INDIVIDUAL DIFFERENCES, PARASITES, AND THE COSTS OF REPRODUCTION FOR BIGHORN EWES (*OVIS CANADENSIS*)

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SUMMARY

(1) The consequences of reproduction for subsequent survival and reproductive success of individually marked bighorn ewes (*Ovis canadensis*) were examined over 8 years in south-western Alberta, Canada.

(2) Ewes that raised sons did not experience a decrease in reproductive success the following year, but their faecal output of lungworm (*Protostrongylus* spp.) larvae increased relative to ewes that raised daughters.

(3) Ewes were seldom known to produce sons in consecutive years. Because lamb sex was not determined at birth, this result could be explained by either an alteration of the birth sex ratio, or differential mortality of sons born in the year after their mother had produced a son.

(4) Ewes that lactated at 2 years of age appeared to be in better condition, and were more likely to lactate at 3 years of age, than ewes that did not lactate at 2 years. Overall, reproductive success in one year did not aversely affect reproduction the following year.

(5) Lactating ewes had greater faecal counts of lungworm larvae than non-lactating ewes. Ewes that had produced a lamb at 2 years of age were more likely to die during a pneumonia epizootic than ewes that had not lambed at 2 years. A decrease in resistance to parasites and pathogens appears to be a consequence of reproduction.

INTRODUCTION

Most life-history models assume that reproduction is costly, so that reproductive effort has a negative effect on subsequent reproductive success (Williams 1966; Gadgil & Bossert 1970; Stearns 1976; Bell 1980). Several studies have found negative correlations between reproductive effort and subsequent reproductive success (Lack 1966; Bryant 1979; Clutton-Brock, Guinness & Albon 1983; Berglund & Rosenqvist 1986; Fink 1986; Gustafsson & Sutherland 1988). However, other studies have not found any such correlations, or have revealed positive correlations between success in different reproductive episodes or between reproduction and survival (DeSteven 1980; Smith 1981; Saether & Haagenrud 1983; Bell 1984; Boyce & Perrins 1987; Murie & Dobson 1987; Pettifor, Perrins & McCleery 1988).

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It is important to understand the fitness consequences of reproduction under natural conditions. If there is no reduction in subsequent reproductive success or survival, the assumption of a cost may be unwarranted (Tuomi, Hakala & Haukioja 1983). Theories of parental investment and reproductive strategies may then have to be reconsidered.

Differences among individuals may affect the costs of reproduction (Clutton-Brock, Guinness & Albon 1983; Cothran *et al.* 1987; Murie & Dobson 1987), and attempts to measure reproductive costs may fail because of individual variations in reproductive capacity. Some costs may occur only under certain ecological circumstances (Boyce & Perrins 1987), such as high population density or low resource availability.

This study aimed to compare survival, reproductive success and parasite levels of bighorn (*Ovis canadensis* Shaw) ewes that weaned lambs of different sex, ewes that succeeded or failed in weaning a lamb in any one year, and ewes that did or did not first produce a lamb at 2 years old.

Bighorn sheep are polygynous, with marked sexual dimorphism. Geist (1971) suggested that male reproductive success was correlated with body size. Increased maternal investment, above that adequate for survival, may be more beneficial if directed towards a son than towards a daughter. Therefore, ewes were expected to invest more in sons than in daughters, and sons were expected to be costlier than daughters in terms of reduced ewe fecundity and survival.

Ewes were expected to be less successful in years following the weaning of a lamb than when their previous year's reproductive investment had been cut short by their lamb's early death. Finally, ewes that had their first lamb at 2 years of age were expected to suffer a decrease in reproductive success in subsequent years relative to ewes that postponed their first reproduction. Two-year-old ewes have not reached adult size (Jorgenson & Wishart 1984), and if they lamb they must bear at the same time the energetic costs of growth and reproduction.

Parasites can have a deleterious effect on reproductive performance of vertebrates (Hudson 1986; Saumier, Rau & Bird 1986). However, no study has investigated the relationship between reproductive effort and parasitism in wild mammals. The immune response against helminth parasites involves inflammation and tissue destruction, is metabolically costly (Larsh & Weatherly 1975; Butterworth 1984) and is impaired in individuals denied access to adequate nutrition (Aschkenasy 1974; Chandra & Newberne 1977). If resources are limited, and are diverted from the immune system to reproduction, individuals with relatively greater reproductive investment may be expected to suffer from greater parasitism. To test this hypothesis, this paper examines the relationship between reproductive effort, faecal output of parasite larvae, and survival during a pneumonia epizootic.

METHODS

Study area, population, and monitoring of ewes

This study was conducted from March 1981 to November 1988 in the Sheep River drainage in south-western Alberta, Canada. Bighorns were captured in a corral trap or with tranquilizer darts (Festa-Bianchet & Jorgenson 1985) and marked with plastic ear tags. Data reported here were collected from eighty-nine ewes aged 2 years or more, that produced 327 singleton lambs during this study. Ages were known for ewes captured as lambs or yearlings ($n = 53$). The minimum age of thirty-six ewes was estimated by counting the horn annuli (Geist 1966).

The winter range (1420–1740 m elevation) was regularly censused ($\bar{X} = 5$ times month^{-1}). Most ewes were in the winter range from September to May (Festa-Bianchet 1986a). The summer range (1800–2550 m elevation) was approximately 12 km west of the winter range and was searched from late May to early October ($\bar{X} = 34$ days year^{-1}). The identity and reproductive status of ewes were recorded. Lambing took place in late May and early June (Festa-Bianchet 1988a). Marked ewes were classed as lactating when they were seen to nurse a lamb, except for eighteen cases when the lamb died before being sighted, and lactation was revealed by obvious swelling of the udder. I am confident that almost all ewes that were not classed as lactating had also not been pregnant, because of the high frequency of sightings near lambing time and the long time (up to 3 weeks) after the death of the lamb during which lactation could still be detected through udder shape and size. Pregnancies interrupted before term (with no evidence of lactation) would have been undetected, but there is no evidence that these are common in bighorn sheep.

Lambs that disappeared were assumed to have died. Sex of young lambs was determined by observation of urination posture. The penis was readily visible in male lambs when they moulted in August. The sex of 84% of lambs that died before August ($n = 58$) was unknown.

Definition and description of variables

Reproductive success. A ewe's reproductive success in any one year was defined as the survival of her lamb to October, which corresponds to the time of weaning (Festa-Bianchet 1988b) and probably to the end of maternal investment.

Successful ewe. A ewe that in the previous year raised a lamb to October.

Yeld ewe. A ewe that in the previous year had not raised a lamb to October. Primiparous ewes were not included in this category. Most (83%) yeld ewes had produced a lamb the previous year, but their lamb had died before October. A few (17%) did not lactate in the previous year.

Adult ewe. Ewes 4 years of age and older, based on age-related differences in reproduction (Festa-Bianchet 1988c).

Larval count. The square root of the number of lungworm (*Protostrongylus* spp.) first-stage larvae per gram of dry faeces. All ewes were infected with lungworms. Faecal samples were collected from individually known ewes in 1981–86 during late pregnancy (March and April). An average of 3·6 samples (range 2–9) were collected from each ewe each year, and the number of larvae was counted using the Baermann technique (Samuel & Grey 1982). A square-root transformation resulted in a normal distribution (Festa-Bianchet 1987). The value used for each ewe was the average of the transformed values of all samples collected from that ewe that year.

Analysis

Larval counts were analysed using parametric statistics. Data on reproductive success and larval counts were collected from the same ewes for several years. To avoid potential statistical problems due to the inclusion of several data points collected from the same individual (Machlis, Dodd & Fentress 1985), only one year of larval count data for each ewe was selected for each lamb sex. Larval counts were the average of several faecal samples each year, and the year with the most samples was selected for analyses. The data set used to analyse the effects of lamb sex included sixty-one data points collected from forty-five ewes in 1981–86.

   Analysis of the effects of lamb sex was performed on ewes for which data were available under both circumstances. Using Wilcoxon's matched-pairs tests, the reproductive success of each individual was compared during years following the weaning of a son or of a daughter. This procedure emphasized individual differences in reproductive performance. Data on reproductive success were available from twenty-seven ewes in years following the weaning of a son and of a daughter ($\bar{X} = 3 \cdot 2$ lambs per ewe, range 2–6, S.D. $= 1 \cdot 15$). When more than 1 year of data following the weaning of a lamb of one sex were available, the average reproductive success in those years was used for analyses. For example, if a ewe had weaned two daughters, and in the years following these two daughters she had been successful once and yeld another time, her reproductive success following the weaning of a daughter was calculated as $0 \cdot 5$.

   This procedure could not be followed to compare yeld and successful ewes, because simulations revealed that even if the pattern of successful and yeld years was random, the procedure would show a significant cost of reproduction. For example, consider the thirty-two possible combinations of successful ($+$) and yeld ($-$) years for a ewe with 5 years of data. Only for four combinations ($+ + - - -$, $+ + + - -$, $- - + + +$, $- - - + +$), would the calculation of the probability of success following successful or yeld years within each combination go against the cost hypothesis (greater average success after successful than after yeld years). Of the remaining twenty-eight combinations, eighteen would suggest a cost of reproduction, six would have the same probability of success after successful and yeld years, and for four combinations the calculation would not be possible, because data would only be available after one type (successful or yeld) of year.

   Reproductive success following successful and yeld years was compared only at the population level, first with a G-test, then using logistic regression (Cox 1970), through the generalized linear model facility in GENSTAT (Alvey, Galwey & Lane 1982), to include in the analysis the effects of ewe age and year of study. This technique has been applied in analyses of reproductive success of red deer (*Cervus elaphus* L.) (Albon *et al.* 1986).

   The analysis of survival emphasized individual differences. Average survival for each ewe was calculated following yeld or successful years, and compared with a paired Wilcoxon test. For example, consider a ewe that died after 1 of 4 years during which she had successfully weaned lambs, and survived after 2 years in which she had been yeld. Her survival after yeld years would be 1, after successful years it would be $0 \cdot 75$.

   Frequency distributions of survival and lactation were compared using G-tests with one degree of freedom. All statistical procedures followed Sokal & Rohlf (1981), and all P values are two-tailed.

RESULTS

Population size and larval counts

   The number of ewes and lambs in the Sheep River herd in March increased from 1981 to 1985, then declined following a pneumonia epizootic (Table 1). The average number of bighorns seen during searches of the winter range in October–March followed a similar pattern (Table 1). The latter is determined by how many ewes and lambs are in the Sheep River herd and by how much the winter range is used by rams (Festa-Bianchet 1986b) and by non-resident ewes (Festa-Bianchet 1986a). The average larval count did not vary between 1981 and 1986 (Table 1; $F_{5,235} = 0 \cdot 89$, $P = 0 \cdot 49$).

TABLE 1. Number of resident ewes and lambs in the Sheep River herd in March 1981–88, average number of bighorn sheep seen in the winter range during censuses in October–March 1981–86, and average square-root transformed count of lungworm larvae in ewe faeces in March and April 1981–86. Numbers in parentheses indicate sample size for larval counts, which include only ewes aged 20 months or older

Year	1981	1982	1983	1984	1985	1986	1987	1988
Number of ewes	49	55	63	62	71	57	49	51
% Ewes marked*	33	76	84	85	86	93	98	94
Number of lambs†	16	36	29	29	27	7	13	14
% Lambs marked*	0	22	38	59	59	86	62	71
$\bar{X}$ total seen	81	115	112	128	119	94		
$\bar{X}$ larval count	19·0	23·8	22·1	21·2	21·8	19·5		
	(14)	(25)	(38)	(55)	(66)	(43)		

* By March of each year.
† 10-months-old.

Effects of lamb sex

Foetal sex did not affect larval count of ewes in late pregnancy ($t = 0·32$, $P > 0·5$; Table 2). The change in larval count to the following year was not significant for ewes that weaned daughters (paired $t = 1·25$, $P = 0·22$), but ewes that weaned sons tended to show an increase in larval count (paired $t = 1·95$, $P = 0·059$). Larval counts of ewes that had weaned sons during the previous year were higher than those of ewes that had weaned daughters ($t = 2·84$; $P < 0·01$).

Reproductive success was 70% following the weaning of a son and 74% following the weaning of a daughter ($n = 27$, $P > 0·5$, Wilcoxon matched-pairs test). The ewe's probability of survival was the same (89%) after weaning a son or a daughter.

For those cases where lamb sex was known in consecutive years, sex in year 2 was not independent of sex in year 1 ($G = 4·48$, $P < 0·05$). This result appeared to be mostly due to the small number of ewes known to produce sons in 2 consecutive years (Table 3).

TABLE 2. Square-root transformed faecal counts of *Protostrongylus* spp. larvae in March and April for bighorn ewes that weaned lambs of different sex (sample size in parentheses)

	Larval count			
	Year 1*		Year 2	
Lamb sex	$\bar{X}$	S.E.	$\bar{X}$	S.E.
Male (35)	20·49	1·58	24·34	1·86
Female (26)	19·69	1·99	16·98	1·66

* Larval count during late pregnancy.

Effects of previous year's reproduction

The prevalence of lactation among adult ewes was 95%, and the fourteen recorded cases of non-lactation were distributed among only eleven ewes. Lactating ewes had

TABLE 3. Sex of lambs produced by bighorn ewes that had produced a son or a daughter in the previous year. In 67% of the cases when lamb sex in year 2 was unknown, the lamb had died before 2 months of age. Ewes that did not lactate in year 2 are not included

Year 1		Year 2			
Lamb sex	n	Lamb sex	n	%*	%†
Male	73	Male	17	23	33
		Female	34	47	67
		Unknown	22	30	
Female	72	Male	30	42	54
		Female	26	36	46
		Unknown	16	22	

* All ewes.
† Only ewes whose lamb's sex was known for year 1 and year 2.

greater larval counts than non-lactating ewes (Table 4). A two-way ANOVA revealed a significant effect of lactation ($F_{1,124} = 10.504$, $P = 0.002$) and a non-significant effect of age ($F_{2,124} = 2.731$, $P = 0.069$), with no ($P > 0.2$) interaction effects. All available data were included in this analysis, and most non-lactating ewes were 2 or 3-year-olds. Within each of these age-classes, lactating ewes had greater larval counts than non-lactating ewes (2-year-olds: $t = 3.28$, $P = 0.003$; 3-year-olds: $t = 2.66$, $P = 0.02$).

The trend in lamb survival was opposite to that predicted by the reproductive cost hypothesis. Survival was 74% ($n = 155$ ewe-years, sixty-five ewes) following a successful year and 65% ($n = 78$ ewe-years, forty-nine ewes) following a yeld year ($G = 1.93$, $P > 0.1$). Logistic regression analysis confirmed this non-significant trend also when the effects of ewe age and year were taken into account.

Lamb survival to October did not affect ewe survival. There were only fourteen ewes with information on survival after yeld and successful years. Survival was greater after yeld than after successful years for five ewes, while the pattern was the opposite in nine cases ($0.1 > P > 0.05$, Wilcoxon matched-pairs test). Overall, ewes survived in 90% of the

TABLE 4. Average square-root transformed faecal counts of *Protostrongylus* spp. larvae in March and April for bighorn ewes that did and did not lactate the following summer 1981–86 (sample sizes in parentheses)

	Ewe age (years)		
	2	3	≥4
Lactating	25·08 (15)	26·60 (12)	20·05 (74)
Not lactating	16·70 (16)	14·64 (5)	17·69 (8)

TABLE 5. Survival from 2 to 3 years of age, and reproductive performance at 3 years of age, of bighorn ewes that did and did not lactate as 2-year-olds (sample sizes in parentheses)

	Survival to 3			Lactation at 3		
Lactate at 2	Yes	No	%	Yes	No	%
Yes (26)	23	3	88	20	3	87
No (23)	22	1	96	13	9	59

years following reproductive succcess ($n = 164$) and in 84% of the years following yeld years ($n = 95$) ($G = 1.59$, $P > 0.2$).

Effects of age of first reproduction

The prevalence of lactation was 52% for 2-year-old ewes ($n = 54$) and 76% for 3-year-olds ($n = 49$). There were no differences in the yearly prevalence of lactation among 3-year-olds. Prevalence among 2-year-olds was lower in 1986 (0%, $n = 7$) than in all other years combined (60%, $n = 47$; $G = 11.36$, $P < 0.001$).

Lactation at 2 years of age affected the frequency of lactation at 3 years ($G = 4.614$, $P < 0.05$; Table 5). The trend in the data was the opposite to that expected. If the 1986 cohort of 2-year-olds was excluded, ewes that lactated at 2 years were even more likely to lactate at 3 years (twenty of twenty-three) than ewes that had not lactated at 2 years (seven of fifteen; $G = 7.19$, $P < 0.01$). Frequency of lactation at 4 years was 85% for ewes that had ($n = 27$) and 75% for those that had not ($n = 8$) lactated at 3 years of age ($G = 0.42$, $P > 0.5$).

Survival from 2 to 3 years was independent of reproduction ($G = 0.88$, $P > 0.2$; Table 5). More ewes that had lactated as 2-year-olds, however, died during a pneumonia epizootic in 1985–86 (six dead of twenty-two) than ewes that had not lactated at 2 years (none dead of eleven; $G = 5.01$, $P < 0.03$). These ewes ranged in age from 2 to 5 years during the epizootic, which appeared to be a stress-related disease (Spraker *et al.* 1984; Festa-Bianchet 1989).

The larval count in March–April 1985 of ewes that did and did not die during the 1985–86 epizootic did not differ significantly. The count averaged 24.1 ($n = 12$, S.E. = 2.8) for ewes that died, and 20.2 ($n = 40$, S.E. = 1.3) for ewes that survived ($t = 1.41$, $P > 0.1$).

DISCUSSION

The results of this study suggest that reproduction of bighorn ewes involves a cost, but does not always affect subsequent reproductive success. For example, lamb sex did not have a significant effect on the ewe's reproductive success the following year, but sons probably obtained greater maternal investment than daughters, and appeared more costly to raise in terms of reduced immunity. Individual differences in reproductive capability strongly affected the manifestation of reproductive costs.

Little is known of what determines counts of *Protostrongylus* larvae. Forrester & Senger (1964) and Uhazy, Holmes & Stelfox (1973) suggested that larval counts were correlated with the number of lungworm-induced lung lesions. There is no evidence, however, that larval counts are strongly correlated with infection intensity. While it is reasonable to suspect that some correlation exists, other factors also affect larval counts.

Survival of first-stage larvae may vary with the host's immune response (Butterworth 1984). One interpretation of the results of this study is that reproductive effort weakened the immune system, so that pregnant ewes and ewes that reared sons were less effective at either preventing new infections or limiting the reproductive performance of parasites already established. Gravid worms may increase egg production in response to a weakening of their host (Gibbs & Barger 1986; Ito *et al.* 1986), and survival of first-stage larvae from hatching to exit from the digestive tract may be greater in stressed ewes. Similar relationships between nematode egg or larval counts and reproductive effort have been found in domestic sheep (Gibbs & Barger 1986).

Nematodes may also vary their egg production in response to hormonal changes related to host pregnancy (Gibbs & Barger 1986). While this alternative may apply to the data on larval counts of pregnant and non-pregnant ewes, it is difficult to see how it may explain the differences related to lamb sex in the previous year.

Faced with a limited amount of body resources, ewes may shift some from the immune system to reproduction. This resource allocation may improve reproductive success, but may also increase the risk of invasion by parasites and pathogens. This hypothesis may explain why ewes that produced their first lamb at 2 years of age were more likely to die during the pneumonia epizootic. During periods of stress, ewes that have allocated much of their resources to reproduction may suffer greater mortality from disease. This hypothesis predicts that small, reproductively unsuccessful individuals may, under certain circumstances, be more likely to survive disease outbreaks than larger, reproductively successful ones. The postulated trade-off between reproductive effort and ability to survive epizootics is similar to that between body growth and survival under stress in juvenile males among polygynous vertebrates (Clutton-Brock, Albon & Guinness 1985). It is interesting to note that during the pneumonia epizootic the mortality of yearling males exceeded that of yearling females (Festa-Bianchet 1987).

Bighorn sheep are polygnous (Geist 1971), and the reproductive success of males is probably more dependent upon body size than that of females. As in other polygynous mammals (Reiter, Stinson & LeBoeuf 1978; Clutton-Brock, Guinness & Albon 1982; Lee & Moss 1986), bighorn ewes may be expected to invest more in sons than in daughters. Evidence from this and other studies (Jorgenson & Wishart 1984) suggests that they do so, but not to the point of affecting their reproductive success the following year. Several studies have shown that mothers invest more in sons than in daughters, but have not shown a direct effect of offspring sex on subsequent reproductive success (Reiter, Stinson & LeBoeuf 1978; Duncan, Harvey & Wells 1984; Johnson 1986; Kovacs & Lavigne 1986; Lee & Moss 1986; Trillmich 1986). The results of this study caution against assuming that greater investment will always lead to lower subsequent reproductive success. Some females that make a greater reproductive investment may recover their body reserves before the next reproduction (Mitchell, McCowan & Nicholson 1976).

The effect of lamb sex upon the sex of the next offspring produced by a ewe (Table 3) is interesting, but the data do not allow us to determine whether it results from an alteration of the birth sex ratio or from differential mortality. The data support the hypothesis that sons are costlier to rear than daughters: what remains to be determined is whether ewes alter offspring sex ratio to avoid producing sons in consecutive years, or whether the greater cost of rearing sons results in greater mortality of sons (but not daughters) born in the following year.

Clutton-Brock, Guinness & Albon (1983) argued that the costs of reproduction should be measured in terms of effects upon subsequent reproductive success, not simply in terms

of energy budgets or metabolism. Long-term studies are especially valuable in this respect, because they may reveal how costs vary with changing ecological circumstances. In the present study, ewes that lactated as 2-year-olds did not appear to suffer any negative consequences until the occurrence of the pneumonia epizootic. From an evolutionary viewpoint, it is important to know that greater reproductive effort will have a negative effect on subsequent reproductive success only under certain circumstances. The intensity of selection against increased reproductive effort should vary according to the frequency of occurrence of those circumstances (Boyce & Perrins 1987). In particular, costs of reproduction may only be manifest when resources are scarce. The bighorn population increased before the pneumonia epizootic. The occurrence of the latter suggests that the population was under stress, possibly because it was near its carrying capacity (Stelfox 1976).

Ewes that lactated at 2 years of age were more likely to lactate as 3-year-olds than ewes that had not lactated at 2 years. This positive correlation between components of reproductive success runs counter to the predictions of most life-history models (Stearns 1976). It does not, however, indicate that early reproduction had no cost. Ewes that lactated at 2 years were probably in better condition than those that did not, and were able to bear the energetic cost of reproduction (evidenced by greater larval counts) without a decrease in subsequent short-term reproductive success. Several studies, empirical and theoretical, have pointed out how adjustment of reproductive effort to individual condition can mask the cost of reproduction (Van Dijk 1979; Hogstedt 1981; Saether & Haagenrud 1983; van Noorwijk & de Jong 1986; Murie & Dobson 1987).

Not all ungulates, however, appear to reproduce early only if in superior condition. A study by Miura, Kita & Sugimura (1987) suggests that in Japanese serow (*Capricornis crispus* Temminck), females that reproduce at 2 years of age might be less likely to produce offspring at 3 years than females that did not reproduce at 2 years (16% and 33% reproduction at 3 years, respectively; $G = 3 \cdot 11$, $0 \cdot 1 > P > 0 \cdot 05$; Miura, Kita & Sugimura 1987, Fig. 5; my calculations and statistics).

Because of individual differences, it is not possible to assess the costs of reproduction by comparing individuals that reproduce with those that do not. Such procedure would probably underestimate reproductive costs (Clutton-Brock, Guinness & Albon 1983). In this study, the data did not allow a comparison of within-individual reproductive success after successful and unsuccessful years. If individual differences in reproductive potential were ignored, an immediate fitness cost of reproduction could not be detected. Some ewes were consistently successful year after year, while others failed to rear lambs in several successive years.

The trend towards lower survival in yeld years, although not significant, is intriguing. Possibly, some ewes in deteriorating condition were unable to provide sufficient maternal investment for their last lamb's survival. More data are required to test this hypothesis, which implies that the costs of reproduction vary within individuals according to age.

ACKNOWLEDGMENTS

of Cambridge, provided hospitality and stimulation during the preparation of the manuscript.

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