Dear Author:

Please find attached the final pdf file of your contribution, which can be viewed using the Acrobat Reader, version 3.0 or higher. We would kindly like to draw your attention to the fact that copyright law is also valid for electronic products. This means especially that:

- You may not alter the pdf file, as changes to the published contribution are prohibited by copyright law.
- You may print the file and distribute it amongst your colleagues in the scientific community for scientific and/or personal use.
- You may make your article published by Springer-Verlag available on your personal home page provided the source of the published article is cited and Springer-Verlag is mentioned as copyright holder. You are requested to create a link to the published article in Springer's internet service. The link must be accompanied by the following text: The original publication is available at http://link.springer.de or at http://link.springer-ny.com . Please use the appropriate URL and/or DOI for the article. Articles disseminated via SpringerLink are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks and consortia.
- Without having asked Springer-Verlag for a separate permission your institute/your company is not allowed to place this file on its homepage.
- Please address any queries to the production editor of the journal in question, giving your name, the journal title, volume and first page number.

Yours sincerely,

Springer-Verlag

Behav Ecol Sociobiol (2003) 54:352–358
DOI 10.1007/s00265-003-0638-8

ORIGINAL ARTICLE

Bjørn Dahle · Jon E. Swenson

Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring

Received: 7 October 2002 / Revised: 1 May 2003 / Accepted: 1 May 2003 / Published online: 13 June 2003

Abstract Length of maternal care, i.e. the interval between successfully raised litters, is the most important factor explaining the variation in reproductive rate among brown-bear (*Ursus arctos*) populations. In this paper, we examine the variation in length of maternal care in radio-marked brown bears and its effect on their offspring in northern Sweden. Young stayed with their mothers for 1.4–1.5 or 2.4–2.5 (in one case 3.5) years and were weaned with body masses varying from 17 to 69 kg. The probability of yearling litters staying with their mother for a 2nd year increased with decreasing yearling body mass, and was higher for litters with two offspring than for litters with one or three to four offspring. Staying with their mothers for a 2nd year had a positive effect on mass gain in yearlings and this effect was more pronounced in litters with two than three to four offspring. Body mass of 2-year-olds was not related to age of weaning, suggesting that keeping offspring for an additional year mainly compensated for low yearling body mass. If large offspring body mass positively affects later offspring survival and reproduction, mothers may be able to optimize the length of maternal care according to the litter size and the size of their yearlings.

Keywords Litter interval · Maternal care · Litter size · Body mass · *Ursus arctos*

Introduction

Life-history theory predicts that animals should show optimal levels of parental investment, with energy expenditure for current offspring balanced against the effects on the parents' probability of survival and future reproduction (Roff 1992; Stearns 1992). In most polygynous species, males provide no parental care and the optimal time span for maternal care then depends only on the effect that maternal care has on offspring survival and the mother's future probability of reproduction. Thus, in such species, maternal investment should be terminated when the fitness pay-off for further investment in an offspring is lower than the pay-off for investing in future reproduction.

Craighead et al. (1995) presented a conditional model based on theories of behavioural polymorphism (Maynard Smith 1982) to explain the age of weaning in North American brown bears. They argued that females in good condition could wean yearling offspring (at least small litters), whereas females in poor condition weaned their offspring as 2.5-year-olds. However, they failed to determine the factors influencing the cessation of maternal care.

In this paper, we examine variation in the length of maternal care in Swedish brown bears. Brown-bear offspring separate from their mothers when they are 1.4–3.5 years old (McLellan 1994). A female brown bear does not mate until she has separated from her offspring, which in nearly all cases coincides with the mating season in late May/early July (Dahle and Swenson 2003) (Table 1). Thus, accompanying their yearling offspring through the mating season increases the litter interval by 1 year, and may impose fitness costs if the positive effect of prolonged maternal care on the offspring does not compensate for the loss of potential reproduction due to the increased litter interval. Length of maternal care, i.e. the interval between successfully raised litters, is more important than litter size and age of maturity in influencing the long-term reproductive rate in brown-bear populations (Swenson and Sandegren 1999). Determining the factors influencing this life-history trait is therefore very important. The study population is suitable to study this life-history trait because preliminary data suggested that about 40% of the offspring separated from their mothers as yearlings and the rest as 2-year-olds (Swenson et al. 1994).

Communicated by F. Trillmich

B. Dahle (✉) · J. E. Swenson
Department of Biology and Nature Conservation,
Agricultural University of Norway,
Post Box 5014, 1432 Ås, Norway
e-mail: bjorn.dahle@ibn.nlh.no
Fax: +47-64948502

Table 1 Reproductive cycles in female brown bears illustrating the effect of varying length of maternal care

Time		Two-year reproductive cycle	Three-year reproductive cycle
Year	Month		
0	January	Cubs born	Cubs born
	May		
	June		
1	May	Separates from yearlings	
	June	Mates	
2	January	Cubs born	
	May		Separates from 2-year-olds
	June		Mates
3	January	Separates from yearlings	Cubs born
	May	Mates	
	June		

According to the resource-allocation theory (Williams 1966), maternal investment may vary according to litter size, offspring sex and maternal attributes, such as body mass or condition and parity, and environmental factors (see Clutton-Brock 1991 for a review). A general trend in the age of weaning seems to be that offspring are weaned when they reach a threshold size (Lee et al. 1991), and hence the length of maternal investment often varies in relation to nutritional and maternal condition (Trillmich 1986; Cheney et al. 1988; Fairbanks and McGurie 1995).

A trade-off exists between the number and size of offspring in a wide variety of taxa (Lloyd 1987; Roff 1992). Because the reproductive value of a litter increases with number of offspring, we should expect prolonged nursing and care in large litters compared to small litters. In species such as the brown bear, which has a long interbirth interval, it may even be beneficial for females to abandon single cubs of the year, because they could then produce a new and perhaps larger litter the next year (Tait 1980).

From the general trend that weaning occurs after a given threshold size is reached, and because the reproductive value of a litter increases with the number of offspring, we predicted that the probability that a litter will stay with its mother for 2 years should be: (1) negatively related to average yearling body mass, and (2) positively related to litter size.

Any relationship between the probability of staying with the mother for 2 years and litter size could be confounded by female size and condition. Litter size has been reported to be positively correlated with female condition in many species, including both the brown bear (Craighead et al. 1995) and the American black bear (*Ursus americanus*) (Samson and Huot 1995), but no such relationship was reported in the polar bear (*U. maritimus*) (Ramsay and Stirling 1988). If litter size is positively related to female condition, then Craighead et al.'s (1995) model predicts that large litters should be weaned earlier than small ones. However, in contrast to Craighead et al. (1995), we include body mass of yearlings, which is positively related to the size and condition of their mothers (B. Dahle and J.E. Swenson, unpublished data), as a factor to explain length of maternal care. Further, in the present study, we consider litter size as yearlings, not the number of cubs born, which may be both difficult to assess and different from yearling litter size due to both care-independent and care-dependent mortality, although the 1st-year mortality is very low in the studied population (Swenson et al. 2001a). We feel that litter size as yearlings is relevant in this context as the options for a mother are to separate or not, based on the given number of yearlings, and this decision should be irrespective of the number of cubs she gave birth to the previous year.

If the amount of parental investment partly determines a young's subsequent adult body size, sex allocation theory predicts that parents should then invest more in individual offspring of the sex with the greater variance in reproductive success (Maynard Smith 1980; Charnov 1982). In polygynous mammals, including the brown bear, adult size of the sexes often differs greatly (e.g. Jarman 1983; J.E. Swenson et al., unpublished data), and large adult size is likely to increase fitness (survival and/or reproductive success) more in males than in females (e.g. Maynard Smith and Parker 1976; Clutton-Brock et al. 1986, but see Hewison and Gaillard 1999). To date, the empirical support of differential parental investment in wild mammals is equivocal, but Lee and Moss (1986) and Ono and Boness (1996) found that male offspring were weaned at an older age than females. For this reason, we predicted: (3) that the probability of a litter staying with the mother for 2 years should be higher in litters with a male-biased sex ratio.

The theory of parent-offspring conflict (Trivers 1974) assumes that an increase in maternal investment will increase offspring fitness. Thus, this theory assumes a positive correlation between offspring size or condition at the time parental effort ceases and lifetime reproductive success. Lifetime reproductive success is very hard to measure in long-lived free-ranging mammals, so with few exceptions (e.g. Festa-Bianchet et al. 2000), some surrogate measure of reproductive success must be used. Survival and growth are assumed to increase during maternal care (Clutton-Brock 1991), and survival has been reported to be positively related to the size at weaning (e.g. McMahon et al. 2000). Growth rate may influence the age for attainment of sexual maturity (e.g. Congdon and Sels 1993) and also later reproductive success (e.g. Tummaruk et al. 2001). In some ungulates, lactating females that do not conceive in the following breeding season may continue to nurse their offspring through the winter, resulting in increased calf growth rate (Clutton-Brock et al. 1982; Green and Rothstein 1991a) and reproductive success of offspring (Green and Rothstein 1991b). In Scandinavian brown bears, yearlings that stayed with their mother did not experience significantly lower intraspecific predation, perhaps the most important mortality factor except human-caused mortality (Swenson et al. 2001b), and the same was found among yearling polar bears (all sources of mortality included) (Ramsay and Stirling 1988). For this reason, we predicted: (4) that staying with their mother should positively affect growth rate in yearling brown bears. In general, growth rate in young is negatively related to litter size (e.g. Mendl 1988; Koskela 1998), and thus we predicted: (5) that growth rate among yearlings that stayed with their mother should be negatively related to litter size, whereas no such effect was expected in yearlings that separated from their mother. In accordance with the sex allocation theory (e.g. Maynard Smith 1980), several studies have reported faster growth in males than females in sexually dimorphic species where males compete for access to females (e.g. Clutton-Brock et al. 1982; Lee and Moss 1986), and we predicted: (6) faster growth in male than female yearlings.

Staying with their offspring for 2 years could be a strategy for producing larger and more competitive young. If so, this predicts: (7) that, at the age of 2 years, offspring then weaned should be larger than those weaned as yearlings.

Methods

The study was performed in southwestern Norrbotten County, Sweden, (67°N, 18°E) during 1989–2000. The rolling landscape is covered with coniferous forest, dominated by Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*), but mountains rise to about 2,000 m in large parts of the area. There, subalpine forest dominated by birch (*Betula pubescens*) and willows (*Salix* spp.), as well as alpine areas, are common. Bears hibernate for about 7 months, but the length of hibernation may vary according to age, sex and reproductive status.

Subadult bears (1–2 years old) and their mothers, which had been almost always radio-marked previously, were darted with immobilizing drugs from a helicopter during early May, prior to any separation between mothers and their offspring. We used 2.5 mg Tiletamin, 2.5 mg Zolazepam and 0.02 mg Medetomidin per kilogramme to immobilize the bears. Atipamezol was used as an antidote for Medetomidin (5 mg per 1 mg Medetomidin). Altogether, 110 bears (54 females and 56 males) were immobilized in 1989–2000, but the present paper is based on the capture/recapture of 17 adult females and their offspring. The immobilized bears were weighed and measured, and fitted with VHF radio transmitters (adults: Telonics model 500 with 3 years life-time, yearlings: Telonics model 400 with 1 year life-time) mounted on neck collars (until 1996). In 1997–2000, transmitters (Telonics model 400L with 4 years life-time) were implanted into the peritoneal cavity of yearlings following the surgical procedures described in Arnemo et al. (1999). Until 1997, growing bears were recaptured each spring to change neck collars and to obtain weights and body measurements. Because bears were captured within a 3-week period in May, and bears generally do not gain weight during this time of the year, we did not adjust mass for capture date. Bears were localized once a week from fixed-winged aircraft or helicopter, weather permitting, and the status of yearlings and 2-year-olds (separated or following their mother) was determined. Throughout the paper, weaning is synonymous with the permanent separation of offspring from their mother.

We combined body length (from the tip of the nose to the base of the tail) and skull circumference (measured in front of the ears) through a factor reduction (principal component analysis) to produce an index of structural body size of adult females (hereafter maternal size). These measures should reflect structural dimensions and be rather uninfluenced by body condition. These body-size indices were regressed against body mass to produce indices (the residuals) of body condition (Cattet et al. 2002).

Staying with the mother for (at least) 2 years can be considered to be a binomial process. Therefore, to explore which factors influenced the probability that litters stayed with their mother for 2 years, we applied logistic regression analysis that fits a generalized model to the data by maximum likelihood techniques (Proc Genmod, logit link function, SAS 1996) (McCullagh and Nelder 1989). The other statistical tests were executed in SPSS/Win v. 10.0 (SPSS Inc., Ill., USA).

Results

Length of maternal care varied among individuals, but also varied within many individuals (Table 2). For this reason, we treated each litter as independent data in our analyses. Yearling litters were made up of 1 (N=7), 2 (N=13), 3 (N=8) and 4 (N=1) offspring, with an average litter size of 2.10±0.15 (SE). For statistical analyses, we pooled the litters with three and four offspring. Offspring became independent with body masses ranging from 17.5 to 69 kg. Using a logistic regression model, we tested if yearling body mass in the litter (average littermate mass), litter size, and sex ratio in the litter, including all possible interactions among these factors, affected the probability for staying with the mother for (at least) 2 years. The probability of staying with the mother for 2 years increased as predicted (1) with decreasing body mass as a yearling (Table 3). Litter size also affected the length of maternal care, but not in the predicted way. The probability of yearlings of a given body mass staying with their mother for an additional year was similar for litters with one and three to four offspring, but higher for litters with two young (Fig. 1, Table 3). Contrary to prediction (3), the probability of staying for an additional year was not related to the sex ratio in the litter [the average proportion of males in litters was 0.49±0.42 (SD)].

Maternal size and condition were not related to yearling litter size ($F_{2,29}$=1.05, P=0.36, and $F_{2,28}$=0.957, P=0.40,

Table 2 Documented length of maternal care for offspring by individual female brown bears in northern Sweden. Figures *in parentheses* refer to the number of litters where sufficient data were obtained to include the litter in the logistic regression model

Bear	Litters nursed for 1.5 years	Litters nursed for 2.5 years	Litter nursed for 3.5 years
BD 1	1 (1)	3 (3)	
BD 7	6 (3)		
BD 10		1 (0)	
BD 16	1 (0)		
BD 18		3 (3)	
BD 23	3 (2)	2 (2)	
BD 25	1 (1)		1 (1)
BD 27		1 (0)	
BD 33	1 (1)	1 (1)	
BD 46	1 (1)		
BD 47	1 (1)		
BD 49	1 (1)	1 (1)	
BD 51	2 (2)	1 (1)	
BD 62	1 (0)	2 (2)	
BD 64		1 (1)	
BD 71	1 (0)		
BD 95		1 (1)	
Total	20 (13)	17 (15)	1 (1)

Table 3 To test factors that influence the probability that a female keeps her young for 2 years (vs 1 year), we applied logistic regression statistics (PROC GENMOD, SAS 1996). The global model included: whether a litter was kept for 2 years (0,1) as a response variable, and average body mass of yearling(s) in each litter, litter size, and sex ratio as explanatory factors. After a successive exclusion of the least significant terms, based on likelihood ratio-tests (type 3-tests), the final model included the variables presented in the table (β denotes the regression coefficient, SE the standard error, *df* denotes degrees of freedom, χ^2 is the chi-square value of the type 3-test). The sample size of the final model was n=29

Explanatory variables	β	SE	*df*	χ^2
Intercept	5.0143	2.9893	1	
Yearling weight	–0.2521	0.1288	1	7.13**
Litter size 1	0.1536	1.1563	1	11.15**
Litter size 2	4.0860	1.7485	1	
Litter size 3	0		0	

** denotes P<0.01.

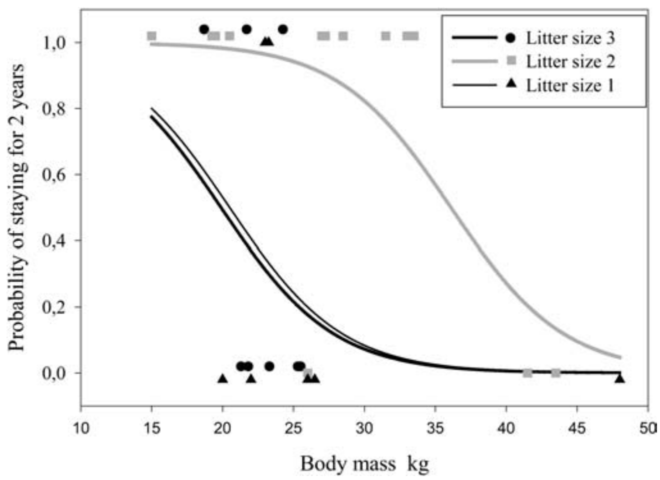

Fig. 1 Probability that young brown bears stay with the mother for 2 years rather than 1 year as a function of average yearling body mass and litter size, based on the multiple logistic regression model presented in Table 3; [a] includes one litter with four offspring. Real data are shown with *symbols*

respectively). Thus, yearling litter size was not merely a function of maternal size or condition, strengthening our findings that the mothers' willingness to invest another year in a litter was higher for litters with two offspring than for litters with one or three to four offspring when the yearlings' average body mass was the same.

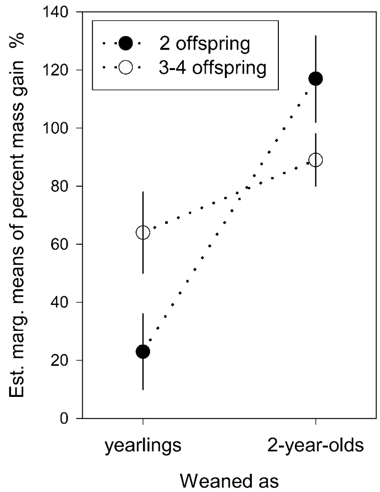

Fig. 2 Profile plot (interaction plot) of estimated marginal means of percent mass gain of yearling brown bears (adjusted for maternal size) in relation to age at weaning and litter size. *Vertical bars* indicate the SE

Thirty-one yearlings were recaptured as 2-year-olds (Table 4). Due to the small sample of litters with 1 offspring (N=3), they were excluded from statistical analyses of yearling growth and body mass at the age of 2 years. General linear models explained 44 and 60% of the variation in absolute and percent mass gain, respectively, among young bears during their 2nd year (Table 5). As predicted (4), mass gain (absolute and percent mass gain) was higher for yearlings that stayed with their mother than for yearlings that separated (Table 5). Mass gain was not related to litter size, but there was a litter size*age-at-weaning interaction. A profile plot indicated, as predicted (5), that the positive effect on yearling-mass gain by staying with their mothers was more pronounced in litters with two than three to four offspring, but that mass gain in weaned yearlings was higher in litters with three to four than two offspring (Fig. 2). Percent mass gain of yearlings was positively related to maternal size, whereas the relationship between absolute mass gain and maternal size was less clear (F=3.03, *df*=1, P=0.096). Contrary to prediction (6), mass gain was not higher in males than females (F=1.92, *df*=1, P=0.18 and F=0.55, *df*=1, P=0.47 for absolute and percent mass gain, respectively).

The effect of staying with the mother for 2 years was substantial in some cases. After the capture of a mother

Table 4 Body growth as absolute mass gain±SE (standard error) and as percent mass gain±SE of brown bears from age 1.4 to 2.4 years and body mass±SE at the age of 2.4 years

Litter size	Weaned as	Mass gain (kg) $\bar{X}$±SE	% mass gain $\bar{X}$±SE	Body mass of 2-year-olds $\bar{X}$±SE	*N*
1	1.5-year-old	19.8±9.3	50±10.4	57±20	2
1	2.5-year-old	15.5	67.4	38.5	1
2	1.5-year-old	9.3±8.7	28.2±21.1	46±11.1	3
2	2.5-year-old	30±2.5	122.8±15.2	56±2.5	9
3	1.5-year-old	15.1±4.2	57.7±13.8	40.1±5.3	7
3–4	2.5-year-old	20.2±1.4	94.2±9.1	42.4±1.9	9

Table 5 To test factors that influence the mass gain (absolute and percent) of yearlings during their 2nd year, we applied General Linear Models (SPSS 10.0). The global models included: absolute (*Abs*) or percent (%) mass gain of yearlings during their 2nd year as response variables, and age at weaning, maternal size, litter size (two or three to four) and sex as explanatory factors (including their interactions). After a successive exclusion of the least significant terms, the final model included the variables presented (β denotes the regression coefficient for variable values in *parentheses*, *Effect size* denotes the proportion of total variability attributable to a factor)

Explanatory variables	*df*	β		SE		*F*		Effect size	
		Abs	%	Abs	%	Abs	%	Abs	%
Age-at-weaning (1.5)	1	−5.2	−26.4	4.4	16.9	12.79**	19.69***	0.348	0.461
Maternal size	1		14.5		5.2		7.95*		0.257
Litter size (2)	1	9.8	32.4	4.1	15.5	0.31	0.031	0.013	0.001
Age-at-weaning*litter size (1.5 years litter size 2)	1	−15.5	−69.6	7.2	27.7	4.62*	6.31*	0.161	0.215
Intercept	1	20.22	85.0	2.88	11.4	106.86***	99.28***	0.817	0.812
Final model	3,24[a] 4,23[b]					6.20**	8.60***	0.437	0.599

*, ** and *** denote $P<0.05$, $P<0.01$ and $P<0.001$, respectively.
[a] is *df* in the model for absolute mass gain.
[b] is *df* in the model for percent mass gain.

(BD 1) with two yearlings, one of the yearlings (female BD 25) was separated from the mother and the female littermate (BD 24) and did not reunite. It is most likely that this separation was inflicted by the capture and marking (1 of 2 marking-induced separations in 85 family groups handled by the research project). However, all bears were healthy and BD 24 and BD 25 weighed 23.5 and 23 kg, respectively. The next spring, BD 24, which stayed with her mother for 2 years, weighed 63 kg, whereas BD 25 weighed only 33 kg.

At the age of 2 years, offspring body mass was higher in litters with two than three to four offspring (F=6.69, df=1, P=0.016). Offspring weaned as 2-year-olds were not heavier than offspring weaned as yearlings, at the age of 2 years (F=2.95, df=1, P=0.099). Offspring body mass at the age of 2 years was not related to maternal size (F=0.03, df=1, P=0.84) and did not differ between males and females (F=3.39, df=1, P=0.078).

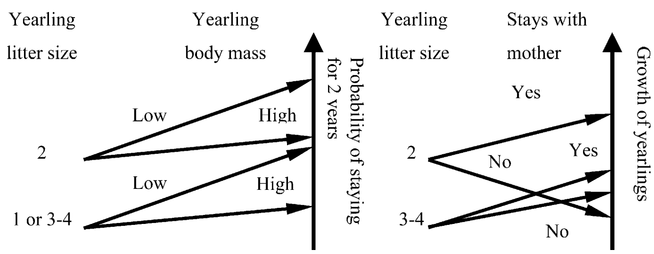

Fig. 3 Conceptual model illustrating the factors influencing the length of maternal care and the effect on offspring in brown bears in northern Sweden. Litters with one offspring are excluded for growth of yearlings and for body mass at the age of 2 years due to the small sample size

Discussion

Our most important findings were that the probability of offspring staying with their mother for 2 years increased with decreasing yearling body mass, and that this relationship was related to litter size, with litters with two offspring having a higher probability of staying for 2 years than litters with one or three to four offspring (Fig. 3). Staying with their mother also had a more pronounced positive effect on growth rate in litters with two than three to four offspring (Fig. 3). The body mass of 2-year-olds was not related to age at weaning, suggesting that prolonged nursing mainly compensated for small size of yearlings, bringing them to about the same size as offspring weaned as yearlings by the age of 2 years.

Derocher and Stirling (1995) reported annual variation in the percentage of yearling polar bears that were still following their mothers. Despite annual variation in the proportion of yearlings that followed their mothers, the proportion was significantly less in years when both yearling and maternal body masses were higher and population density lower. They suggested that mothers might wean offspring as yearlings under favourable conditions, whereas mothers may keep their offspring for an additional year when conditions are poor. The same suggestion was made by Craighead et al. (1995) for brown bears. However, neither Derocher and Stirling (1995) nor Craighead et al. (1995) showed this statistically. The negative relationship between yearling body mass and probability of staying with their mothers for 2 years, which we predicted (1) and found, supported these suggestions, as offspring mass and condition are positively related to maternal mass and condition (B. Dahle and J.E. Swenson, unpublished data).

Craighead et al. (1995) did not find any significant relationship between litter size and age at weaning, and Derocher and Stirling (1995) only reported that yearling litter size varied annually, but did not analyse this variation in relation to the probability of yearlings following their mother for an additional year. Contrary to prediction (2), we found that litters with two offspring had the highest probability of staying with their mother for 2 years. Prolonged nursing had a more pronounced positive effect on the mass gain in litters with two than three to four offspring. Thus the benefit obtained by offspring of staying another year may be reduced in large litters. The relative importance of milk transfer to yearlings from their mother compared to their own feeding is not known, but milk production by polar bears with yearlings is only about 25% of the production by females with cubs (Arnold and Ramsay 1994). However, milk production is probably not related to litter size in bears (Arnold and Ramsay 1994), and competition for both milk and food would increase with litter size, having a negative impact on mass gain. Hilderbrand et al. (2000) studied body mass and fat content of adult female brown bears and suggested that keeping yearlings from spring to autumn is as energetically costly as nursing cubs during the same period, Thus, nursing yearlings is probably not a cheap alternative to mating and raising a new litter the next year.

Many females varied their length of maternal investment among litters, so it is likely that this life-history trait is flexible for each litter size, reflecting variation in food availability and maternal condition acting on offspring size. As litter size of yearlings was unrelated to maternal body size or condition, it is unlikely that the observed effect of litter size on the probability of offspring staying with the mother for 2 years, was related to size or condition of mothers.

Age of weaning was not related to the sex ratio in the litter. This contradicts prediction (3), but confirms the results of Craighead et al. (1995). It seems that female brown bears do not adjust the length of maternal care in relation to the sex of offspring.

In sum, it seems that litters with one and three to four offspring are only kept for 2 years in our study area if the yearlings are very small. Rather than being weaned at a threshold body mass, as seems to be the general trend for mammals, the litters were weaned as yearlings only if their body mass was above a certain threshold. However, this threshold was dependent on litter size, a result not reported previously, to our knowledge. Our results suggest that females assess both the size and number of their yearlings before deciding to end or continue further care.

Young brown bears in northern Sweden were, on average, weaned earlier than in North American populations living under comparable climatic and nutritional conditions (see McLellan 1994 for a review). In these populations, young are rarely weaned as yearlings and most young stay with their mother for 2.4–2.5 or 3.4–3.5 years. In southern Sweden and in populations elsewhere in Europe, most brown bears are weaned as yearlings (Swenson et al. 1994; Frković et al. 2001). Brown-bear yearlings are heavier in southern European populations than in northern European populations (J.E. Swenson et al., unpublished data), which may explain why all offspring are reported to be weaned as yearlings in the southern European populations.

As predicted (4), yearlings staying with their mothers gained more mass than yearlings staying on their own, and as discussed above, this effect was more pronounced in litters with two than three to four offspring. In most species, prolonged nursing has a positive effect on the mass gain in young (e.g. Green and Rothstein 1991a, 1991b; Festa-Bianchet et al. 1994), but it is also reasonable to assume that mass loss during hibernation may be reduced in bears hibernating together in the same den, as they may save energy by decreasing the surface/volume relationship if huddling with conspecifics (Arnold 1990).

As predicted (5), mass gain was higher in litters with two offspring than in litters with three to four offspring. We have previously found a negative relationship between litter size and yearling body mass (B. Dahle and J.E. Swenson, unpublished data) and, as discussed above, it suggests that resources provided by females are not proportional to litter size and/or that yearlings in large litters suffer from competition for other food. We found no significant difference in growth of males and females from 1 to 2 years of age. Mass gain in yearlings was affected by factors other than those we considered, because much of the variation remained unexplained in our models. Due to the small sample size, we were not able to include year as a variable in our models of mass gain. Yearling body mass varies among years (Swenson et al. 2001b) and thus growth probably varies among years as well.

Because body mass of 2-year-olds was not related to age at weaning, it seems that prolonged nursing was mainly a compensation for low yearling body mass. As prolonged nursing is energetically costly for the mother and increases the interbirth interval by 1 year, reproductive success in 2-year-old bears should be positively affected by body mass. Little is known about this relationship in brown bears, but in mammals in general, large young survive and reproduce better than small ones (Green and Rothstein 1991b; Festa Bianchet et al. 2000; Hall et al. 2001).

We have used the term maternal care and not maternal investment, because we did not measure reproductive costs. However, considering the increased litter interval and the large energetic cost associated with nursing yearlings measured by Hilderbrand et al. (2000), this maternal care probably reflects maternal investment.

Acknowledgements This study was funded by the Norwegian Directorate for Nature Management, the Swedish Environmental Protection Agency, the Norwegian Institute for Nature Research, the Swedish Association for Hunting and Wildlife Management, WWF Sweden and the Research Council of Norway. We thank the personnel in the Scandinavian Brown Bear Research Project, especially Robert Franzén, Peter Segerström and Sven Brunberg for their assistance in the field, and we thank Thor H. Ringsby for assistance with the logistic regression model. Andreas Zedrosser, Ole-Gunnar Støen, Phyllis C. Lee and an anonymous reviewer gave valuable comments on a draft of the paper. All animal capture and handling reported in this paper comply with the current laws regulating the treatment of animals in Sweden and were approved by the appropriate ethical committee.

References

Arnemo JM, Linnell JDC, Wedul SJ, Ranheim B, Odden J, Andersen R (1999) Use of intraperitoneal radio-transmitters in lynx *Lynx lynx* kittens: anaesthesia, surgery and behaviour. Wildl Biol 5:245–250

Arnold JPY, Ramsay MA (1994) Milk production and milk consumption in polar bears during the ice-free period in western Hudson Bay. Can J Zool 72:1365–1370

Arnold W (1990) The evolution of marmot sociality. II. Costs and benefits of joint hibernation. Behav Ecol Sociobiol 27:239–246

Cattet MRL, Caulkett NA, Obbard ME, Stenhouse GB (2002) A body-condition index for ursids. Can J Zool 80:1156–1161

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Cheney DL, Seyfarth RM, Andelman SJ, Lee PC (1988) Reproductive success in vervet monkeys. In: Clutton-Brock TH (ed) Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, pp 384–402

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago

Clutton-Brock TH, Albon SD, Guinness FE (1986) Great expectations: dominance, breeding success and offspring sex ratios in red deer. Anim Behav 34:460–471

Congdon JD, Sels RVC (1993) Relationships of reproductive trait and body-size with attainment of sexual maturity and age in blandings turtles (*Emyoidea blandingi*). J Evol Biol 6:547–557

Craighead JJ, Sumner JS, Mitchell JA (1995) The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem 1959–1992. Island, Washington DC

Dahle B, Swenson JE (2003) Family break-up in brown bears: are young forced to leave? J Mammal 84

Derocher AE, Stirling I (1995) Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. Can J Zool 73:1657–1665

Fairbanks LA, McGurie MT (1995) Maternal condition and the quality of maternal care in vervet monkeys. Behaviour 132:733–754

Festa-Bianchet M, Jorgenson JT, Wishart WD (1994) Early weaning in bighorn sheep, *Ovis canadensis*, affects growth of males but not females. Behav Ecol 5:21–27

Festa-Bianchet M, Jorgenson JT, Reale D (2000) Early development, adult mass and reproductive success in bighorn sheep. Behav Ecol 11:633–639

Frković A, Huber D, Kusak J (2001) Brown bear litter sizes in Croatia. Ursus 12:103–106

Green WCH, Rothstein A (1991a) Sex bias or equal opportunity? Patterns of maternal investment in bison. Behav Ecol Sociobiol 29:373–384

Green WCH, Rothstein A (1991b) Trade offs between growth and reproduction in female bison. Oecologia 86:521–527

Hall AJ, McConnell BJ, Barker RJ (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. J Anim Ecol 70:138–149

Hewison AJM, Gaillard JM (1999) Successful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investment in ungulates. Trends Ecol Evol 14:229–234

Hilderbrand GV, Schwartz CC, Robbins CT, Hanley TA (2000) Effects of hibernation and reproductive status on body mass and condition of coastal brown bears. J Wildl Manage 64:178–183

Jarman P (1983) Mating system and sexual size dimorphism in large terrestrial mammalian herbivores. Biol Rev 58:485–520

Koskela E (1998) Offspring growth, survival and reproductive success in the bank vole: a litter size manipulation experiment. Oecologia 115:379–384

Lee PC, Moss CJ (1986) Early maternal investment in male and female African elephant calves. Behav Ecol Sociobiol 18:353–361

Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning and maternal investment from a comparative perspective. J Zool 225:99–114

Lloyd DG (1987) Selection of offspring size at independence and other size versus number strategies. Am Nat 129:800–817

Maynard Smith J (1980) A new theory of sexual investment. Behav Ecol Sociobiol 7:247–251

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Maynard Smith J, Parker G (1976) The logic of asymmetric contests. Anim Behav 24:159–175

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London

McLellan B (1994) Density dependent population regulation in brown bears. In: Taylor M (ed) Density dependent population regulation in black, brown and polar bears. Monograph series no. 3. International Association for Bear Research and Management, Port City, Washington DC, pp 15–25

McMahon CR, Burton HR, Bester MN (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leeonina* at Macquarie Island. Antarct Sci 12:149–153

Mendl M (1988) The effects of litter size on mother offspring relationships and behavioural and physical development in several mammalian species (principally rodents). J Zool 215:15–34

Ono KA, Boness DJ (1996) Sexual dimorphism in sea lion pups: differential maternal investment, or sex specific differences in energy allocation. Behav Ecol Sociobiol 38:31–41

Ramsay MA, Stirling I (1988) Reproductive biology and ecology of female polar bears (*Ursus maritimus*). J Zool 214:601–634

Roff DA (1992) The evolution of life histories; theories and analysis. Chapman and Hall, New York

Samson C, Huot J (1995) Reproductive biology of female black bears in relation to body mass in early winter. J Mammal 76:68–77

Stearns SC (1992) The evolution of life histories. Oxford University Press, New York

Swenson JE, Sandegren F (1999) Conservation of European brown bear populations: experinces from Scandinavia. In: Layna JF, Heredia B, Palomero G, Doadr I (eds) La conservación del oso pardo en Europa: un reto de cara al siglo XXI. (io), Madrid

Swenson JE, Sandegren F, Bjärvall A, Söderberg A, Wabakken P, Franzén R (1994) Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. Biol Conserv 70:9–17

Swenson JE, Sandegren F, Segerström P, Brunberg S (2001a) Factors associated with loss of brown bear cubs in Sweden. Ursus 12:69–80

Swenson JE, Dahle B, Sandegren F (2001b) Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. Ursus 12:81–92

Tait DE (1980) Abandonment as a reproductive tactic—the example with grizzly bears. Am Nat 115:800–808

Trillmich F (1986) Maternal investment and sex allocation in the Galapagos fur seal, *Arctocepahalus galapagoensis*. Behav Ecol Sociobiol 19:157–164

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Tummaruk P, Lundeheim N, Einarsson S, Dalin AM (2001) Effect of birth litter size, birth parity number, growth rate, backfat thickness and age at first mating of gilts on their reproductive performance as sows. Anim Reprod Sci 66:225–237

Williams GC (1966) Natural selection, the cost of reproduction and a refinement of Lack's principle. Am Nat 100:687–690