Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations

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Abstract. In iteroparous mammals, conditions experienced early in life may have long-lasting effects on lifetime reproductive success. Human-induced mortality is also an important demographic factor in many populations of large mammals and may influence lifetime reproductive success. Here, we explore the effects of early development, population density, and human hunting on survival and lifetime reproductive success in brown bear (Ursus arctos) females, using a 25-year database of individually marked bears in two populations in Sweden. Survival of yearlings to 2 years was not affected by population density or body mass. Yearlings that remained with their mother had higher survival than independent yearlings, partly because regulations prohibit the harvest of bears in family groups. Although mass as a yearling did not affect juvenile survival, it was positively associated with measures of lifetime reproductive success and individual fitness. The majority of adult female brown bear mortality (72%) in our study was due to human causes, mainly hunting, and many females were killed before they reproduced. Therefore, factors allowing females to survive several hunting seasons had a strong positive effect on lifetime reproductive success. We suggest that, in many hunted populations of large mammals, sport harvest is an important influence on both population dynamics and life histories.

Key words: brown bear; early development; fitness; hunting; individual-based studies; lifetime reproductive success; population dynamics; survival; Sweden; Ursus arctos.

INTRODUCTION

Fitness, the expected contribution of an allele, genotype, or phenotype to future generations (Stearns 1992), is the currency of Darwinian evolution. Thus, ecologists seek to understand why some individuals leave more descendants than others, and how phenotype and genotype interact to shape individual fitness (Endler 1986, Kingsolver et al. 2001). The fitness of an individual will generally be affected by its phenotype as well as the environmental conditions experienced (Falconer and Mackay 1996). Early development can be a key factor influencing an individual’s lifetime reproductive success, LRS (Stearns 1992, Lindström 1999), and thus affect population ecology in long-lived species (Festa-Bianchet et al. 2000). To understand the evolution of life histories, it is therefore important to identify which quantitative characteristics are most important for fitness, and to tease apart the relative importance of environment vs. phenotype under field conditions.

Body mass usually has an overwhelming effect on the life history, fitness, and ultimately the population dynamics of animals (Peters 1983). In mammals, body mass affects the relative importance of female survival and juvenile recruitment, as well as litter size and the costs of reproduction, on population dynamics (review in Hamel et al. 2010). Thus, female longevity increases with body mass, and the elasticity of population dynamics to variability in litter size and juvenile survival is greater for small than for large species (Gaillard and Yoccoz 2003). In smaller species, such as long-lived birds, LRS is affected by an individual’s clutch size (Charmantier et al. 2006). In large mammals, longevity typically has a greater effect on LRS than other individual traits (Bérubé et al. 1999, Kruuk et al. 1999, Robbins et al. 2011). Most species of large mammals produce only one or two offspring per litter and thus can only improve reproductive performance by living longer. Therefore, it is important to examine the determinants of LRS in large mammals, such as large carnivores, that show variation in both longevity and litter size (Mech...
Several studies have shown that early development can have permanent effects in mammals and birds (Lindström 1999, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002, Hamel et al. 2009, Cam and Aubry 2011), and that early deficits in growth are costly and not always possible to remediate, especially in long-lived species (LeBlanc et al. 2001, Metcalfe and Monaghan 2001, Jobling 2010). Environmental conditions early in life, including weather and population density, can have profound effects on body size and other life history traits. For example, Albon et al. (1987) reported that in red deer (Cervus elaphus), adverse weather during the first year of life delayed primiparity and decreased adult survival. Festa-Bianchet et al. (2000) showed a negative effect of population density on mass of young bighorn sheep (Ovis canadensis).

Almost all individual-based studies exploring the effects of individual variation in body size on the survival and reproduction of large vertebrates have been conducted on ungulate populations protected from hunting (e.g., Kruuk et al. 1999, Clutton-Brock and Pemberton 2004, Jones et al. 2005, Hamel et al. 2009). Currently, however, most populations of large terrestrial mammals are exploited by humans for management, food, or recreation (Darimont et al. 2009). Harvest-induced selection differs from natural selection (Coltman et al. 2003, Hendry et al. 2008, Bonenfant et al. 2009), yet we know little about how human-caused mortality affects the life history and, ultimately, the evolution of wild mammals (Darimont et al. 2009).

Many important questions in ecology and evolutionary biology can only be answered with data on the life histories of recognizable individuals that extend over decades (Clutton-Brock and Sheldon 2010). Here we examine the early determinants of survival and reproductive success of female brown bears (Ursus arctos), based on 25 years of individual-based studies in two hunted populations in Sweden. We quantified three reproductive measures of individual fitness, i.e., the number of litters produced (lifetime breeding success, LBS), the number of yearlings weaned (lifetime reproductive success, LRS), and the Caswell matrix measure (CMM), which takes into account age at maturity and reproductive success at different ages (McGraw and Caswell 1996). We examined whether early development (i.e., mass as a yearling) and population density in the yearling year affected survival to two years of age, cause of death (natural or human-caused), age at death, and LBS, LRS, and CMM. Assessing how phenotypic individual differences affect lifetime reproductive success is crucial for understanding the evolution of life histories. It is important to extend our investigation to several species and quantitative characteristics in a broad range of environmental conditions to document general patterns of the link between early-life development and lifetime reproductive success. Our work contributes directly to this growing literature.

**Methods**

**Study areas and populations**

The southern study area (south) was located in Dalarna and Gävleborg counties in south-central Sweden (approximately 61°N, 15°E), and includes a rolling landscape of coniferous forest dominated by commercial plantations of Scots pine (Pinus sylvestris) and Norway spruce (Picea abies). The northern study area (north) in Norrbotten County (67°N, 15°E) was located in northern Sweden, and is mountainous, with altitudes up to 2000 m. It is covered by coniferous forest of Scots pine and Norway spruce at lower altitudes, and subalpine forests dominated by birch (Betula pubescens) and willow (Salix spp.) at higher altitudes. The study areas are separated by 600 km.

The duration of maternal care differs between study areas. In the south, 95% of litters were weaned as yearlings, whereas in the north, 45% of litters were weaned as 2-year-olds (Dahle and Swenson 2003a, b). The study areas also differed in absolute population density (Støen et al. 2006, Zedrosser et al. 2006). The average density index (see Individual population density index) was 11.1 bears/1000 km² in the north and 29.3 bears/1000 km² in the south (Støen et al. 2006). Because age at primiparity differed between study areas (Zedrosser et al. 2009), we considered females as adults at 4 years in the south and at 5 years in the north. Cub-of-the-year mortality was as high as 40% in both areas (Swenson et al. 1997, 2001b, Zedrosser et al. 2009). Because we did not capture cubs-of-the-year for animal welfare reasons, we focus our study on yearlings.

Bears are hunted in both areas, with the exception of national parks in the north (Zedrosser et al. 2007a). The bear hunting season generally starts in late August or early September and lasts 1–2 months. Anyone with hunting rights to an area and a weapon legal for big game hunting can kill bears. The harvest is limited by an annual quota and stops either at the scheduled season end date or when the quota is reached (Bischof et al. 2008). Until the quota is filled, hunters may shoot any solitary bear encountered, regardless of sex and age. The only protected segment of the population is family groups, composed of mothers and their accompanying offspring of any age.

Every bear found dead is by law examined by the Swedish State Veterinary Institute to determine cause of death. In addition to legal hunting, brown bears in Sweden die from a variety of other causes, such as intraspecific predation, vehicle collision, depredation control, and poaching (Swenson et al. 2001a, Bischof et al. 2009). Bischof et al. (2009) calculated estimates of cause-specific mortalities of brown bears in Sweden and found that yearling females suffer hunting mortality, dependent upon annual and geographic variations in hunting pressure, of 1.9–5.4% in the south and 0% in the
north, and a mortality of 17.7% from causes other than
general hunting (defense of life or property, poaching,
capture or traffic accidents, unknown causes) in the
north and south combined. Subadult females (ages 2–4
years) suffer an annual hunting mortality of 2.1–5.8% in
the south and 2.3–3.6% in the north, and a mortality due
to other reasons of 6.0% in both areas combined. For
adult females, annual hunting mortality is 3.1–8.6% in
the south and 1.2–1.9% in the north, and the mortality
rate due to other reasons is 6.6% in both areas combined
(Bischof et al. 2009).

Capture

Radio-marked females and all their yearling cubs were
immobilized by darting from a helicopter shortly after
emergence from the winter den (late April in the south
and early May in the north). Body mass was measured
to the nearest kilogram. Because all bears were captured
within a two-week period in each study area, we did not
adjust mass for capture date. For further details regarding
capture and handling of bears, see Arnemo
et al. (2011) and Zedrosser et al. (2007b). Our analyses
include only females of known age that were first
captured as yearlings. Litter size was determined by
counting cubs-of-the-year accompanying radio-collared
mothers from the air or the ground three times annually.
When a lactating female was captured without cubs, we
assumed that her cubs had died in the den or shortly
after leaving it (Zedrosser et al. 2009).

Individual population density index

We estimated an individual population density index
as the population density within a circular buffer around
the centroid of the home range of each individual (radius
= 17.84 km, area = 1000 km²). Density estimates were
facilitated by the high proportion of radio-marked bears
and documented population growth rates (Zedrosser et
al. 2006). In the south, population size was estimated
based on DNA analysis of scats collected throughout
the area in 2001 and 2002 (Bellemain et al. 2005). The
density index around each radio-marked individual in
our analysis was based on the location of individuals
genetically identified by scat sampling in those two years
(71% of the radio-marked bears were represented in the
scats samples (Bellemain et al. 2005), and then adjusted
using the population growth rate both before 2001 and
after 2002 (Seether et al. 1998, Kindberg et al. 2011). In
the north, virtually every adult male and female and all
subadult female bears were radio-marked (Swenson et
al. 2001b). We used the locations of radio-marked bears,
a correction to include the estimated number of subadult
males, and data on growth rate of the population to
calculate an individual density index as in the south
(Zedrosser et al. 2006).

Definitions of reproductive success

All females included in our analyses had complete
records of reproductive events until death. We estimated
lifetime reproductive success as the number of litters
born (LBS) and the number of yearlings produced
(LRS). Brown bears are commonly weaned as yearlings
in our study areas (Swenson et al. 2001a), and those that
stay with their mother for a second year could have
survived on their own. In addition, most natural
mortality of females <5 years old (i.e., before reaching
primiparity; Zedrosser et al. 2009) occurs in the yearling
year (Swenson et al. 2001a; see also Fig. 1). Litter loss is
common (up to 40% annually), probably due primarily
to infanticide during the mating season (Swenson et
al. 1997, 2001b). Most females that lose offspring during
the mating season produce a new litter the following
year (Zedrosser 2006). Reproductive success in bears
may vary with age (Fig. 2).

Data Analysis

We evaluated the factors affecting yearling survival to
age 2 years (0 = dead; 1 = survived) with a generalized
linear mixed-effects model with a binomial error
structure and a logit link function. We assessed the
effects of the following factors: study area (north, 0;
south, 1), mass as a yearling (9.5–45 kg), independence
from the mother as a yearling (0 = dependent; 1 =
independent), population density around a yearling
female (0.9–67.7 bears/1000 km²), and the interactions
of these variables. We included maternal identity and
year as random effects. We used a backward procedure
to select the best models, based on \( P \) values with a
significance level of \( \alpha = 0.05 \), starting with a full model
of all covariates and relevant second-order interactions
(Crawley 2007). The “lme4” package in R (Bates et al.
2012) was used to fit mixed-effects models. Significance
of random effects was assessed using likelihood ratio
tests, with the restricted maximum likelihood method
(Pinheiro and Bates 2000). Because neither mother
identity nor year were significant as random effects
We did not adjust for changes in population size (e.g., Schwartz et al. 2003, Bischof et al. 2010, Dobson et al. 2012), because brown bears have a slow life history with low birth rates and natural mortality of adults (Schwartz et al. 2003, Bischof et al. 2009). Brown bear populations are thus expected to be stable from year to year and to not show the substantial population fluctuations often observed in small mammals and some ungulates (e.g., Coulson et al. 2001, Hoffmann et al. 2003). The resulting fitness measure, termed individual fitness, was a highly bimodal continuous variable, with values clustered around 1 and 0. We therefore used a two-step conditional approach for modeling the effect of covariates on individual fitness. First we fit a logistic regression of whether individual fitness was zero or nonzero. For individuals with nonzero fitness (those that reproduced at least once), we then fitted a linear regression with untransformed individual fitness as the response. The same set of covariates was considered in both models; population density around a yearling female (0.9–67.7 bears/1000 km$^2$), study area (north: 0; south: 1), and mass as a yearling (9.5–45 kg). The least significant terms were excluded in a stepwise manner until the final model consisted of only significant ($P \leq 0.05$) terms (Crawley 2007). All analyses were conducted in R version 2.12.0 (R Development Core R Development Core Team 2012).

**RESULTS**

We documented complete life histories for 92 female bears from 1988 to 2008. Of those, 66 (71.7\%) died due to human causes, 18 (19.6\%) died of natural causes, and for 8 (8.7\%) the cause of death was unknown (Fig. 1). All but four natural mortalities occurred during the yearling year. Thirty-six (39.1\%) females reached reproductive age, and 28 (30.4\%) made at least one breeding attempt. Of 64 females with complete life histories that died before breeding, 42 (65.6\%) died due to human causes, 16 (25\%) died of natural causes, and 6 (9.4\%) died of unknown causes. Yearling mass ($P = 0.17$), population density ($P = 0.62$), study area ($P = 0.42$), and their interactions (all $P > 0.10$) did not affect yearling survival to age 2. Yearling females that were independent of their mother, however, were less likely to survive ($β = -2.499 \pm 1.051$ SE, $z = -2.377$, $P = 0.017$). Of the 30 females that died in their yearling year, we were able to establish whether 27 of them were dependent or independent of their mother at the time of death. Only one was dependent, and died of unknown causes. Of the 10 independent bears dying from human causes, nine were shot. None of the yearlings included in our study was shot while accompanying its mother.

The average age-specific number of yearlings weaned was lowest for 5 year-old females and increased with age; however, the variation in the age-specific number of yearlings weaned also increased with age, partly due to low sample sizes of females that were >18 years of age (Fig. 2). LBS increased with longevity, was higher for females that were heavier as yearlings, and for females that experienced high population density as yearlings (Table 1A, Fig. 3A–C). Other variables and interactions were removed in the following order from the analysis: yearling mass \times population density, age at death \times study area, age at death \times population density, study area \times...
LIFETIME REPRODUCTION IN FEMALE BEARS

Table 1. Generalized linear models of the early determinants of lifetime reproductive success of female brown bears in two study areas in Scandinavia in 1988–2008: (A) lifetime number of litters produced, and (B) the number of cubs that survived to one year of age over a female’s lifetime.

<table>
<thead>
<tr>
<th>A) Litters born</th>
<th>df</th>
<th>β</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>36</td>
<td>-2.799</td>
<td>0.734</td>
<td>-3.812</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Age at death</td>
<td>36</td>
<td>0.203</td>
<td>0.024</td>
<td>8.378</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mass as yearling</td>
<td>36</td>
<td>0.060</td>
<td>0.026</td>
<td>2.306</td>
<td>0.028</td>
</tr>
<tr>
<td>Population density at yearling age</td>
<td>36</td>
<td>0.013</td>
<td>0.006</td>
<td>2.143</td>
<td>0.040</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B) Yearlings produced</th>
<th>df</th>
<th>β</th>
<th>SE</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>36</td>
<td>-4.186</td>
<td>0.992</td>
<td>-4.218</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Age at death</td>
<td>36</td>
<td>0.283</td>
<td>0.033</td>
<td>8.659</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Mass as yearling</td>
<td>36</td>
<td>0.108</td>
<td>0.033</td>
<td>3.235</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Notes: Variables included were study area (North = 0; South = 1), age at death, mass as a yearling, population density in the yearling year, and interactions of these variables. After a successive exclusion of the least significant term, the final result is shown in the table; β is the quasi-Poisson regression coefficient, and N = 38 adult female brown bears with complete records of reproductive events until death.

The probability of having an estimated individual fitness (>0) increased with increasing age (β = 1.518 ± 0.467 SE, exp(β) = 4.562, z = 3.251, P = 0.001). This effect was retained also when bears that died before reaching reproductive age were excluded from the analysis (β = 1.351 ± 0.252, exp(β) = 3.861, z = 2.600, P = 0.009). Conditional on having weaned at least one yearling offspring, both age at death (Fig. 4A) and mass as a yearling (Fig. 4B) had a positive effect on individual fitness (age at death: β = 0.016 ± 0.004, t = 4.379, P < 0.001; yearling mass: β = 0.011 ± 0.003, t = 3.296, P = 0.005).

Discussion

Our study produced three main findings. First, body mass early in life is an important life history trait for female brown bears, because mass as a yearling was positively related to all three fitness measures evaluated. Second, yearlings that remained associated with their mother had higher survival than independent yearlings, partly because they were protected from hunting, which could possibly lead to artificial selection on maternal investment. Finally, we confirmed that longevity is an important determinant of lifetime reproductive success. The best strategy to increase fitness for female brown bears was to stay alive; longevity alone explained 52% and 68% of the variance in lifetime production of litters and yearlings, respectively. In Sweden, adult female brown bears that survived the longest were generally those that avoided being shot (Bischof et al. 2009).

Our results may underestimate the fitness effects of early development, because the analysis was restricted to individuals that survived to 1 year of age, and ultimately to primiparity (see also Festa-Bianchet et al. 2000). Sources of mortality in brown bear cubs and yearlings are different (Swenson et al. 2001a, b). Infanticide appears to be the major cause of cub mortality in Scandinavia (Swenson et al. 1997, Zedrosser et al. 2009). It is unknown whether larger cubs are more likely to survive an attack by an adult male.

Body mass did not affect yearling survival. In small mammals, such as rodents, subadult survival is sometimes higher than adult survival (e.g., Julliard et al. 1999, Prevot-Julliard et al. 1999), whereas in large mammals, such as ungulates, yearlings typically suffer higher mortality than adults (Gaillard et al. 2000, Gaillard and Yoccoz 2003). We found a typical large-mammal pattern in brown bears, as female mortality peaked during the yearling year (Fig. 1). Almost 90% of natural mortalities (16/18) occurred during the yearling year, mainly because female yearlings were killed by adults during the mating season (Swenson et al. 2001a). These inraspecific killings are poorly understood, but they appear to be independent of yearling size (Swenson et al. 2001a).

In mammals, smaller individuals tend to reproduce later and less frequently, and have fewer and smaller offspring per breeding attempt compared to larger individuals (Stearns 1992). Among pre-industrialized humans, women with reduced early growth and low birth weight tend to have small babies who suffer high mortality (Lummaa and Clutton-Brock 2002). A positive effect of early body size on reproductive success has been suggested in several ungulates, mostly in males (e.g., Kruuk et al. 1999, Festa-Bianchet et al. 2000). Although body mass as a yearling did not affect survival
to 2 years in our study, it was positively associated with lifetime reproductive success, as well as individual fitness, despite evidence for compensatory growth between the ages of 1 and 4 (Zedrosser et al. 2006). As reported in red squirrels *Tamiasciurus hudsonicus* (Descamps et al. 2008), this correlation suggests a “silver-spoon effect” (Grafen 1988) in female brown bears. Similarly to other mammals, larger mothers have larger offspring (e.g., Clutton-Brock et al. 1988, Wauters et al. 1993, Dahle et al. 2006, Skibiel et al. 2009). In addition, larger female yearling brown bears establish their home range closer to or within their natal home range, which probably gives them a reproductive advantage through familiarity with the area and better access to resources facilitated by their mother (Zedrosser et al. 2007b). Although compensatory growth can have short-term benefits, it may involve costs that are not evident until much later (Metcalfe and Monaghan 2001).

Environmental conditions, such as population density, early in life can have pronounced effects on body size and ultimately on survival and reproductive success (Albon et al. 1987, Festa-Bianchet et al. 2000). Subadult survival is often lower at high densities than at moderate densities (Clutton-Brock et al. 1997, Bonenfant et al. 2009); however, similar to body size, population density during the yearling year did not affect survival of female brown bears until age 2. Among deaths of known cause during the yearling year, roughly half are human-caused.
and half are from intraspecific killing (Fig. 1). It is possible that a potential negative effect of population density on yearling brown bear survival was masked by the high rate of human-caused mortality.

Population density was positively associated with LBS, but not with other fitness measures, suggesting that litter loss due to infanticide may be greater in areas of higher density (Palombit 2003). Almost all females reproduce the year after a litter is lost (Swenson et al. 1997), so that infanticide shortens the interbirth intervals (Hrdy 1979) and increases the number of litters born, while reducing a female’s weaning success. LBS also may be indirectly affected by hunting. Cub mortality increases in years after adult males are shot, probably because potentially infanticidal neighboring males realign their home range or immigrant males occupy the home range of the dead male (Swenson et al. 1997, Swenson 2003). More adult males are shot in high-density than in low-density areas in Sweden (Kindberg et al. 2009). Consequently, LBS may be a poor measure of fitness in species with infanticide, such as the brown bear.

Age at weaning and yearling survival were positively associated, which may appear surprising at first, because yearlings that remain associated longer with their mother are often smaller (Dahle and Swenson 2003a). However, this result is partly explained by hunting regulations. Because it is illegal to kill bears from a family group, remaining with the mother for an additional year increases the survival of female yearlings. In addition, adult females that keep their young for an additional year spend more years protected from hunting. Rughetti and Festa-Bianchet (2011) found a similar result in chamois (Rupicapra rupicapra); because hunters tend to avoid shooting females with an offspring, nonlactating females had a higher probability of being harvested than lactating females. High harvest pressure has been suggested to affect life history traits and population productivity in both fish and mammals (Conover and Munch 2002, Proaktor et al. 2007, Darimont et al. 2009). In both chamois and brown bears, high hunting pressure could select for early primiparity and protracted mother–offspring associations.

Longevity was strongly correlated with the fitness measures used in our study, similar to results reported in several small as well as large mammals and birds (e.g., Kruuk et al. 1999, von Holst et al. 2002, Jensen and Miller 2004, Neuhaus et al. 2004, Robbins et al. 2011). The average age of female brown bears at primiparity is 4.7 years in our southern study area and 5.3 years in the northern study area (Zedrosser et al. 2009). The average age at death of brown bears in Sweden, however, is 4.8 years (Bischof et al. 2008), with almost all mortality caused by humans (Table 1; Bischof et al. 2009). A female brown bear’s ability, or good fortune, to survive several hunting seasons therefore has an overwhelming effect on her fitness.

Our results provide insights into the evolution of the extremely diverse life histories of carnivores (Paemelaere and Dobson 2011). Bears are long-lived species with restricted and seasonal reproduction. Accordingly, longevity was the most important life history trait explaining LRS and individual fitness. As predicted by life history theory (e.g., Stearns 1992, Lindström 1999), early mass had long-lasting effects on female lifetime reproductive success. In contrast to prevalent life history theory (e.g., Sutherland et al. 1986, Stearns 1992, Dobson and Oli 2008) and other studies on juvenile
and subadult survival in birds and mammals (e.g., Moreno et al. 1999, Owen-Smith and Mason 2005, Bonenfant et al. 2009, Cleasby et al. 2010), survival of yearling bears was not related to body size or population density. Hunting regulations favored yearlings that remained with their mother. Because the probability of staying with the mother for a second year is inversely related to yearling body mass (Dahle and Swenson 2003a), these regulations may increase the mortality of large, high-quality yearlings.

The effects of hunting on wild populations are pervasive and include direct and indirect demographic effects (Williams et al. 2002), ecological effects on community structure and ecosystem functioning that go beyond the harvested species (Fenberg and Roy 2008), as well as evolutionary effects (Allendorf and Hard 2009). Persecution by humans appears to cause greater and more rapid changes in traits in wild populations than do other selective pressures (Darimont et al. 2009), and the importance of harvest-induced selection has been recognized in both aquatic (Olsen et al. 2004) and terrestrial systems (Coltman et al. 2003). Human-caused mortality is important in most large carnivore species, even inside protected areas (Woodroffe and Ginsberg 1998, Liberg et al. 2012). This is also the case in our study populations, where most mortality occurs before primiparity (Bischof et al. 2009, Zedrosser et al. 2009). Thus, high hunting pressure could select for prolonged maternal care, which might have demographic consequences (Zedrosser et al. 2011). Together, our results support the contention that sport hunting has the potential to become an artificial selective pressure on the reproductive strategy, and ultimately the life history, of carnivores.

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