

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

ANDREAS ZEDROSSER,^{1,2,3,6} FANIE PELLETIER,⁴ RICHARD BISCHOF,³ MARCO FESTA-BIANCHET,⁴
AND JON E. SWENSON^{3,5}

- 1) Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College,
NO-3800 Bø i Telemark, Norway
- 2) Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and
Applied Life Sciences, Vienna, Gregor Mendel Str. 33, A-1180 Vienna, Austria
- 3) Department for Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432
Ås, Norway
- 4) Université de Sherbrooke, Département de Biologie et Centre d'Études Nordiques, Sherbrooke, Canada J1K2R1
- 5) Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

Ecology. 2013, 94 (1), 231-240.

DOI: [10.1890/12-0229.1](https://doi.org/10.1890/12-0229.1)

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. This article is protected by copyright. All rights reserved.

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

ANDREAS ZEDROSSER,^{1,2,3,6} FANIE PELLETIER,⁴ RICHARD BISCHOF,³ MARCO FESTA-BIANCHET,⁴ AND JON E. SWENSON^{3,5}

¹Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, NO-3800 Bø i Telemark, Norway

²Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Applied Life Sciences, Vienna, Gregor Mendel Str. 33, A-1180 Vienna, Austria

³Department for Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

⁴Université de Sherbrooke, Département de Biologie et Centre d'Études Nordiques, Sherbrooke, Canada J1K2R1

⁵Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

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 (Charmanier 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

Manuscript received 9 February 2012; revised 6 July 2012; accepted 16 July 2012; final version received 17 August 2012. Corresponding Editor: F. S. Dobson.

⁶Present address: Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, NO-3800 Bø i Telemark, Norway. E-mail: andreas.zedrosser@hit.no

1988, Schwartz et al. 2003, Sidorovich et al. 2007, Steyaert et al. 2012).

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 develop-

ment 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 legal 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 (Sæther 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



FIG. 1. Number of female brown bears with complete life histories and their causes of mortality in two study areas in Sweden, 1988–2008 ($N = 92$ female bears). Human-caused mortalities are legal hunting, poaching, roadkills, or management removals; natural mortalities refer to traumas due to fall or being killed by another bear.

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 (χ^2

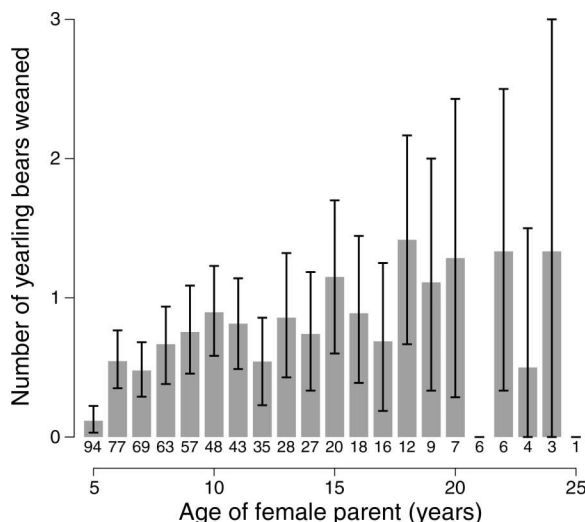


FIG. 2. Average age-specific number of yearlings weaned (gray bars) by female brown bears in Scandinavia, 1988–2008 ($N = 126$ females aged ≥ 4 , for 643 years). Confidence limits (95%) were calculated as the 0.025 and 0.975 quantile of 1000 bootstrapped replicates of the average number of yearlings weaned. The sample size per age class is indicated below the bars.

$= 0.001$, $P = 0.979$), we reported results from a generalized linear model.

We used generalized linear models to examine the relationship between the two measures of reproductive success for all females reaching reproductive age with the following variables: study area (as binomial variable: with north = 0; south = 1), age at death (4–18 years), body mass as a yearling, population density, and all possible two-way interactions. We assumed a Poisson data distribution for age at death and reproduction and corrected for over-dispersion using a quasi-GLM model (Crawley 2007, Zuur et al. 2009). The least significant terms were excluded in a backward stepwise manner until the final model consisted of only significant ($P \leq 0.05$) terms.

We followed McGraw and Caswell (1996) in calculating individual fitness for all females with complete life histories. We first constructed a separate population projection matrix for each individual, accounting for both survival and fecundity. Survival from one age to the next is 1 until the age of death is reached. Recruitment by the focal individual is the number of yearlings weaned in each year of her life, divided by two to exclude the father's contribution. We calculated individual fitness as the dominant eigenvalue using the "popbio" package in R (Stubben and Milligan 2007). We did not adjust for changes in population size (e.g., Viblanc 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 km²), 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 ($\beta = -2.499 \pm 1.051$ 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

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.

Explanatory variables	df	β	SE	<i>t</i>	<i>P</i>
A) Litters born					
Intercept	36	-2.799	0.734	-3.812	<0.001
Age at death	36	0.203	0.024	8.378	<0.001
Mass as yearling	36	0.060	0.026	2.306	0.028
Population density at yearling age	36	0.013	0.006	2.143	0.040
B) Yearlings produced					
Intercept	36	-4.186	0.992	-4.218	<0.001
Age at death	36	0.283	0.033	8.659	<0.001
Mass as yearling	36	0.108	0.033	3.235	0.003

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.

population density, study area \times yearling mass, study area, and age at death \times yearling mass (all $P > 0.17$).

LRS increased with female longevity, and was higher for females that were heavier as yearlings (Table 1B, Fig. 3D, E). The other variables and interactions were removed in the following order from the analysis: age at death \times population density, study area \times population density, study area \times yearling mass, age at death \times study area, yearling mass \times population density, population density, study area, and age at death \times yearling mass (all $P > 0.33$). As expected, LBS and LRS were correlated (Spearman's rank correlation, $\rho = 0.790$); see Fig. 3F.

The probability of having an estimated individual fitness >0 increased with increasing age ($\beta = 1.518 \pm 0.467$ SE, $\exp(\beta) = 4.562$, $z = 3.251$, $P = 0.001$). This effect was retained also when bears that died before reaching reproductive age were excluded from the analysis ($\beta = 1.351 \pm 0.520$, $\exp(\beta) = 3.861$, $z = 2.600$, $P = 0.009$). 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: $\beta = 0.016 \pm 0.004$, $t = 4.379$, $P < 0.001$; yearling mass: $\beta = 0.011 \pm 0.003$, $t = 3.296$, $P = 0.005$).

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 intraspecific 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

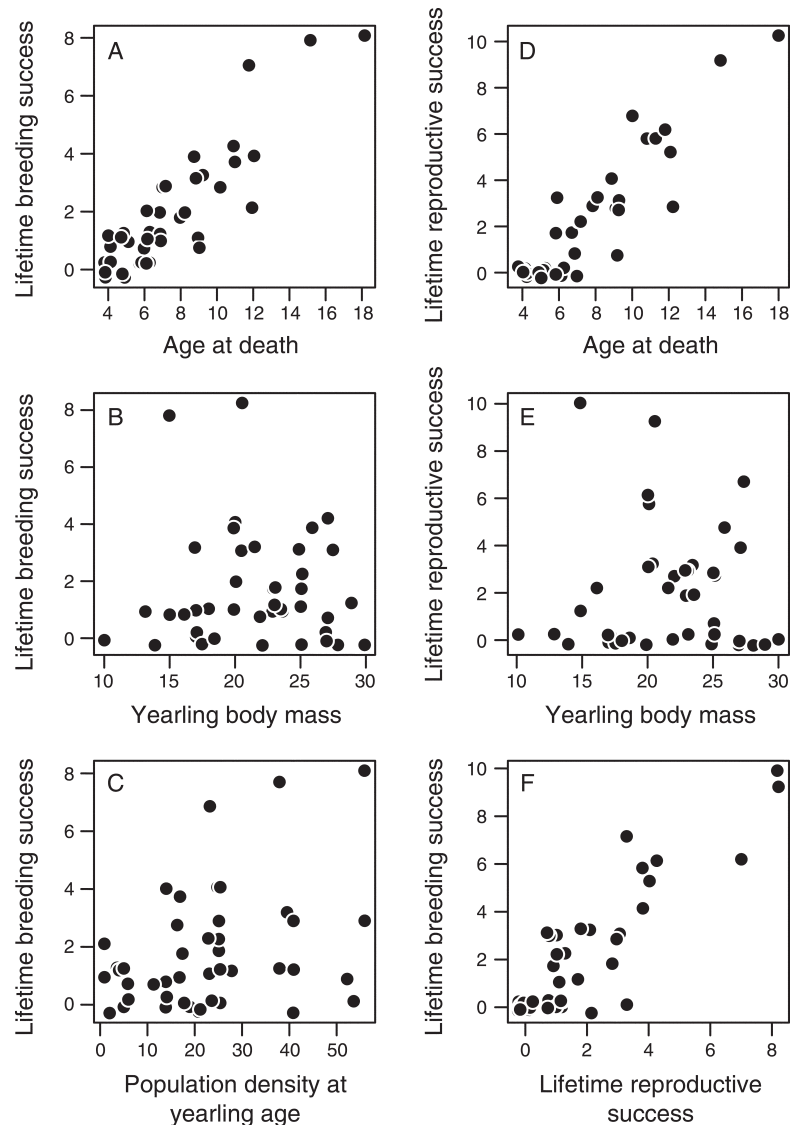


FIG. 3. Determinants of lifetime reproduction of female brown bears in Scandinavia. Lifetime breeding success (number of litters born in a lifetime) in relation to (A) age at death, (B) body mass as a yearling, and (C) population density experienced in the yearling year. Lifetime reproductive success (number of yearlings in a lifetime) in relation to (D) age at death, and (E) body mass as a yearling. (F) Lifetime reproductive success in relation to lifetime breeding success. Data points are jittered to avoid overlap.

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, Skibieli 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 (Metcalf 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 (Hrady 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. Rugghetti 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.

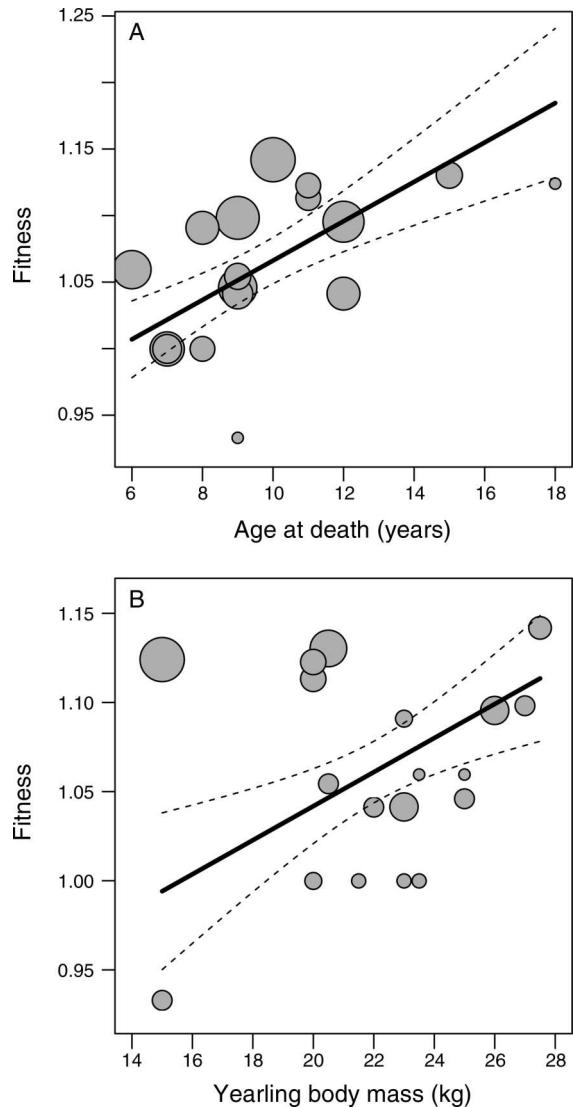


FIG. 4. Raw data (gray dots) and predictions from a linear regression model (solid lines) relating individual fitness of female brown bears to (A) age at death and (B) mass as a yearling. Point sizes indicate the relative value of the mass as a yearling in panel (A) and age at death in panel (B); regression predictions for a given term are made with the other term set to its mean value. Confidence intervals (95%) around the fit are indicated with dashed lines.

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.

ACKNOWLEDGMENTS

We thank the field personnel of the Scandinavian Brown Bear Research Project (SBBRP). A. Zedrosser was supported financially by the Research Council of Norway. R. Bischof was partially funded by grant 204202/F20 from the Research Council of Norway. F. Pelletier and M. Festa-Bianchet were funded by NSERC Discovery grants, and F. Pelletier by the Canada Research Chair in Evolutionary Demography and Conservation. The SBBRP was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Swedish Association for Hunting and Wildlife Management, WWF Sweden, the Research Council of Norway, and the Austrian Science Fund. All capture and handling was approved by the appropriate authority and ethical committee (Djuretiska nämnden i Uppsala, Sweden). This is paper No. 130 from the Scandinavian Brown Bear Research Project.

LITERATURE CITED

- Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. 2. Density-independent effects and cohort variation. *Journal of Animal Ecology* 56:69–81.
- Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences USA* 106:9987–9994.
- Arnemo, J. M., A. Evans, and Å. Fahlman. 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Norwegian Directorate for Nature Management, Trondheim, Norway.
- Bates, D., M. Maechler, and B. Bolker. 2012. Package 'lme4'. Linear mixed-effects models using eigen and S4 classes. <http://cran.R-project.org/package=lme4>
- Bellemain, E., J. E. Swenson, D. Tallmon, P. Taberlet, and S. Brunberg. 2005. Estimating population size of elusive animals with DNA from hunter-collected feces: Four methods for brown bears. *Conservation Biology* 19:150–161.
- Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* 80:2555–2565.
- Bischof, R., R. Fujita, A. Zedrosser, A. Soderberg, and J. E. Swenson. 2008. Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. *Journal of Wildlife Management* 72:79–88.
- Bischof, R., J. E. Swenson, N. G. Yoccoz, A. Mysterud, and O. Gimenez. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* 78:656–665.
- Bonenfant, C., J. M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit, and P. Duncan. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* 41:313–357.
- Cam, E., and L. Aubry. 2011. Early development, recruitment and life history trajectory in long-lived birds. *Journal of Ornithology* 152:187–201.
- Charmanier, A., C. Perrins, R. H. McCleery, and B. C. Sheldon. 2006. Evolutionary response to selection on clutch size in a long-term study of the mute swan. *American Naturalist* 167:453–465.
- Cleasby, I. R., S. Nakagawa, D. O. S. Gillespie, and T. Burke. 2010. The influence of sex and body size on nestling survival and recruitment in the house sparrow. *Biological Journal of the Linnean Society* 101:680–688.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1988. Reproductive success in male and female red deer. Pages 325–343 in T. H. Clutton-Brock, editor. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, Illinois, USA.
- Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. *American Naturalist* 149:195–219.
- Clutton-Brock, T. H., and J. M. Pemberton, editors. 2004. *Soay sheep: dynamics and selection in an island population*. Cambridge University Press, Cambridge, UK.
- Clutton-Brock, T. H., and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution* 25:562–573.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* 297:94–96.
- Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* 292:1528–1531.
- Crawley, M. J. 2007. *The R book*. John Wiley, Chichester, UK.
- Dahle, B., and J. E. Swenson. 2003a. Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology* 54:352–358.

- Dahle, B., and J. E. Swenson. 2003b. Family breakup in brown bears: Are young forced to leave? *Journal of Mammalogy* 84:536–540.
- Dahle, B., A. Zedrosser, and J. E. Swenson. 2006. Correlates with body size and mass in yearling brown bears (*Ursus arctos*). *Journal of Zoology* 269:273–283.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences USA* 106:952–954.
- Descamps, S., S. Boutin, D. Berteaux, A. G. McAdam, and J. M. Gaillard. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. *Journal of Animal Ecology* 77:305–314.
- Dobson, F. S., and M. K. Oli. 2008. The life histories of orders of mammals: Fast and slow breeding. *Current Science* 95:862–865.
- Dobson, F. S., V. A. Viblanc, C. M. Arnaud, and J. O. Murie. 2012. Kin selection in Columbian ground squirrels: direct and indirect fitness benefits. *Molecular Ecology* 21:524–531.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, New Jersey, USA.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. Addison Wesley Longman, Boston, Massachusetts, USA.
- Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology* 17:209–220.
- Festa-Bianchet, M., J. T. Jorgenson, and D. Réale. 2000. Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology* 11:633–639.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: A case of environmental canalization? *Ecology* 84:3294–3306.
- Grafen, A. 1988. On the use of data on lifetime reproductive success. Pages 454–471 in T. H. Clutton-Brock, editor. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, Illinois, USA.
- Hamel, S., J. M. Gaillard, M. Festa-Bianchet, and S. D. Cote. 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* 90:1981–1995.
- Hamel, S., J. M. Gaillard, N. G. Yoccoz, A. Loison, C. Bonenfant, and S. Descamps. 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecology Letters* 13:915–935.
- Hendry, A. P., T. J. Farrugia, and M. T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology* 17:20–29.
- Hoffmann, I. E., E. Millesi, S. Huber, L. G. Everts, and J. P. Dittami. 2003. Population dynamics of European ground squirrels (*Spermophilus citellus*) in a suburban area. *Journal of Mammalogy* 84:615–626.
- Hrdy, S. B. 1979. Infanticide among mammals: review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1:13–40.
- Jensen, A. L., and D. H. Miller. 2004. Modeling emigration of wolves from a wilderness area into adjacent agricultural regions. *Ecological Modelling* 175:115–120.
- Jobling, M. 2010. Are compensatory growth and catch-up growth two sides of the same coin? *Aquaculture International* 18:501–510.
- Jones, O. R., M. J. Crawley, J. G. Pilkington, and J. M. Pemberton. 2005. Predictors of early survival in Soay sheep: cohort-, maternal- and individual-level variation. *Proceedings of the Royal Society B* 272:2619–2625.
- Julliard, R., H. Leirs, N. C. Stenseth, N. G. Yoccoz, A. C. Prevot-Julliard, R. Verhagen, and W. Verheyen. 1999. Survival-variation within and between functional categories of the African multimammate rat. *Journal of Animal Ecology* 550–561.
- Kindberg, J., J. E. Swenson, and G. Ericsson. 2009. Björnstammens storlek i Sverige 2008—länsvisa uppskattningar och trender. Report, Scandinavian Brown Bear Research Project, Umeå, Sweden.
- Kindberg, J., J. E. Swenson, G. Ericsson, E. Bellemain, C. Miquel, and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear (*Ursus arctos*) population. *Wildlife Biology* 114–123.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *American Naturalist* 157:245–261.
- Kruuk, L. E. B., T. H. Clutton-Brock, K. E. Rose, and F. E. Guinness. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London B* 266:1655–1661.
- LeBlanc, P. J., M. Obbard, B. J. Battersby, A. K. Felskie, L. Brown, P. A. Wright, and J. S. Ballantyne. 2001. Correlations of plasma lipid metabolites with hibernation and lactation in wild black bears *Ursus americanus*. *Journal of Comparative Physiology B* 171:327–334.
- Liberg, O., G. Chapron, P. Wabakken, H. C. Pedersen, N. Thompson Hobbs, and H. Sand. 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B* 279:910–915.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14:343–348.
- Lummaa, V., and T. Clutton-Brock. 2002. Early development, survival and reproduction in humans. *Trends in Ecology and Evolution* 17:141–147.
- McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life-history data. *American Naturalist* 147:47–64.
- Mech, L. D. 1988. Longevity in wild wolves. *Journal of Mammalogy* 69:197–198.
- Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* 16:254–260.
- Moreno, J., A. Barbosa, A. De Leon, and J. A. Fargallo. 1999. Phenotypic selection on morphology at independence in the Chinstrap penguin *Pygoscelis antarctica*. *Journal of Evolutionary Biology* 12:507–513.
- Neuhaus, P., D. Broussard, J. Murie, and F. Dobson. 2004. Age of primiparity and implications of early reproduction on life history in female Columbian ground squirrels. *Journal of Animal Ecology* 73:36–43.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935.
- Owen-Smith, N., and D. R. Mason. 2005. Comparative changes in adult vs. juvenile survival affecting population trends of African ungulates. *Journal of Animal Ecology* 74:762–773.
- Paemelaere, E., and F. S. Dobson. 2011. Fast and slow life histories of carnivores. *Canadian Journal of Zoology* 89:692–704.
- Palombit, R. A. 2003. Male infanticide in wild savanna baboons: adaptive significance and intraspecific variation. Pages 367–412 in C. B. Jones, editor. *Sexual selection and reproductive competition in primates: new perspectives and*

- directions. American Society of Primatologists, Norman, Oklahoma, USA.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.
- Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York, New York, USA.
- Prevot-Julliard, A. C., H. Henttonen, N. G. Yoccoz, and N. C. Stenseth. 1999. Delayed maturation in female bank voles: optimal decision or social constraint? *Journal of Animal Ecology* 68:684–697.
- Proaktor, G., T. Coulson, and E. J. Milner-Gulland. 2007. Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology* 76:669–678.
- R Development Core Team. 2012. R version 2.12.0. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Robbins, A. M., T. Stoinski, K. Fawcett, and M. M. Robbins. 2011. Lifetime reproductive success of female mountain gorillas. *American Journal of Physical Anthropology* 146:582–593.
- Rughetti, M., and M. Festa-Bianchet. 2011. Effects of early horn growth on reproduction and hunting mortality in female chamois. *Journal of Animal Ecology* 80:438–447.
- Sæther, B. E., J. E. Swenson, S. Engen, O. Bakke, and F. Sandegren. 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: The effects of uncertain parameter estimates. *Oikos* 83:403–416.
- Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear. Pages 556–586 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Sidorovich, V. E., V. P. Stolyarov, N. N. Vorobei, N. V. Ivanova, and B. Jedrzejska. 2007. Litter size, sex ratio, and age structure of gray wolves, *Canis lupus*, in relation to population fluctuations in northern Belarus. *Canadian Journal of Zoology* 85:295–300.
- Skibieli, A. L., F. S. Dobson, and J. O. Murie. 2009. Maternal influences on reproduction in two populations of Columbian ground squirrels. *Ecological Monographs* 79:325–341.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.
- Steyaert, S. M. J. G., A. Endrestøl, K. Hackländer, J. E. Swenson, and A. Zedrosser. 2012. The mating system of the brown bear *Ursus arctos*. *Mammal Review* 42:12–34.
- Støen, O. G., A. Zedrosser, S. Sæbø, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* 148:356–364.
- Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:1–23.
- Sutherland, W. J., A. Grafen, and P. H. Harvey. 1986. Life-history correlations and demography. *Nature* 320:88.
- Swenson, J. E. 2003. Implications of sexually selected infanticide for the hunting of large carnivores. Pages 171–190 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C., USA.
- Swenson, J. E., B. Dahle, and F. Sandegren. 2001a. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12:81–92.
- Swenson, J. E., F. Sandegren, S. Brunberg, and P. Segerstrom. 2001b. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- Viblan, V. A., C. M. Arnaud, F. S. Dobson, and J. O. Murie. 2010. Kin selection in Columbian ground squirrels (*Urocyon columbianus*): littermate kin provide individual fitness benefits. *Proceedings of the Royal Society B* 277:989–994.
- von Holst, D., H. Hutzelmeyer, P. Kaetzke, M. Khaschei, H. Rodel, and H. Schrutka. 2002. Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). *Behavioral Ecology and Sociobiology* 51:245–254.
- Wauters, L., L. Bijnens, and A. A. Dhondt. 1993. Body mass at weaning and juvenile recruitment in the red squirrel. *Journal of Animal Ecology* 62:280–286.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.
- Zedrosser, A. 2006. Life history aspects of brown bears. Dissertation. Norwegian University of Life Sciences, Ås, Norway.
- Zedrosser, A., E. Bellemain, P. Taberlet, and J. E. Swenson. 2007a. Genetic estimates of annual reproductive success in male brown bears: The effects of body size, age, internal relatedness and population density. *Journal of Animal Ecology* 76:368–375.
- Zedrosser, A., B. Dahle, O. G. Stoen, and J. E. Swenson. 2009. The effects of primiparity on reproductive performance in the brown bear. *Oecologia* 160:847–854.
- Zedrosser, A., B. Dahle, and J. E. Swenson. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87:510–518.
- Zedrosser, A., S. M. J. G. Steyaert, H. Gossow, and J. E. Swenson. 2011. Brown bear conservation and the ghost of persecution past. *Biological Conservation* 144:2163–2170.
- Zedrosser, A., O. G. Støen, S. Sæbø, and J. E. Swenson. 2007b. Should I stay or should I go? Natal dispersal in the brown bear. *Animal Behaviour* 74:369–376.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in Ecology with R. Springer-Verlag, New York, New York, USA.