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Litter reductions reveal a trade-off between offspring size and number in brown bears

Ofelia Gonzalez · Andreas Zedrosser · Fanie Pelletier · Jon E. Swenson · Marco Festa-Bianchet

Abstract Experimental manipulations have revealed positive effects of litter reduction on offspring mass in small mammals, but little is known about this trade-off in large mammals. We examined the determinants of natural litter size variation and quantified the effects of litter size, maternal characteristics, and litter composition on yearling mass using 24 years of data on marked brown bears (*Ursus arctos*) in Sweden. Infanticide by adult males is a major cause of cub-of-the-year mortality, leading to litter size reductions. Litter size ($n=265$) at den emergence ranged from one to four cubs (average, 2.7) and increased with maternal age. Litter size, however, appeared independent of maternal size, population density, interlitter interval, study area, or previous litter sex ratio. Yearling body mass increased with maternal body size but was independent of litter sex ratio. Litter size and yearling mass were negatively correlated, mostly because singletons were about 30 % heavier than yearlings from litters of two to four cubs. In reduced litters, survivors were on average 8 % heavier as yearlings than individuals from intact litters, suggesting that sibling competition reduces growth. Trade-offs between litter size and yearling mass in bears appear similar in magnitude to those found in small mammals.

Keywords Body mass · Brown bear · Litter size · Maternal effect · Sibling competition · *Ursus arctos*

Introduction

Life-history theory predicts that, if energy is limited, individuals face trade-offs between life history traits (Williams 1966; Stearns 1992). One of the most studied trade-offs is between offspring size and number (Godfray and Parker 1991). Limited resources also lead to sibling competition, decreasing individual fitness as offspring number increases (Clutton-Brock 1991; Godfray and Parker 1991). Quantification of this trade-off is typically done through experimental manipulations (Godfray et al. 1991; Stearns 1992). Most experimental studies found negative effects of litter size enlargements and positive effects of litter size reductions on offspring size (Mappes et al. 1995; Koskela 1998). Experimental litter size manipulations, however, have been carried out mostly in small mammals (Humphries and Boutin 2000; Neuhaus 2000; Koivula et al. 2003; Oksanen et al. 2003) and birds (Korpimäki 1988; Dijkstra et al. 1990; Roulin et al. 1999). Although a trade-off between litter size and offspring mass also should be expected in large mammals, it is unknown whether the magnitude of this trade-off is comparable to that reported for small mammals. Large mammals, with over 25–30 kg body mass, produce fewer offspring than

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small mammals (Krohne 1981; Gaillard et al. 1989; Carranza 1996). In a small litter, loss of a single sibling will free up a larger proportion of maternal resources for survivors than in a large litter.

Under natural conditions, litter size often increases with food availability (Risch et al. 1995; Koskela et al. 1998; Jonsson et al. 2002). Although most studies found that litter size tends to decrease as population density increases (Morris 1998; Forchhammer et al. 2001), a positive relationship between these variables also has been reported (Festa-Bianchet and King 1991). Maternal conditions affect litter size in small mammals, as suggested by a positive relationship between maternal mass and litter size (Campbell and Slade 1995; Risch et al. 1995; Kasparian et al. 2005). Litter size may also vary with maternal age, first increasing as mothers gain mass and experience, reaching a plateau during prime age and declining with senescence (Derocher and Stirling 1994).

Litter size manipulations in large mammals are logistically challenging, and none have been conducted in the wild. In some species, infanticide may lead to litter size reductions. Infanticidal males cause offspring mortality that is probably independent of maternal reproductive potential because they seek to kill the entire litter to accelerate the return of the mother to estrus (Hrdy 1977; Agrell et al. 1998). Failure to kill a whole litter leads to litter size reduction and occurs either because the mother can defend part of her litter or because some cubs-of-the-year (hereafter referred to as cubs) escape the infanticidal male (Swenson 2003).

Here, we use a 24-year data set of individually marked Scandinavian brown bears (*Ursus arctos*) with detailed information on female reproduction to examine the factors affecting the trade-off between litter size and offspring size in a large mammal with pronounced sexual size dimorphism. Brown bears have a polygamous mating system, and adult males can be twice as heavy as adult females (Steyaert et al. 2012). Females give birth during hibernation to cubs weighing 350–500 g (Pasitschniak-Arts 1993). Because litter mass at parturition is very small compared to maternal mass (Ramsay and Dunbrack 1986), the greatest reproductive costs in this species likely arise from lactation (Farley and Robbins 1995). Assuming that energy was limited during lactation, we expected a trade-off between number and size of offspring in a litter. In Scandinavia, age of primiparity is between 4 and 7 years, litter size ranges from one to four cubs (Zedrosser et al. 2009), and offspring are weaned at 1 or 2 years of age (Dahle and Swenson 2003). Cub mortality is about 40 % and appears mostly due to sexually selected infanticide (Swenson et al. 1997, 2001b; Zedrosser et al. 2009). Infanticidal males seek to kill cubs sired by other males to induce estrus in females (Bellemain et al. 2006). Attempts at infanticide can cause

partial reduction of some litters (Swenson et al. 2001a; Zedrosser et al. 2009). We assumed that survival of infanticide attempts was independent of offspring or maternal condition and evaluated the effects of litter size reduction on offspring characteristics. There is currently no published information about the relationship between offspring size and litter size in brown bears. In polar bears (*Ursus maritimus*), cub mass decreases with increasing litter size (Derocher and Stirling 1998).

We had three objectives. First, we sought to explain variation in unmanipulated litter size within and among females. We evaluated the effects of maternal age and body size, study area, population density, interlitter interval, and sex ratio of the previous litter on the number of cubs produced by each female. We predicted that litter size would increase with maternal age and size, be lower at high population density, increase with interlitter interval, and decrease with the number of males in the previous litter. Second, we expected that maternal characteristics and sibling sex would affect yearling mass. In sexually dimorphic species, mothers may increase their fitness by modifying the amount of care they provide according to offspring sex (Clutton-Brock et al. 1981) if one sex provides greater potential returns on investment. In ungulates, sons require more nutrition than daughters (Clutton-Brock et al. 1985; Bérubé et al. 1996). We expected a similar effect in bears because male reproductive success is affected by intrasexual competition that depends largely on body size (Zedrosser et al. 2007a). Assuming that sons would demand more care than daughters, we expected that sibling competition should vary with litter sex ratio. We therefore evaluated litter composition and maternal effects on yearling body mass. Because offspring growth is influenced by maternal condition and food availability in black bears (*Ursus americanus*) (Rogers 1976; Samson and Huot 1995), we expected that yearling mass would increase with maternal age and size. Finally, we expected a negative relationship between yearling mass and litter size and that yearlings from intact litters should be lighter than those from litters that experienced cub loss.

Methods

Study areas and captures

Our study areas were located in Norbotten County, northern Sweden (~67° N, 18° E) and about 600 km to the south in Dalarna and Gävleborg counties, south-central Sweden (~61° N, 14° E) (Zedrosser et al. 2006). The mountainous northern study area (north) is about 8,000 km² and includes three national parks (Zedrosser et al. 2006, 2007b). Bears are protected in the national parks, but hunting is allowed in the surrounding areas (Bjärvall 1990; Zedrosser et al. 2006;

Bischof et al. 2008). The southern study area (south) is about 13,000 km^2, and its rolling landscape with boreal forest is intensively managed. Bear hunting is allowed in the entire area (Bjärvall 1990; Zedrosser et al. 2006).

Individually marked bears have been monitored since 1984 in the north and 1985 in the south. Radiomarked females with yearlings were darted from a helicopter. We used 2.5 mg tiletamine, 2.5 mg zolazepam, and 0.02 mg medetomidine per kilogram body mass to immobilize bears (Zedrosser et al. 2007b). Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg medetomidine). We used VHF radio transmitters (Telonics®, model 500) for adult females; from 2003, most adult females were fitted with GPS-GSM transmitters (GPS Plus, Vectronic Aerospace GmbH®). Yearlings were not fitted with a radiocollar due to their rapid growth. Instead, a sterile radiotransmitter (Telonics®, model IMP/400/L HC) was implanted in their peritoneal cavity following a standard biomedical protocol (Zedrosser et al. 2007b). For ethical reasons, we did not capture females with cubs. All captures were conducted as soon as possible after den emergence, in mid-April in the south, and early May in the north. We collected a vestigial premolar tooth from all females not captured as yearlings, to estimate age based on the cementum annuli in the root (Craighead et al. 1970). Head circumference (at the widest part of the zygomatic arch between eyes and ears) was measured with a tape measure (Zedrosser et al. 2006) and was used as an indicator of adult female body size (Bischof et al. 2009).

Litter size

Female brown bears with cubs were monitored by direct observation from a helicopter three times a year: at den emergence in spring (late April, early May), after the breeding season (middle of July), and in autumn (late September, early October) before den entrance (Støen et al. 2006). We used the number of cubs seen with each mother at the first sighting following den emergence to determine litter size. To avoid risk of abandonment by the mother, we did not capture cubs. Offspring were first captured and weighed at age 1 (hereafter referred to as yearling). We use "cub litters" to refer to the number of cubs-of-the-year and "yearling litters" for the number of 1-year-olds. Litter size reduction was defined as the difference in number of offspring between yearling and cub litter size.

Individual population density index

The population density within a radius of 17.84 km around each individual, corresponding to bears/1,000 km^2, was estimated based on the high proportion of radio-collared bears and documented population growth rates (see Zedrosser

et al. (2006) for a detailed description). In the south, population size was estimated based on a DNA analysis of scats in 2001 and 2002, which identified scats of 71 % of radio-collared bears (Bellemain et al. 2005). The density index around each radio-collared individual was based on locations of individuals genetically identified by scat sampling (Bellemain et al. 2005) and adjusted each year for the population growth rate (Sæther et al. 1998; Kindberg and Swenson 2006).

No corresponding population estimate was available for the north, but over 90 % of adult male and female and all subadult female bears were radio-collared (Swenson et al. 2001b). We used the locations of radio-collared bears, corrected to account for subadult males, and growth rate of the population to calculate the same individual density index used in the south (Zedrosser et al. 2006).

Statistical analyses

We used a linear mixed model with a normal distribution to study cub litter size at den emergence. We evaluated the effects of maternal age, age^2 (to account for possible nonlinear effects), study area, maternal head circumference (not adjusted for capture date because all individuals were captured within a 2-week period in each study area (Zedrosser et al. 2006)), interlitter interval, population density, and sex ratio of the previous yearling litter on cub litter size. No explanatory variables had correlation higher than 0.3 so they were all included in our model. As some mothers contributed several litters to our datasets during their lifetime, we included maternal identity and year as random effects to account for non-independence (Pinheiro and Bates 2000). We tested for interactions between study area and population density and also between study area and interlitter interval. We used a linear regression to evaluate the effects of maternal age on total yearling litter mass. Residuals from all final models were visually inspected to ensure that the assumptions of constancy of variance and normality of errors were met.

We used a linear mixed model, including maternal identity and year as random effects, to evaluate the consequences of variation in cub litter size on yearling body mass. This analysis included only mothers that weaned offspring during at least two reproductive events. We coded yearlings from intact cub litters as "0" and yearlings from reduced litters as "1." Analyses of the specific decrease in numbers from cub to yearling litter did not increase our ability to explain variability in yearling mass (data not shown); therefore, we only classified litters according to whether or not they were reduced.

We evaluated the effects of cub litter size, maternal age, maternal size, yearling sex (Dahle et al. 2006), study area, and population density on yearling body mass. We tested for interactions between yearling sex and study area. We

evaluated the effects of yearling litter composition on yearling mass with a one-way analysis of variance (ANOVA). We used a multiple comparisons test (Tukey honestly significant difference) with a significance level of 0.05.

All analyses began with a full model including all covariates, the interactions previously mentioned, and random effects. Then, we tested the significance of random effects with likelihood ratio tests, using restricted maximum likelihood (Pinheiro and Bates 2000). If random effects were not significant, we continued our analyses using linear or generalized linear models depending on the response variable. We then used backward selection to remove nonsignificant fixed effects (Crawley 2007). All analyses used R version 2.11.1 (R Development Core Team 2010). The "lme4" package (version 0.999375-37) was used to fit generalized mixed effects models (Bates et al. 2008).

Results

Cub litter size

We monitored 265 litters produced by 53 different females aged 4–26 years from 1984 to 2008. Litter size at den emergence was either one ($n=53$), two ($n=93$), three ($n=108$), or four ($n=11$) cubs, averaging 2.7 ± 0.8 (SE). Maternal identity ($x^2<0.001$, $p=0.99$) and year ($x^2<0.001$, $p=0.99$) as random effects did not affect cub litter size; therefore, we report results from linear models.

Cub litter size increased up to 8 years of maternal age (Fig. 1), then reached a plateau (estimates from a linear model: age, $\beta=0.209\pm0.046$, $t=4.498$, $p\leq0.001$; age^2, $\beta=-0.006\pm0.002$, $t=-3.331$, $p\leq0.001$). Removing one 26-year-old female (Fig. 1) did not affect the quadratic effect of age (results not shown). Of 85 litters born to mothers aged between 4 and 7 years, 30 (35.3 %) were from primiparous females (Zedrosser et al. 2009), 37 (43.5 %) were from multiparous females, and for 18 litters (21.2 %), we could not establish whether the mother was primi- or multiparous. Cub litter size appeared independent of study area ($\beta=-0.083\pm0.165$, $t=-0.506$, $p=0.61$), maternal head circumference ($\beta=0.015\pm0.019$, $t=0.793$, $p=0.43$), interlitter interval ($\beta=0.083\pm0.090$, $t=0.918$, $p=0.36$), population density ($\beta=-0.001\pm0.002$, $t=-0.855$, $p=0.39$), or sex ratio of the previous yearling litter ($\beta=-0.197\pm0.190$, $t=-1.040$, $p=0.30$). None of the interactions in this analysis were significant (all $p>0.05$).

Maternal effects on yearling mass

Yearling mass varied from 8 to 48 kg (mean±SE; 23.2 ± 0.4) and increased with maternal head circumference ($r^2=0.03$; Table 1; Fig. 2a). That relationship, however, appeared
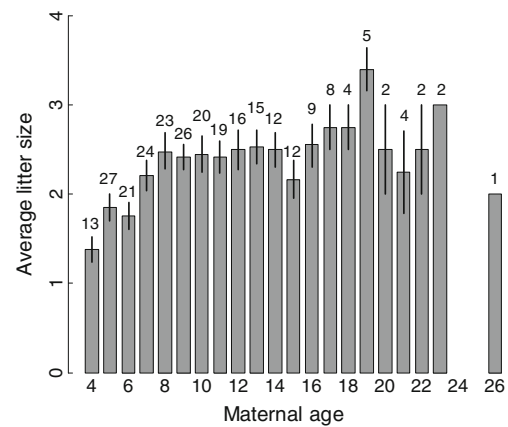

Fig. 1 Average litter size of brown bear cubs-of-the-year at den emergence in relation to maternal age, in Sweden from 1984 to 2008. *Bars* indicate standard errors; sample sizes are given *above the bars*. Data are from 265 litters produced by 53 females

driven mostly by four small females that produced small yearlings (Fig. 2a). After excluding those females and their 13 yearlings from the analysis, we found no effect of maternal head circumference on yearling mass ($\beta=0.271\pm0.278$, $t=0.977$, $p=0.33$). There was no effect of maternal age on yearling mass ($\beta=-0316\pm0.436$, $t=-0.725$, $p=0.47$). Total yearling litter mass increased with maternal age (linear regression; $\beta=1.625\pm0.351$, $t=4.636$, $p<0.001$, $r^2=0.13$; Fig. 2b).

### Effects of litter composition on yearling body mass

In litters of two yearlings, mean mass of males was independent of whether the sibling was a brother (kg, mean±SE; 25.7 ± 1.5, $n=34$) or a sister (25.7 ± 1.3, $n=28$). Likewise, we found no difference in the yearling mass of females with a

Table 1 Factors affecting body mass of 254 yearling brown bears produced by 46 females in Sweden from 1984 to 2007

Fixed effects	Estimate	SE	t value	p value
Intact/reduced litter	2.239	0.942	2.378	0.018
Sex	2.460	0.607	4.053	<0.001
Litter size 2	−5.522	2.011	−2.746	0.006
Litter size 3	−8.161	2.060	−3.962	<0.001
Litter size 4	−12.417	2.571	−4.830	<0.001
Study area (North/South)	3.859	1.605	2.404	0.017
Population density	−0.121	0.040	−3.038	0.003
Maternal head circumference	0.503	0.253	1.992	0.047

Estimates±standard errors (SE) are from a linear mixed effects model ($r^2=0.280$) including maternal identity and year as random effects. As random effects, maternal identity accounted for 31.5 % of the variance (SD=3.560, $x^2=130.256$, $p<0.001$) and year for 20.8 % (SD=2.927, $x^2=110.934$, $p<0.001$)

Fig. 2 Maternal effects on body mass of yearling brown bears in Sweden from 1984 to 2007; **a.** yearling mass (kg) in relation to maternal maximum head circumference (cm) for 305 yearlings in 138 litters produced by 51 females and **b** total yearling litter mass (kg) in relation to maternal age, from 305 yearlings in 138 litters produced by 51 females
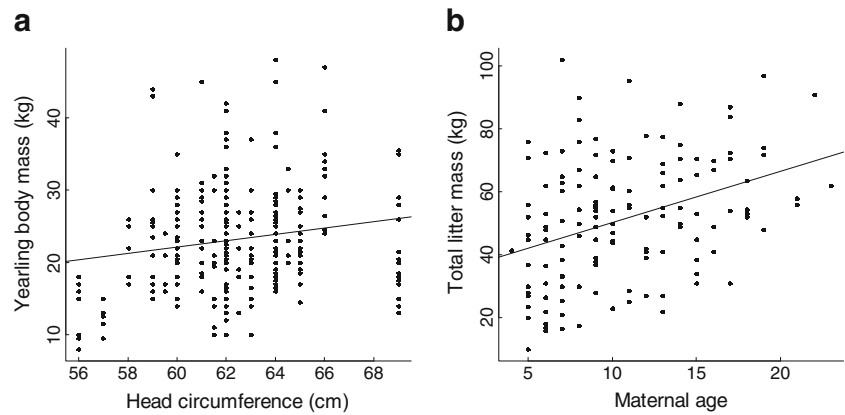
sister (20.6±0.9, $n=28$) or a brother (23.7±1.3, $n=28$). In litters of three yearlings, we observed the same pattern of no effects of sex ratio ($F=0.6$, $df=140$, $p=0.67$) for either males (kg, mean±SE; 22.3±1.1) or females (21.6±1.1). The sample size for litters of four ($n=16$) was too small for analysis.

Effects of litter size on yearling body mass

Of 305 yearlings of known mass, 254 were from intact litters. Among those, males were heavier than females (Table 1). Yearling mass decreased as yearling litter size increased (Fig. 3a), and singletons were ~30 % heavier than yearlings born in larger litters. Yearlings in the south were heavier than in the north (Table 1). In both study areas, yearling mass decreased with increasing population density (Table 1). None of the interaction terms in this analysis were significant (all $p>0.05$).

Effects of litter size reduction on yearling body mass

We monitored 51 yearlings from 33 litters that had experienced cub loss the previous year. An additional 49 litters were lost completely, whereas in 105 litters

all cubs survived to yearling age. Yearlings from reduced litters were 8 % heavier (kg, mean±SE; males, 26.0±1.4; females, 23.6±1.3) than those from intact litters (males, 23.7±0.6; females, 22.0±0.6; Table 1 and Fig. 3b). The effect of partial litter loss appeared independent of cub litter size ($p=0.09$).

Discussion

Our main objective was to quantify a possible trade-off between offspring size and number in a large mammal. Our analyses produced three main findings. First, maternal age was the main determinant of cub litter size. Second, yearling mass varied with yearling litter size and maternal body size, but appeared independent of litter sex ratio. Finally, yearlings from reduced litters were heavier than those from intact litters, revealing a trade-off between litter size and yearling mass likely due to sibling competition and suggesting that mothers redirect care to surviving offspring following litter size reduction.

Long-lived mammals with a high adult survival rate are expected to show weak evidence of reproductive senescence (Williams 1957). Cub litter size first increase with maternal

Fig. 3 Mean body mass (kg) of male (*open bars*) and female (*solid bars*) yearling brown bears **a** in relation to litter size as cubs, from 254 yearlings from 105 litters that experienced no cub loss, produced by 46 females and **b** from intact litters and from reduced litters, from 305 yearlings produced in 138 litters by 51 females, in Sweden from 1984 to 2007. *Bars* indicate standard errors; sample sizes are given *above the bars*
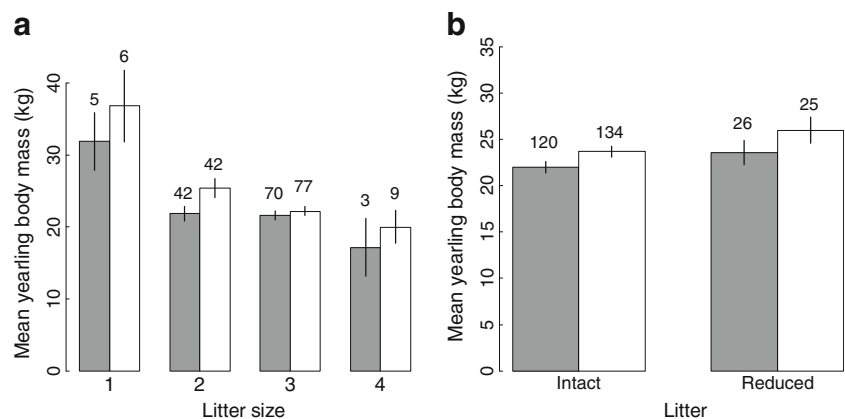
age, then reached a plateau, and showed no evidence of senescence (Fig. 1). A senescent decline in cub litter size starting at 14–16 years of age was reported for female polar bears (Derocher and Stirling 1994). Schwartz et al. (2003) reported that brown bears showed a very slight decline in litter production between 8 and 25 years of age, followed by a drastic decline from about 28 years of age. Although we monitored 37 females older than 15 years, we found no evidence of senescence in either cub litter size or yearling mass. Hunting pressure in Sweden, however, reduces female longevity (Bischof et al. 2008) compared to that expected under natural conditions. More than 95 % of females in our study die from hunting (Bischof et al. 2008), and few survive to the onset of reproductive senescence. Total year-ling litter mass increased linearly with maternal age (Fig. 2b), but that relationship was weak and older mothers did not produce larger offspring. Because adult female mor-tality from sport hunting appears to be random (Bischof et al. 2008), it is unlikely that an increase in litter mass with age could be due to greater longevity of females with higher reproductive potential. Our data appear to confirm William's (1957) prediction and suggest that reproductive senescence plays a minor role in the life-history strategy and the popu-lation dynamics of brown bears. In hunted populations such as the one we studied, it may play no role at all as very few females survive to old age.

Previous analyses found no difference in yearling body mass between the two study areas (Dahle et al. 2006). With a larger sample size and 9 years of additional data, we documented that yearlings in the south were heavier than yearlings in the north. The northern area has lower mean temperature, shorter growing season, and lower primary pro-ductivity than the southern area, reducing resource availability (Zedrosser et al. 2006). Population density did not affect cub litter size but reduced yearling mass, consistent with Dahle et al. (2006) findings. Zedrosser et al. (2006) reported a negative effect of density on adult female body size, suggesting that the reduction in yearling mass at high density could be a maternal effect.

Yearlings raised as singletons were about 30 % heavier than yearlings raised with littermates. The effect of having siblings was greater than the effect of having more than one sibling, suggesting that costs of reproduction do not increase linearly with litter size. Competition among siblings for ma-ternal resources, became evident through litter size reductions because surviving yearlings in reduced litters were heavier than yearlings from intact litters. Female brown bears appear to face a trade-off between offspring size and number. Similarly to our results, small mammal studies have reported that survivors in reduced litters enjoyed about an extra 8 % of mass gain (e.g., Koskela 1998; Neuhaus 2000). We suggest that female reproductive strategy in large mammals is partly shaped by a trade-off between offspring number

and size of similar magnitude to that seen in small mammals. Yearlings from litters of two, three, or four, however, did not differ much in mass (Fig. 3a). Although the small number of very large litters may have limited the statistical power of our analysis, this result suggests that female bears produce litter sizes based on the amount of maternal care that they are likely able to provide. The amount of care may depend on differences in both individual reproductive potential and resource availability within each home range. Thus, larger litters are not produced at the expense of smaller young, but when one or more cubs were removed, females appeared to redirect care to the remaining young, so that survivors received a greater amount of resources.

Most cub mortality was likely due to infanticide as almost 85 % of cub disappearances occur during the mating season (Swenson et al. 2001b). We could not, however, always distinguish between infanticides and cub deaths from other causes. Our assessment of the strength of the trade-off between offspring size and number may be biased if surviving cubs had been in better condition than those that died. In theory, litter loss caused by infanticidal males is expected to be random (Hrdy 1977; Agrell et al. 1998) and should be equivalent to an experimental reduction in cub litter size. We currently cannot distinguish if surviving cubs were in the same condition as those that were killed.

Contrary to our prediction, yearling mass appeared to be independent of yearling litter sex ratio. As yearlings, male brown bears are, on average, 2.6 % larger and 7.8 % heavier than females (Dahle et al. 2006). Our analysis took into account the sex difference (Table 1), but the moderate amount of dimorphism appeared insufficient to affect sibling compe-tition in the first year of life. Body mass of male and female polar bears in twin litters are not different, suggesting that females do not provide more care to male cubs (Derocher and Stirling 1998).

Our results underline some differences in the effects of litter size variation for small and large mammals. Although the effect of maternal age on litter size in brown bears was consistent with those reported for ungulates (Ericsson et al. 2001; Wilson et al. 2009) and small mammals (Fleming and Rauscher 1978; Neuhaus et al. 2004), other variables such as population density did not affect litter size as reported for small mammals (Morris 1998). Our results also underline that litter reductions through infanticide provide insights to life-history trade-offs in species that might not be easy to manipulate. Sibling competition is common in species where parents provide essential resources to the young, as it is the case in most bird and in every mammal species (Mock and Parker 1997). However, the preva-lence of small litters among large mammals makes

sibling competition difficult to assess. In other large mammals where infanticide plays a major role in offspring mortality, such as some carnivores (e.g., lions; *Felis leo*, wild dogs; *Lycaon pictus*) (Agrell et al. 1998), natural litter size reductions could provide valuable insights into reproductive costs.

Ethical Standards

All capture and handling procedures were approved by the appropriate authority and ethical committee (Djuretiska nämden i Uppsala, Sweden).

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