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LETTER

Condition-dependent reproductive success in bighorn ewes

Marco Festa-Bianchet
Groupe de Recherche en Écologie, Nutrition et Énergétique, Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada J1K 2R1.
E-mail: mbianche@courrier.usherb.ca

Abstract

Individual bighorn ewes (*Ovis canadensis*) at 4–14 years of age were 1.5% heavier preceding years when they weaned a lamb than preceding years when their lamb died before weaning. Intra-individual differences in mass between years of successful and unsuccessful reproduction appeared independent of a ewe's multiyear average mass. Relative mass loss both in the winter before and in the winter after a given reproductive episode increased with reproductive success. Long-term monitoring of individual mass and reproductive success is a promising technique to study life histories in capital breeders, because it allows to partially account for differences in reproductive potential.

Keywords

Bighorn sheep, body condition, body mass, capital breeder, condition-dependent, *Ovis canadensis*, reproductive strategy.

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INTRODUCTION

Characters that affect individual reproductive success are of great interest for evolutionary ecology and for population dynamics. Body mass may affect an individual's probability of survival and reproduction (Berger 1989; King *et al.* 1991; Dobson & Michener 1995; Illius *et al.* 1995). Body mass has two major components: skeletal size and body composition, including different relative amounts of muscle, adipose, and other tissues. Skeletal size and body composition can have different effects on reproductive success and may respond to different selective pressures. Although methods exist to evaluate fat content of live animals (Gerhart *et al.* 1991; Chan-McLeod *et al.* 1994; Arnould *et al.* 1996), none are easy to use in the field, particularly in situations where captured animals cannot be confined or reliably recaptured at predetermined times. Morphometric methods such as condition indices based on feeling the animal's body (Gerhart *et al.* 1997) or on dividing mass by a skeletal measurement (Dobson & Michener 1995) may not be very accurate (Cattet *et al.* 1997).

Mass of adult bighorn sheep (*Ovis canadensis* Shaw) ewes has a positive effect on subsequent ability to reproduce, and lactation has a negative effect on year-to-year mass changes. Compared with heavy ewes, light ewes suffer greater mass and fitness costs of reproduction, and the advantage of large mass increases with population density (Festa-Bianchet *et al.* 1998). That study, however, could not distinguish between the effects of size and those of body condition: a large ewe in poor condition could have the same mass as a small ewe in good condition. The ewe in good condition should have greater reproductive success than the one in poor condition (Doughty & Shine 1997). Here, I use repeated observations of the same individuals to test whether body condition affects individual reproductive performance. Long-lived animals offer the opportunity to use each individual as its own control to assess the role of body condition in reproductive success. I expected that ewes would have greater reproductive success following years when they were heavy relative to their multiyear average mass. To explore the relationships between reproduction and changes in mass, I also compared different levels of reproductive success to relative mass loss in winter.

STUDY AREA AND METHODS

Marked bighorn ewes were monitored at Ram Mountain (52°N, 115°W, elevation 1082–2173 m), Alberta, Canada, from 1973 to 1997. Body mass was adjusted to June 5 and to September 15 each year using each ewe's individual rate of mass gain, determined from repeated weightings during the summer. Most ewes were caught at least three times each summer and only ewes with one capture within 50 days of the adjustment dates were included. Reproductive status was assessed through udder examination at capture and from observations of lamb–ewe interactions. Ewe summer mass gain is linear when plotted over the

square root of capture date: further details are in Festa-Bianchet *et al.* (1996). Relative mass loss during winter was the proportion of a ewe's mass on September 15 that she had lost by June 5 the following year. To compare mass and reproductive success for each ewe, her average mass adjusted to September 15 in year x according to her reproductive success in year $x + 1$ was calculated. Ewes aged 4–14 years were included. Younger and older age classes were excluded because of strong age effects on mass (Festa-Bianchet *et al.* 1996; Bérubé 1997). Adult body mass was calculated by averaging all mass measurements adjusted to September 15 while the ewe was 4–14 years old. The following categories of reproductive success were considered: barren (no evidence of lactation), summer loss (the ewe gave birth to a lamb that died before October; in most cases the lamb died at or soon after birth), weaned a lamb (the lamb survived to October, then died overwinter), and lamb survival to 1 year. Data were available from 132 individual ewes, each contributing an average of 5.2 years of data (SD = 2.49, range 2–11). Paired t tests were used to compare levels of progressively higher reproductive success. Repeated-measures ANOVA were unfeasible because data on all four categories of reproductive success were available for less than 20 individuals. Means are reported ± SD and all tests are two-tailed.

RESULTS

The average mass adjusted to September 15 for ewes included in this analysis was 70.3 ± 4.7 kg (range 57–84 kg). Although individuals were on average 1.5% lighter preceding years when they were barren than preceding years when they lactated but failed to wean lambs, this trend was not significant, possibly because of wide individual variation (Table 1). Data for barren ewes were few because almost all ewes aged 4–14 years produced lambs (Bérubé *et al.* 1996). Ewes were about 1.5% lighter preceding years when their lamb died during summer than preceding years when their lamb survived to weaning, whereas there were no mass differences according to whether the ewe's lamb did or did not survive the winter (Table 1). The difference in individual mass between years when the ewe did and did not wean a lamb was not related to her average body mass on September 15 between 4 and 14 years of age (linear regression, $N = 97$ ewes, $P = 0.23$). Therefore, a single extra kilogram of mass by mid-September appeared to affect a ewe's chances of weaning a lamb the following year, regardless of her average adult mass.

Relative winter mass loss averaged 19.5% of the ewe's mass in mid-September, and was greater if the following year the ewes lactated than if they were barren (Table 2a). Parturient ewes lost more mass preceding years when they weaned a lamb than preceding years when their lamb died before weaning (Table 2). For ewes that weaned lambs, relative mass loss during the following winter was 3.1% greater in years when the lamb survived to 1 year (average loss of 20.9% of September 15 mass) than in years when the lamb died overwinter (average loss of 17.8%) (Table 2b).

Table 1 Differences in body mass adjusted to September 15 (kg ± SD) for individual bighorn sheep ewes aged 4–14 years at Ram Mountain, Alberta, according to reproductive success the following year

Intra-individual comparison	Mass difference	No. ewes	paired t	P
Barren *versus* summer loss	–1.04 ± 5.61	22	0.866	0.40
Summer loss *versus* weaned lamb	–1.06 ± 3.79	84	2.579	0.01
Weaned lamb died overwinter *versus* lamb survival to 1 year	–0.36 ± 3.35	41	0.686	0.50

Table 2 Effects of reproduction on relative mass loss from September 15 to June 5 the following year for individual bighorn sheep ewes at Ram Mountain, Alberta. Values (% ± SD) indicate the difference between two negatives: for example individual ewes lost 5.1% more of their September 15 body mass if the next summer their lamb died before weaning than if they were barren, and lost 3.1% more mass during winters when their lamb survived to 1 year than when their lamb died before the following June

Intra-individual comparison	Difference in relative loss	No. ewes	paired t	P
(a) Winter before reproduction				
Barren *versus* summer loss	0.051 ± 0.106	20	2.135	0.046
Summer loss *versus* weaned lamb	0.024 ± 0.066	78	3.126	0.008
Weaned lamb died overwinter *versus* lamb survival to 1 year	–0.016 ± 0.065	39	1.518	0.14
(a) Winter after reproduction				
Barren *versus* summer loss	–0.007 ± 0.084	20	0.375	0.71
Summer loss *versus* weaned lamb	–0.010 ± 0.074	84	2.180	0.24
Weaned lamb died overwinter *versus* lamb survival to 1 year	0.031 ± 0.0870	44	2.375	0.022

DISCUSSION

Body condition in late summer appeared to affect reproductive success, because ewes were 1.5% heavier in mid-September preceding years when they weaned lambs than when their lambs died before weaning. The small difference in mass suggests that minor yearly differences in body condition may affect reproductive success, but the wide individual variation also indicates that much variation in reproductive success is unrelated to body condition. Because of wide inter-individual variation in adult body mass (Festa-Bianchet *et al.* 1996), it would have been impossible to detect the small effects of body condition on reproduction without comparing repeated measurements of the same individuals.

For capital breeders, manipulations of energy stores and monitoring of subsequent reproduction and body condition provide valuable insights into the evolution of reproductive strategies (Doughty & Shine 1997). Although experimental manipulations are desirable, they are logistically problematic for mammals. Long-term monitoring of individual reproductive success and body mass is also a valid technique to investigate reproductive strategies in capital breeders. Data on individual body mass or condition may partly control for the individual differences in reproductive potential that often invalidate nonexperimental approaches to life-history evolution (Reznick 1985). Long-term studies of vertebrates can compare body condition and reproductive success of the same individual in different reproductive seasons. This approach is limited by the practical difficulties of observing different levels of reproductive success for each individual, and cannot take into account the effects of environmental variations in resource abundance or population density (Festa-Bianchet *et al.* 1998), but it is a valuable addition to a more general approach of including individual mass in multivariate analyses of reproductive success. For bighorn sheep, year-to-year differences in mass have a small but significant effect on a ewe's ability to reproduce successfully. Because only adult ewes were included in this analysis, it is reasonable to assume that year-to-year differences in mass were mostly due to differences in fat and muscle tissue accumulation and therefore in body condition.

The effects of body condition did not vary with average body mass, therefore interindividual body mass effects on reproductive success (Festa-Bianchet *et al.* 1998) may be due mostly to differences in skeletal size. Both large size and good condition have positive effects on reproduction.

Successful reproduction may depend partly on the amount of maternal investment before and just after parturition: ewes lost less mass preceding years when their lamb died during summer compared with before they weaned a lamb. High maternal expenditure during gestation or early lactation may both increase maternal mass loss from September to June and enhance lamb survival (Festa-Bianchet & Jorgenson 1998).

Following summers when they weaned lambs, ewes lost a greater proportion of their mass overwinter if their lamb survived than if it disappeared during winter. Experimental early weaning had a negative effect on development of male lambs (Festa-Bianchet *et al.* 1994). The results presented here confirm that maternal care continues into autumn, and that this late care increases overwinter mass loss.

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BIOSKETCH

M. Festa-Bianchet's long-term research program on individually marked ungulates aims at understanding the selective pressures that shape life-history evolution and at identifying the factors responsible for changes in population size. His interests include social behaviour, population dynamics, and reproductive strategies. His research also has a strong applied component as he is very interested in the conservation and management of biodiversity in mountain ecosystems.

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