Brown bear conservation and the ghost of persecution past

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ABSTRACT

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

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1. Introduction

People and large carnivores have been in conflict throughout their common history (Linnell et al., 2001; Woodroffe, 2000). In contrast to other large mammals, such as ungulates, carnivores were not killed primarily for consumption, but to prevent them from killing livestock, other wildlife, or people. Emperor Charlemagne was the first to establish a dedicated large carnivore hunting corps around 800 AD (Boitani, 1995), but it took many centuries to gradually eliminate large carnivores from Western Europe (Frank and Woodroffe, 2001). In contrast, the technology of poison, traps, and firearms eradicated large carnivores from much of eastern North America in two centuries, and organized predator control programs eliminated them from most of the American West within a few decades (Frank and Woodroffe, 2001). A shift in the management paradigm towards more conservation-oriented management has occurred in the 20th cen-

tury, and today many large carnivore populations are again on the increase in North America and Europe (e.g. Boitani, 2000; Breitenmoser, 1998; Linnell et al., 2001; Schwartz et al., 2006b; Servheen et al., 1999; Swenson et al., 2000; Woodroffe, 2000). The present conservation challenges regarding large carnivores include their large area requirements and predatory behavior (Linnell et al., 2001; Nowell and Jackson, 1996), as well as their comparatively low population densities and slow life histories. Especially small populations of large carnivores are very vulnerable to stochastic events and the loss of key individuals (Linnell et al., 2005).

Large carnivore conservation today must take place on different ecological stages. In North America the focus of recovery is mostly aimed at protected, remote, and wilderness areas, whereas conservation in Europe must be achieved in a cultural landscape with high human densities, where protected areas are comparatively small, and remote or wilderness areas are virtually nonexistent (Frank and Woodroffe, 2001; Linnell et al., 2001; Woodroffe, 2000). For example, Woodroffe (2000) has suggested that population declines of brown bears (Ursus arctos) in North America occurred at critical historical human population densities of 4.2 people/km². Today, with modern management, several populations of brown bears are increasing again in North America in association with a mean human population density of

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5.8 people/km^2 (Linnell et al., 2001). In Europe brown bear populations are increasing as well, however at mean human population densities >80 people/km^2 (Linnell et al., 2001). Despite the fact that European bears live in areas that are seemingly less suited (i.e. higher human densities, higher habitat alteration, higher landscape fragmentation), they seem to be able to tolerate more human pressure and respond faster to conservation activities than North American populations. For example, brown bear population growth rates of 14% and 16% annually have been documented in Europe (Sæther et al., 1998), whereas the highest population growth rates documented in North America are considerably smaller; 8.5% in British Columbia, Canada (Hovey and McLellan, 1996), and 4.2–7.6% in the Greater Yellowstone Ecosystem (Harris et al., 2007; Schwartz et al., 2006a).

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

Interspecific competition among carnivores can limit spatial distributions, constrain habitat selection, reduce prey encounter rates, reduce food intake, and increase mortality rates (Creel et al., 2001). The usual direction of the relationship between two carnivore species is that large carnivores commonly affect the distribution, demography, and population dynamics of medium-sized carnivores, which in turn limit smaller carnivores (Creel et al., 2001). For example, the distribution and population size of coyotes (*Canis latrans*) in Yellowstone National Park has decreased as a result of the reintroduction of wolves (*Canis lupus*) (Berger and Gese, 2007). However, smaller carnivores can also potentially limit larger species, when there is extensive dietary overlap, their density is higher, and when they are more efficient using a low density of the same food resource. For example, Mattson et al. (2005) suggested that the American black bear (*Ursus americanus*) has a negative impact on brown bear populations through competitive exclusion from common food sources in areas where brown bear populations have been reduced and where black bear populations are robust.

Also human-caused selection can influence the life-history of a species. There is growing evidence of human-induced selection on morphology (Hendry et al., 2008) and life-history traits (Darimont et al., 2009) from wild animal populations, the latter especially from commercially exploited fish populations (Hutchings and Fraser, 2008). In large mammals, effects on morphological traits have been documented (Coltman et al., 2003; Jachmann et al., 1995), however modeling suggests that also life histories can be affected (Proaktor et al., 2007).

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

We aim to evaluate the differences in reproductive allocation of brown bear populations in relation to population density, habitat quality (normalized difference vegetation index; NDVI (Pettorelli et al., 2005)), interspecific competition, as well as differences in nonselective human persecution history (short persecution history: <150 years, equivalent to <15 generations; long persecution history: >500 years, equivalent to >50 generations with a ~10-year generation length (Harris and Allendorf, 1989; Tallmon et al., 2004). The length of persecution histories (i.e. long, short) reflects the time period with intense persecution in Europe and North America, respectively.

2. Methods

We collected data from 28 different brown bear populations in North America, Asia, and Europe with population size >100 to avoid potential Allee effects on life history traits (Table 1). The decline of brown bear populations started early in Europe (Jakubiec, 1993), and it chronicles the expanding human population (Breitenmoser, 1998). Eradication of large carnivores due to their threat to livestock and as competitor for game species was a political objective of all European agricultural societies (Breitenmoser, 1998). Killing of bears was indiscriminant of sex, age, or reproductive class, and they were trapped, shot, or poisoned whenever encountered. For example, brown bears disappeared in Denmark 3500 years ago, in Britain during the Middle Ages, and in the German lowlands by 1600 (Breitenmoser, 1998; Jakubiec, 1993). In comparison, brown bear populations in North America south of Canada collapsed rapidly during 1850–1920 and most remnant populations disappeared during 1920–1970, due to persecution by settlers with modern weapons (Frank and Woodroffe, 2001; Mattson and Merrill, 2002). Several brown bear populations in Asia were included into the analysis in order to increase the sample size. The persecution history of these populations is very similar to that of North America (i.e. short persecution history) (Servheen et al., 1999).

Female body masses were estimated by summing the average adult (⩾5 years) April–July weight and the average August–November weight and dividing by 2 (McLellan, 1994; Stringham, 1990). In our own study populations (northern and southern Sweden) body mass was estimated by averaging spring body mass of adult females captured in the course of our study. To obtain comparable weight estimates, the mean spring weights in populations where bears only were weighed in spring were multiplied by 1.28 to obtain an estimate of the annual mean mass. This correction factor is based on populations where bears were weighed in both seasons (McLellan, 1994; Stringham, 1990). Female body mass was log-transformed in the analysis to obtain a better model fit.

Table 1

Data used to analyze the relative degree of female reproductive allocation in brown bear populations. Continent refers to the geographic location of the population (NA = North America, EU = Europe, A = Asia); NDVI is the mean normalized difference vegetation index around the center location of each study area for the months May–July in the years 2000–2005; density is the reported population density in bears/1000 km^2; salmon refers to whether populations have access to spawning salmon as food source; persecution refers to length of persecution by modern man (long: >500 years; short: <150 years); black bear = presence (Yes) or absence (No) of sympatric black bear populations; mean female mass = mean adult female body mass in kg, and N = sample size of adult females used to calculate mean adult female mass; mean litter size = mean number of cubs per litter, and N = sample size of litters used to calculate mean litter size. The column "reference" indicates the source(s) of the data.

Population	Continent	NDVI	Density	Salmon	Persecution	Black bear	Mean female mass	N	Mean litter size	N	Reference
Populations with short persecution history											
Admiralty Island	NA/USA-Alaska	0.320	419[a]	Yes	Short	No	169[b]	18	1.80	32	Miller et al. (1997), Schoen and Beier (1990)
Alaska Range	NA/USA-Alaska	0.595	15	No	Short	No	154[c]	52	2.10	71	Miller et al. (1997), Reynolds (1997)
Black Lake	NA/USA-Alaska	0.336	191	Yes	Short	No	256[c]	34	2.57	46	Miller et al. (1997), Miller et al. (2003)
Denali National Park	NA/USA-Alaska	0.522	37	No	Short	Yes	125[c]	65	2.10	42	Miller et al. (1997), Miller et al. (2003)
East Front Montana	NA/USA-Montana	0.362	7	No	Short	Yes	125[b]	6	2.20	41	Aune and Kasworm (1989)
Eastern Brooks Range	NA/USA-Alaska	0.276	4	No	Short	Yes	108[b]	31	1.80	13	Reynolds (1976)
Flathead	NA/Canada-British Columbia	0.542	64	No	Short	Yes	114[b]	16	2.20	26	McLellan (1989a,b,c)
Katmai NP	NA/USA-Alaska	0.284	551	Yes	Short	No	207[c]	12	2.06	51	Miller et al. (2003)
Kenai Peninsula	NA/USA-Alaska	0.501	230[f]	Yes	Short	Yes	202[b]	14	2.36	56	Farley et al. (2001)
Kluane NP	NA/Canada-Yukon	0.297	37	No	Short	Yes	121[b]	35	1.97	29	Ferguson and McLoughlin (2000), McCann (1998), Pearson (1975), Smith and Van Daele (1991)
Kodiak Island	NA/USA-Alaska	0.324	280	Yes	Short	No	202[b]	16	2.50	29	LeFranc et al. (1987), McLellan (1994)
Kuskokwim Mountains	NA/USA-Alaska	0.428	18	Yes	Short	Yes	170[c]	23	1.90	33	Van Daele et al. (2001)
MacKenzie Mountains	NA/Canada-Yukon, NW Territories	0.437	12	No	Short	Yes	110[b]	28	1.80	6	Miller et al. (1982)
McNeil Sanctuary	NA/USA-Alaska	0.407	370[g]	Yes	Short	No	160[h]		2.15	137	McLellan (1994), Sellers and Aumiller (1994a), Stringham (1990)
Middle Susitna	NA/USA-Alaska	0.460	21[i]	No	Short	Yes	170[c]	50	2.09	91	Miller et al. (1987), Miller et al. (2003), Tobey (2001)
Northern Hokkaido	A/Japan	0.412	328[d]	Yes	Short	No	103[b]	31	1.59	13	Kohira et al. (2006)
Northern Yukon	NA/Canada-Yukon	0.486	28	No	Short	No	116[b]	35	2.00	6	Nagy et al. (1983a)
Sakha	A/Sakha Republic	0.472	9	No	Short	No	142		1.89	119	Yakovlev, F., pers. com.; Mordosov (1993)
Southern Hokkaido	A/Japan	0.641	93	No	Short	No	102[b]	17	1.60	13	Mano and Tsubota (2002), Hokkaido Institute of Environmental Sciences (2000)
Tuktoyaktuk	NA/Canada-NW Territories	0.482	4	No	Short	No	124[b]	36	2.30	18	Nagy et al. (1983b)
Western Brooks Range	NA/USA-Alaska	0.448	24	No	Short	No	117[b]	35	2.02	57	Reynolds and Hechtel (1984)
Yellowstone	NA/USA-Wyoming, Montana	0.484	16	No	Short	Yes	135[b]	63	2.00	102	Blanchard (1987), Mattson et al. (2005), Schwartz et al. (2006b)
Populations with long persecution history											
Dinara	EU/Slovenia, Croatia	0.807	41[d]	No	Long	No	128[b]	67/69	2.39	56	Frkovic et al. (2001), Swenson et al. (2007), Zedrosser et al. (2001)
Finish/Russian Karelia	EU/Finland, Russia	0.631	15	No	Long	No	132[e]	81	2.50	31	Kojola, I. (pers. com.)
Leningrad Oblast	EU/Russia	0.720	21	No	Long	No	127[b]	15	2.35	31	Danilov et al. (1993), Novikov et al. (1969)
Northern Sweden	EU/Sweden	0.438	11	No	Long	No	120[c]	46	2.40	33	Støen et al. (2006), Swenson et al. (2001b)
Southern Sweden	EU/Sweden	0.592	29	No	Long	No	117[c]	59	2.30	55	Støen et al. (2006), Swenson et al. (2001b)
Western Cantabria	EU/Spain	0.711	17	No	Long	No	94[e]	12	2.26	23	Fernández Gil (2009), Naves et al. (1999), Wiegand et al.(1998)

[a] Mean of two estimates in Miller et al. (1997).
[b] Spring and fall body mass divided by 2.
[c] Spring body mass multiplied by 1.28.
[d] Total number of bears divided by area occupied by bears.
[e] Hunter-killed females in fall.
[f] Data extracted from Hilderbrand et al. (1999).
[g] Estimate derived from 2 study areas close by Sellers and Aumiller (1994b).
[h] Estimate based on captured bears (Stringham, 1990).
[i] Mean of 2 estimates given in Tobey (2001).

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

We used NDVI as a predictor of habitat quality and productivity (Pettorelli et al., 2005). The Global Land Cover Facility freely provides time series of NDVI, covering the entire world in biweekly and continental-wide mosaics since 1986. The spatial resolution (pixel size) of these NDVI layers is 8 km × 8 km. The data originate from imagery recorded by the Advanced Very High Resolution Radiometer Sensors on board the National Oceanic and Atmospheric Administration satellites (Pinzon et al., 2005; Tucker et al., 2005). NDVI layers for Eurasia and North America were downloaded from http://glcf.umiacs.umd.edu/data/gimms/ (accessed September 2010). We placed the center locations of each study area (based on the study area descriptions) in large and unfragmented areas suitable for bears (i.e. we avoided placing the center points in e.g. large open water bodies or glaciers). Because the populations used in this analysis were studied at different points in time from the 1970s until after the turn of the millennium, we were not able to calculate NDVI values for all studies exactly at the time they were carried out. We therefore calculated the mean NDVI per pixel across all layers of the months May–July for the years 2000–2005 with Erdas Imagine software. We imported this averaged NDVI layer into ArcGIS 9.3.1, and assigned "NoData" to all water to avoid bias because of its default value. We then smoothed the averaged layer with a moving window approach to calculate the mean NDVI for each pixel within a radius of 17.845 km around a given pixel (this radius approximates an area of 1000 km^2, and fully or partially contains 32 8 km × 8 km pixels). This radius was chosen because an area of 1000 km^2 covers the home ranges of several adult females, and because the density measure we used was expressed in bears/1000 km^2 (see below). We then extracted the NDVI-value of the pixel corresponding to each study area center location.

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

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

Individuals in bear populations with access to spawning salmon as a food source are on average larger and heavier than bears in populations without access to spawning salmon (Hilderbrand et al., 1999). Because access to spawning salmon is highly correlated with population density (all populations with densities >100 individuals/1000 km^2 had access to spawning salmon (Table 1) (Spearman's rho = 0.668, $p < 0.001$; variance inflation factor = 5.251, Zuur et al. (2009)), we considered whether or not a population had access to spawning salmon only to subsample populations for analysis, and not as variable in the analysis itself.

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

3. Results

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

Table 2

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

Variable	β	S.E.	T	p	R^2
Model a: Including populations with access to salmon					0.57
Log (body mass)	0.635	0.146	4.337	⩾0.001	
Factor (persecution history)			5.048	⩾0.001	
Short persecution history	0	0			
Long persecution history	0.435	0.086			
Model b: Excluding populations with access to salmon					0.63
Log (body mass)	0.571	0.258	2.213	0.041	
Factor (persecution history)	0		5.284	⩾0.001	
Short persecution history	0	0			
Long persecution history	0.391	0.074			
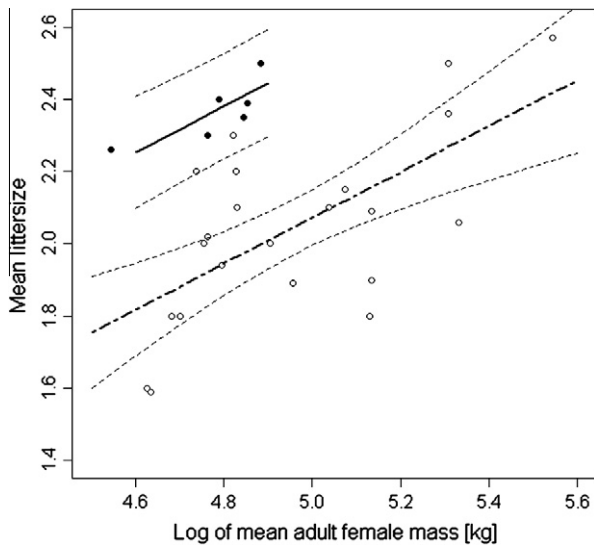
Fig. 1. Predicted relationship between mean litter size and mean female mass in brown bears in relation to persecution history. Predicted brown bear litter sizes and 95% confidence intervals from the linear model with mean adult female mass (kg) and persecution history (long-term = upper, solid line, short-term = lower, dashed line) as model factors. The data are represented by points (filled = populations with long-term history of persecution; open = populations with short-term history of persecution). $N = 28$ populations of brown bears. A small amount of noise was added to locations of data points on the x-axis to allow for the distinction of overlapping points.

$p = 0.528$; factor(presence/absence of black bears), $\beta = 0.0233$, $p = 0.777$; NDVI, $\beta = 0.436$, $p = 0.246$; log(mean adult female body mass) $\times$ log(population density), $\beta = 0.149$, $p = 0.206$; log(population density), $\beta = -0.042$, $p = 0.138$.

Removing populations with spawning salmon as a food source gave similar results and did not affect the relationships of mean adult female body mass and length of persecution on mean litter size (Table 2, R^2 model b = 0.63; Fig. 1). The following variables and interactions tested were not significant and were removed from the analysis in this order: log(mean adult female body mass) $*$ log(population density), $\beta = -0.194$, $p = 0.832$; log(mean adult female body mass) $\times$ factor(presence/absence of black bears), $\beta = 0.336$, $p = 0.767$; log(mean adult female body mass) $\times$ NDVI, $\beta = 1.583$, $p = 0.564$; factor(presence/absence of black bears), $\beta = 0.070$, $p = 0.486$; log(population density) $\times$ NDVI; $\beta = -0.409$, $p = 0.258$; NDVI, $\beta = 0.065$, $p = 0.872$; log(population density), $\beta = -0.035$, $p = 0.419$.

Populations with short persecution history had a significantly lower NDVI than populations with long persecution history (including populations with access to spawning salmon: two-sample t-test, mean NDVI$_{short\ persecution}$ = 0.433 ± 0.100 SD, mean NDVI$_{long\ persecution}$ = 0.650 ± 0.128, $t = 4.454$, $df = 26$, $p < 0.001$; excluding populations with access to spawning salmon: two-sample t-test, mean NDVI$_{short\ persecution}$ = 0.650 ± 0.128, mean NDVI$_{long\ persecution}$ = 0.465 ± 0.102, $t = 3.468$, $df = 18$, $p = 0.003$).

4. Discussion

A species life history is shaped by its physical and ecological environment through the processes of natural selection (Stearns, 1992). Our results showed significant differences in reproductive allocation among populations of brown bears between especially North America and Europe. In addition, females in European brown bear populations also have a shorter mean interlitter interval (2.8 years; data recalculated from Steyaert et al. (in press)) and a younger mean age at primiparity (5.3 years; data recalculated from

Steyaert et al. (in press)) than females in North American populations (mean interlitter interval: 3.6 years; mean age at primiparity: 6.9 years; data recalculated from Steyaert et al. (in press)). These life-history differences among bear populations may be a reason why the highest documented reproductive rates for brown bears are from European populations (i.e. 16% in Sweden, Europe (Sæther et al., 1998). Differences in the population growth rates translate also into differences in sustainable hunting rates for the species in North America and Europe. Brown bear populations can sustain a hunting rate of ~10% annually without declining in Europe (Bischof and Swenson, 2009), whereas maximum sustainable hunting mortality has been estimated to be 5.7% in North America (Miller, 1990).

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

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

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

High levels of centuries-long human persecution may have contributed to an evolutionary life-history change in brown bears, causing females to invest relatively more in reproduction in relation to body mass. Because life-history strategies often involve trade-offs between body growth and reproduction, life-history theory predicts that animals in populations with a high adult mortality rate should prioritize reproduction over body growth to increase the probability of reproducing before death (Stearns, 1992). The duration of persecution of brown bears by humans differed between Europe compared with North America and northern Asia. Europeans conducted extermination campaigns for centuries with primitive weapons and traps; thus the mortality was likely nonselective. Populations declined relatively slowly until effective firearms became available in the 1800s (Curry-Lindahl, 1972;

Swenson et al., 2000). In North America south of Canada, brown bear populations collapsed rapidly during 1850–1920 and most remnant populations disappeared during 1920–1970, due to persecution by settlers with modern weapons (Frank and Woodroffe, 2001; Mattson and Merrill, 2002). In much of northern North America and in northern Asia, settlers arrived later and in smaller numbers, and brown bear populations have remained large over vast areas (Servheen et al., 1999). Aboriginal North Americans may have truncated the expansion of the brown bear to the east and competed with them at salmon spawning streams (Mattson and Merrill, 2002), however no organized extermination efforts were carried out as in Europe. In fact, although some tribes had bear-hunting cults or made a sport of killing brown bears (Schullery, 2002), historical accounts suggest that North American aboriginals had only a minor effect on brown bear mortality, due to fear, respect, or taboos on killing and/or eating them (Hallowell, 1926; Storer and Tevis, 1955).

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

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

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

Conservation of carnivores with a world-wide distribution has to be achieved in different settings and at different paces in different parts of the world. Whereas remote and protected areas in, for example, North America are large enough to support substantial

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

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

Acknowledgements

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