0.104	0.097	4.000
(subadults)	Julian day	3.341	0.001	0.003	0.001	1876.1	642.71	10.614	0.001			
	Country (Slo)	-4.739	0.297	-1.408	0.000	1922.0	651.27	27.775	0.000			
	Category (Problem)	-3.201	0.307	-0.984	0.001	1832.7	634.50	10.245	0.001			
(7) Males,	Intercept	44.137	0.064	2.824	0.000					0.104	0.095	5.000
(subadults,	Julian day	3.407	0.000	0.001	0.001	63.239	-838.73	11.194	0.001			
response	Country (Slo)	-4.372	0.054	-0.238	0.000	64.870	-829.60	24.273	0.000			
sq-root transformed)	Category(Nuisance)	-3.172	0.085	-0.268	0.002	61.403	-847.60	6.458	0.002			
	(Depredators)	-1.887	0.072	-0.135	0.060							

Table 13 Best models for different age/sex categories explaining differences in BCI between nuisance bears, bears shot in self defence and nonproblem bears in Sweden and Finland

Model				Estimated		Forward and forward/backward selection					Best subsets	
description	Variables	*t* value	SE	difference	*p* value	RSS	AIC	F	Pr (F)	R^2	R^2adj	Cp
(1) All bears (no sex/age separation)	Intercept	32.802	0.097	3.168	0.000					0.544	0.542	7.000
	Subadults	-30.868	0.018	-0.561	0.000	314.83	-2510.9	587.682	0.000			
	Julian day	6.393	0.000	0.002	0.000	198.06	-3231.1	44.666	0.000			
	Country (Swe)	-27.550	0.019	-0.527	0.000	210.42	-3140.3	777.566	0.000			
	Sex (males)	7.609	0.018	0.094	0.054	203.71	-3189.0	51.567	0.000			
	Category (Nuisance)	-0.165	0.089	-0.015	0.868							
	(Self-defence)	1.929	0.049	0.094	0.054							
(2) All bears, (adult)	Intercept	10.855	0.809	8.782	0.000					0.168	0.164	5.000
	Sex (males)	9.048	0.156	1.414	0.000	3802.1	1233.0	79.790	0.000			
	Julian day	4.397	0.003	0.014	0.000	3491.4	1171.5	19.434	0.000			
	Country (Swe)	-6.652	0.166	-1.107	0.000	3580.1	1188.8	47.510	0.000			
	Category (Self defence)	-0.036	0.033	-0.012	0.971							
(3) All bears, (subadults)	Intercept	12.477	0.737	9.197	0.000					0.671	0.669	5.000
	Sex (males)	0.836	0.132	0.110	0.404							
	Julian day	4.176	0.003	0.012	0.000	2514.6	919.2	17.971	0.000			
	Country (Swe)	-38.658	0.135	-5.199	0.000	2572.7	935.1	1515.577	0.000			
	Category (Self-defence)	2.426	0.571	1.386	0.016	2495.2	915.2	6.023	0.014			

Effect of previous natural food conditions on occurrence of problem bears

Southern population

I performed correlation analysis to search for a possible relation between standardized residuals of the bears' BCI corrected for Julian date (Table 14), with the number of problem bears occurring during periods in each year. The correlation was significant only when considering the mean standardized residuals from the autumn of the year (x) and spring of the year (x+1), with problem bears occurring in autumn (x+1), and ending with spring (x+2) (Table 15, Fig. 8).

Table 14 The number of problem brown bears in Slovenia and the mean standardized residuals of all nonproblem brown bears each year.

	Problem bears		Autumn (x) + Spring (x+1)		Spring (x) + Autumn (x)
Year (x)	Spring	Autumn	st.res.	BCI (kg/cm)	st.res.
1996	0	3	0.003	8.300	0.084
1997	1	4	-0.047	8.443	-0.057
1998	0	0	-0.040	8.354	0.067
1999	2	1	-0.018	8.292	0.012
2000	4	0	-0.145	8.074	-0.144
2001	3	0	-0.015	8.522	0.026
2002	10	4	-0.016	8.225	0.026
2003	2	7	0.014	8.452	-0.065
2004	5	7	-0.240	7.520	-0.082
2005	6	19	0.010	8.327	-0.166
2006	11	4	0.133	8.785	-0.166
2007	4	4	-0.037	8.393	0.057
2008	5	4	0.016	8.191	-0.133

Table 15 Correlation analyses between the annual condition index, standardized residuals and problem bear occurrences in Slovenia, 1996-2009

Problem bear occurrences	Periods with mean BCI and standardized residuals calculated for Autumn (x) + Spring (x+1)	Spring (x) + Autumn (x)
Spring (x) + Autumn (x)		St.res. (-0.377) P=0.227
Autumn (x) + Spring (x+1)	St.res. (0.058) P=0.851	St.res. (-0.421) P=0.152
Spring (x+1) Autumn (x+1)	St.res. (-0.347) P=0.269	St.res. (-0.278) P=0.382
Autumn (x+1)	St.res. (-0.475) P=0.119	
Autumn (x+1) + Spring (x+2)	St.res. (-0.602) **P=0.038**	

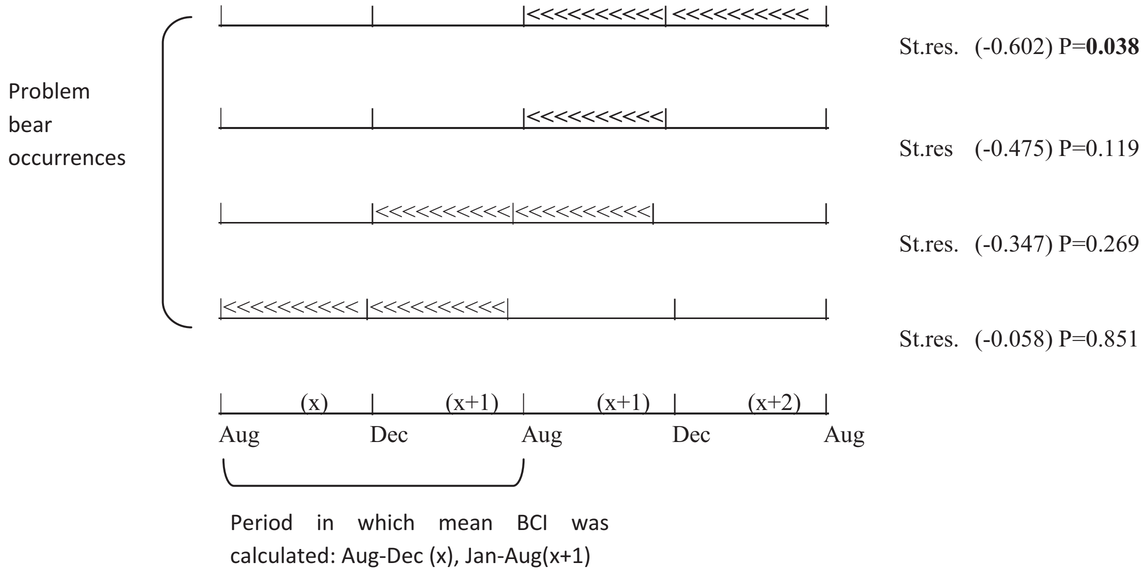

Fig 8 Correlation analysis between mean BCI and standardized residuals and problem brown bear occurrences in Slovenia

Fig. 9 shows the mean standardized residuals in relation to the number of problem bear occurrences in the next seasons. The lowest standardized residual corresponds to the lowest mean BCI occurred in the year 2004 (7.5 kg/cm), after which we had the maximum number of problem bears (30). There were no other extreme values of BCI or of problem bear occurrences in other years.

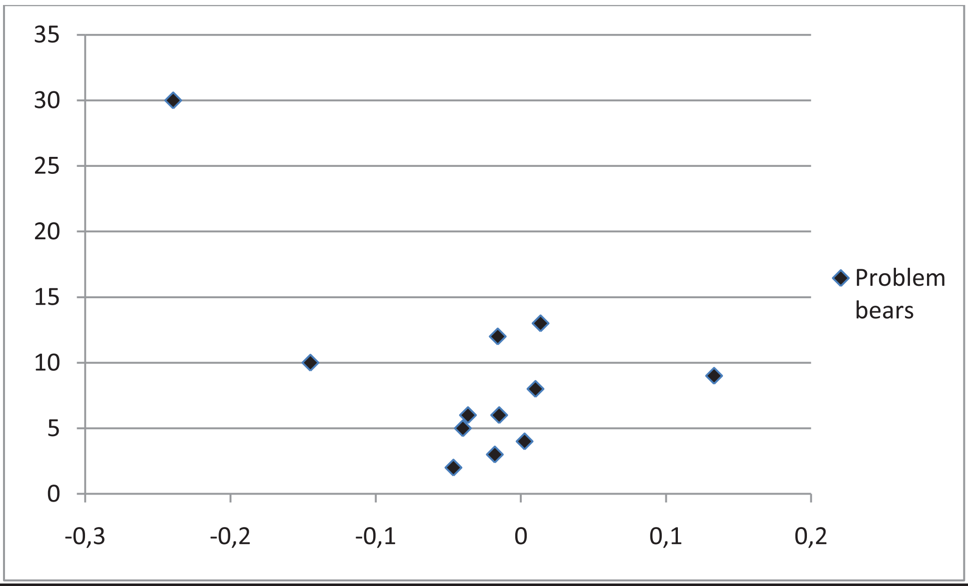

Fig 9 Problem brown bear occurrences in autumn of the year (x+1) and spring (x+2) in Slovenia (1996-2009) in relation to mean standardized residuals in autumn (x) and spring (x+1)

Northern population

The correlation analysis for the northern population was performed only for Sweden. No correlation was found between problem bear occurrence and previous years' body condition index (Table 17, Fig. 10).

Table 16 The number of problem brown bears in Sweden and the mean standardized residuals of body condition index for all nonproblem brown bears in each year.

	Problem bears		Standardized.residuals	BCI
Year (x)	Spring	Autumn	Autumn (x)	Autumn (x)
1990	0	0	-0.102	9.76
1991	0	0	-0.256	9.19
1992	0	0	-0.242	8.75
1993	0	0	0.081	9.76
1994	0	0	-0.235	8.73
1995	0	0	-0.411	8.27
1996	1	0	0.160	9.83
1997	0	1	-0.024	9.48
1998	0	1	-0.142	9.18
1999	0	0	-0.161	8.62
2000	1	1	-0.152	8.68
2001	0	1	0.032	9.48
2002	1	0	-0.001	9.27
2003	1	0	0.159	9.87
2004	0	0	0.040	9.86
2005	0	0	0.099	9.75
2006	0	0	0.035	9.70
2007	0	1	-0.084	9.22
2008	3	2	0.103	9.91

Table 17 Correlation analysis between mean body condition index and standardized residuals and problem brown bear occurrences in_Sweden

Problem bear occurrences	Periods with mean BCI and standardized residuals calculated Aug-Dec (x)
Aug-Dec (x)	St.res. (0.142) P=0.563
Jan-Aug (x+1)	St.res. (-0.155) P=0.540
Jan-Dec (x+1)	St.res. (-0.093) P=0.714
Aug-Dec (x+1) + Jan-Aug (x+2)	St.res. (-0.094) P=0.720

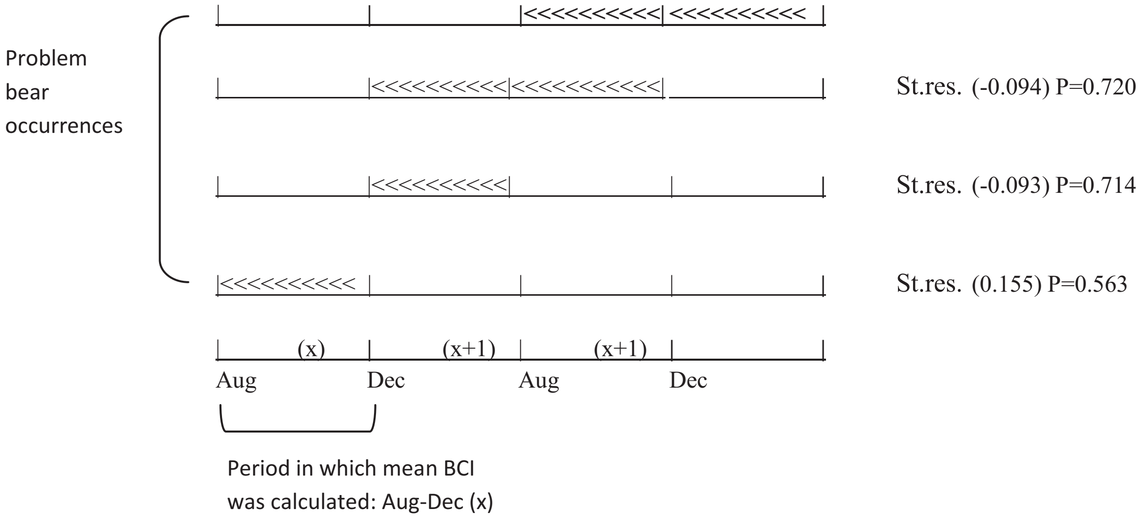

Fig 10 Correlation analysis between mean standardized residuals of the body condition index and problem brown bear occurrences in Sweden

DISCUSSION

The aim of this thesis was to analyze the characteristics of problem bears in northern and southern Europe in relation to predictions of two hypotheses. The social-organization hypothesis, which states that problem bears do not approach humans to search for food, but as a consequence of social constraints imposed by older, dominant individuals, and the food search-hypothesis, which states that problem bears approach people to find food.

Presence of food in relation to problem bear category

According to the social-organization hypothesis, food is not necessarily always present near human settlements, and therefore, not the primary reason why some bears occur close to people. As seen from the data, most problem bears in the south (55 of 120) and all in the north (17) were nuisance bears. Some of them were scavenging on garbage, but did not cause other damage, and the rest were only showing no fear and/or aggressive behavior. This suggests they have probably been seen, and might be more habituated to humans as a consequence of occupying an area close to the settlements. However, except the cases with garbage, none of them were reported damaging livestock or other food resources, which supports the prediction that food is not always the only reason for bears to choose being in human habituated areas, i.e. the social-organization hypothesis.

Age difference between problem and nonproblem bears

In the southern population there was a significantly different age distribution between problem and nonproblem bears. Nonproblem bears consisted of: 64% subadults and 36% of adults, whereas problem bears had a higher proportion of subadults: 78% and 23% adults. This supports the prediction of the social-organization hypothesis. Younger bears, which are more subordinate individuals, should avoid older dominant bears and their territories, and therefore, more subadults are expected among problem bears than among nonproblem bears. In Croatia and Slovenia, bears are given supplemental food at the feeding stations. It is possible that large and older individuals select and defend habitats with the best food resources, which include feeding stations. Those habitats, besides having more food available, are also located in the core area with minimal human presence and disturbance. Thus most young bears would have little other option than to seek less favorable free areas near human settlements. A study conducted in Sweden found as well that radio-marked bears near human settlement were mostly young bears, and that these areas contained only 8% of the adult males (Nellemann et al. 2007). In addition, adult bears in Croatia and Slovenia are mainly nocturnal, whereas younger individuals could be active at any time of the day (Kaczensky et al. 2006). This increases their chances of being seen and perceived by people as a threat, and as a consequence, being killed as problem bears.

However, the more subadults among problem than among nonproblem bears also could be an artifact of hunting habits and rules in Croatia and Slovenia. “Nonproblem” bears consisted mainly of hunter-killed bears. They might not represent the true natural age distribution in the southern population, due to selective hunting, and therefore the comparison of age composition between problem and nonproblem bears must be viewed with caution. Shooting is always performed from high hides near feeding stations on moonlit nights (Ministry of the Environment and Spatial Planing, Slovenia, 2002), which allows hunters to choose the bears to be killed.

According to the Brown bear management strategy in Slovenia (2002), at least 75% of killed bears have to be under 100 kg, at most 15% from 100 to 150 kg, and at most 10% over 150 kg. However, the proportion of killed bears over 100 kg is higher, about 36% for the period 1994-2002, which biases the natural age distribution towards younger bears, which are those that are more often responsible for conflict situations with humans (Akcijski nacrt upravljanja z rjavim medvedom (*Ursus arctos L.*) v Sloveniji 2003-2005).

In contrast, in Croatia there are no recommendations about the preferable proportions of size or age classes to be killed, and it is only illegal to hunt females and young following their mother (Huber et al. 2008b). Therefore the proportions might be even more skewed, in fact, as 66% of Croatian nonproblem bears from 2005 to June 2009 were adults (Table 5).

In the northern population a suggestive difference in age among problem and nonproblem bears was found. There were only 19 problem bears (5 adults and 14 subadults), if we include those with missing Julian dates, and all of them were nuisance bears, which means that none of them were depredating on livestock or caused any other damage near human settlements. In conclusion, the fact that subadults represent as much as 77.5 % of all problem bears in the south, and 74% in the north gives clear support for the social-organization hypothesis.

Sex differences between problem and nonproblem bears

The social-organization hypothesis predicted that I would find more subadult males and females with cubs among problem than among nonproblem bears. My results of the sex distribution in southern population show that nonproblem bears consisted of 66 % males and 34 % females, whereas problem bears were found to have a significantly different distribution; an equal proportion of both sexes (48% and 52% respectively). Hence more females were found than expected by the social-organization hypothesis. As already seen, most of the problem bears were subadults, and only 12% of male problem bears were adults (7 out of 58 bears). This is in line with our expectations from the social-organization hypothesis. Among females there were 32% of adults (20 out of 62 bears), (a somewhat higher percentage than among males), and of those 20 adults, 4 surely had cubs. Compared to the total number of females and our predictions, four females with cubs is a relatively small proportion.

This unexpectedly high number of subadult females is interesting. Although they are commonly found to be philopatric (Kojola et al. 2003; Jerina & Adamič 2009), a study conducted in Sweden found that 32% of females disperse from their natal home range in the north of Sweden and 46% in the south (Støen et al. 2006a). Dispersing females were found to have a smaller body size than non-dispersing females, suggesting that dominance hierarchy based on body size is likely to determine which sibling will be constrained to leave (Zedrosser et al. 2007). The dispersal of subadult females has not been studied in the southern European population, but we could expect a similar pattern to occur in Slovenia and Croatia as well. They probably would not disperse as far as males, but they might move towards the edges of the Core Area. My results show that among subadult females in the southern population, problem females (both nuisance and depredators) had a significantly lower BCI than nonproblem individuals, supporting the social-organization hypothesis and suggesting they might be the subdominant siblings dispersing due to social constraints.

Another explanation for the surprisingly high numbers of females could be related to the hunting practices in Croatia and Slovenia. Most of nonproblem killed bears from the dataset are males (66%), and also from 1994-2000 in Slovenia, males made up 61% of the hunter-killed bears (Ministry of the Environment and Spatial Planning, 2002). This could indicate that the sex structure in the population has been changed, and as a consequence there are more females than males. But, because most of the problem females are subadults and therefore younger than 4 years, this is probably not the reason. Besides, there are some indications that the natural gender balance has not been altered by hunting yet, because in a study including live captures of 56 bears, 64% were males (Huber et al. 2008b), and a genetic study involving sex determination from scat samples revealed a 50:50 sex ratio among 67 randomly selected bears (Huber 2008c).

In the northern population, 13 of 17 problem bears were males, as predicted by the social-organization hypothesis, but the sample size was low.

Timing of problem bears occurrences

Most of the nuisance bears in the southern population (54%) occurred in the "high aggression" period from April to June, as predicted by social-organization hypothesis. This is the time when most intraspecific predation occurs and coincides with breeding and dispersal period. Bears from the northern population showed a similar pattern, with a peak period of nuisance bears from mid-May to Mid-June.

Difference in BCI between problem and nonproblem bears

According to the social-organization hypothesis, I expected problem bears to show a lower BCI, or no difference from nonproblem bears. In the southern population, all models showed that problem bears have a significantly lower BCI, except for adult females, and for males which had too small sample size to run a model. When problem bears were separated, both nuisance and depredators showed a significantly lower BCI, the difference for depredators was only suggestive for males, being significant at $\alpha=0.10$. This was predicted by the social-organization hypothesis, as problem bears were expected to have a significantly lower BCI, or no difference from nonproblem bears. I should mention that, although some problem bears were utilizing human food resources, there was not enough time for them to significantly increase their body mass before being shot. As already said, bears in Slovenia are shot a maximum of two weeks after the bear was seen or first damages had been reported. In Croatia the times could be longer, but there were only 8 problem bears from Croatia compared to 112 from Slovenia; therefore a great majority was surely shot shortly after appearing in the village. However, "country" was always a significant predictor in the model, with Slovenian bears having lower BCI values than Croatian.

A lower BCI also was predicted for problem than nonproblem bears by the food-search hypothesis. Among females, depredators showed a somewhat lower BCI than nuisance bears, which could be interpreted as an indicator of undernourishment, and therefore support the food-search hypothesis.

There was no difference in BCI between problem and nonproblem bears in the northern population, but the sample size was low.

Effect of previous food condition on occurrence of problem bears

A significant correlation was found in Slovenia comparing the BCI corrected for date (autumn index + following spring index) and occurrences of problem bears from the following autumn until the end of spring (Table 15, Fig. 8). This gives a partial support to the food-search hypothesis, as more problem bears occurred after a year with lower mean BCI. An extremely low BCI occurred in autumn of 2004 and spring 2005: 7.52 kg/cm compared to the overall mean of 8.30 kg/cm (Fig 9). The next season (autumn 2005 + spring 2006) there were 30 problem bears (Table 14), which was 28% of all problem bears in 13 years. From the damage reports listed in the brown bear conservation and management plan in Slovenia, the year 2005 had the most damage cases in all years from 1994 to 2006 (Ministry of the Environment and Spatial Planing, Slovenia 2007). I conclude that only a very poor year (no other year had a BCI lower than 8 kg/cm) might lead to an increased occurrence of problem bear in the next fall and spring, which supported the food-search hypothesis is this extreme year. I recommend that a special management strategy be developed in such circumstances, (e.g. an increased amount of supplemental feeding). However, other correlations of time periods were not significant. In Sweden no correlation was found at all, but the sample size was low, which also suggests that no year had so poor food resources that would have caused a peak of problem bears.

Effects of feeding stations on occurrence of problem bears

According to the management plans in Slovenia and Croatia, regularly supplied feeding stations located far from human settlements decrease problem bear occurrences. They should reduce the movement of bears towards human settlements, increase the carrying capacity, and allow monitoring, and safer hunting. Feeding stations might also render adult males more predictable and females with cubs could be able to avoid them more successfully. It was seen in Croatia that females with particularly large litters do not visit feeding stations (Frkovic et al. 2001). It seems that feeding stations successfully keep adult bears inside the desired area of the habitat, but the same cannot be said about subadults. They may avoid feeding stations and probably seek adult-free habitats, therefore the feeding strategies does not appear to keep subadults away from humans settlements, and may even cause more of them to occur near humans. This pattern was not as clear in the north, where baiting for hunting is not allowed (Bischof et al 2008, Pulliainen et al 1996).

Other considerations regarding the feeding stations:

The brown bear management plan in Croatia states that, during the feeding period of 120 days, a maximum of 300 kg of cereals, 300 kg of wet fodder and 400 kg of meat per adult bear may be supplied. If significantly lower quantities are supplied, feeding stations could become an important food resource to be protected by adult males, and other sex/age classes will not be able to obtain food. As seen among brown bears in Alaska, a significantly higher degree of aggression occurred around garbage dumps when its size decreased (Peirce & Van Daele 2006), and after the closure of garbage dumps in Yellowstone, very many problem bears appeared (Robbins et al 2004). If the quantities of supplied food vary from one year to another, it could cause a disproportional reproduction and survival in years with high abundance and cause more problem bears in years with a lower supply. This might be particularly critical if it coincides with years with poor natural food abundance.

Special attention should be given to the types of food that are supplied. In a way, supplemental feeding may have an opposite effect and encourage the bears to become problem bears, e.g. an excessive amount of domestic animal carcasses could induce the bears to seek for similar food when supplemental feeding ends, and the human scent at the feeding stations might make them associate humans with food (Gray et al. 2004, and references within). In Slovenia bears have not been fed with meat since 2004, as required by EU regulations. The feeding stations contain only grain and fruit and are used by other animals as well. The amounts of food are regulated according to the natural food abundance (Jonozovic M., Slovenian Hunting Association, personal communication).

This sudden change of regulations occurred in mid-2004, and interestingly, it was autumn 2004 and spring 2005 when bears had extremely low BCI values and high numbers of problem bears occurred the following season. It is possible that this was due to the inevitable adjustments that had to be made regarding the quantities of food. Therefore the total amounts might have been lower, and the sudden transition to only vegetarian food, might have induced the bears to search for other food elsewhere. However, the year 2005 was different also regarding hunting quotas, which were issued later than usual. Therefore, the supposed amount of 70% of the total hunting quota could not be carried out in spring, as is the usual practice, so more bears might have appeared because of this reason as well.

(It was found that with greater availability of human food, black bears reduced their home range, increased their body mass and reproductive success (Hristienko & McDonald 2007, and references therein), and Frkovic et al. (2001) linked the availability of human food to larger litter sizes in brown bears. More studies are needed to analyze the use of feeding stations, determine sex/age categories using them and their timing, in order to prevent major modifications of brown bear natural behavior and ecology.)

Bears shot in self-defense

Bears shot in self-defense in the north occurred mostly (77%) in autumn (1 September-30 November). We do not know the exact circumstances, but it is probable that the majority of them were shot as a consequence of surprise encounters with hunters during the hunting season in autumn. Most of them (83%) were adults. A study in Sweden showed adult bears to be more tolerant to humans coming in their proximity and fled at shorter distances than younger bears (Moen, 2009). Therefore there is a greater chance to encounter an adult than a subadult. There was no difference in BCI among adult bears shot in self-defense and nonproblem bears, whereas subadults showed a higher BCI than nonproblem bears, but the sample size was low. This indicated that bears that confronted hunters were not bears in poor condition.

Final conclusions

The outcome of the predictions for both hypotheses can be seen from the table 18, the symbol ✓was used if a prediction was supported, ×/✓ when it was partially supported, and × if it received no support. When considering the results, the social-organization hypothesis had more support than the food-search hypothesis. A clear support is given by the age composition of problem bears: more subadults than adults than among nonproblem bears, and the time of the year they appeared most was during the "aggression" period. Furthermore, food other than garbage was not always present near human settlements, and some problem bears caused no damage at all. Only an extreme year with very low BCI value caused a major appearance of problem bears in the following season.

On the other hand, the BCI value of problem bears was significantly lower, which suggests their subdominant status, but could also indicate undernourishment. An equal proportion of males and females among problem bears in the southern population could support both hypotheses.

Table 18 Overview of the outcome of the predictions for food-search and social-organization hypotheses regarding problem brown bears in Europe.

Variables of problem bears in relation to nonproblem bears		Food-search hypothesis		Social-organization hypothesis	
Age	Subadults	Yes	✓	Yes, to a higher degree	✓
	Adults	Yes, to a higher degree	×	Yes, to a lower degree	✓
Sex	Females	Yes	✓	Mostly females with cubs	×
	Males	Yes	✓	Yes, mostly subadult	✓
Problem bear category	Depredators	Yes	✓	Yes	✓
	Nuisance	No	×	Yes	✓
Timing of major problem		Den-emergence	×/✓	"Aggression period"	✓
		Hyperphagia	×/✓		
Food presence		Yes, always	×	Not necessarily	✓
Influence of natural food availability		High	×/✓	Little or none	×/✓
BCI		Lower	✓	Lower or no difference	✓

The predictions of the social-organization and food-search hypotheses were often not mutually exclusive and thereforre difficult to separate. Nevertheless, my results suggest that problem bear occurrence may be due to a combination of factors involving both social constraints and food abundance.

New management strategies should therefore be developed considering social-organization and behavioral ecology of bears, besides the food availability, and keeping in mind that bears are not displaying "unnatural" behavior by occupying areas close to settlements.

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