

INDIVIDUAL DIFFERENCES, LONGEVITY, AND REPRODUCTIVE SENESENCE IN BIGHORN EWES

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Abstract. Within individual iteroparous mammals, a high rate of reproduction in early life may occur at the cost of decreased reproduction near the end of life, leading to reproductive senescence. Using long-term data on marked individuals from two populations of bighorn sheep (*Ovis canadensis*), we tested for the existence of reproductive senescence and of trade-offs between longevity and early reproductive success in ewes, which have an observed maximum life-span of 19 yr. Lamb production decreased in older ewes, while weaning success for parous ewes was independent of age in one population and decreased with age in the other. The age-related decrease in lamb production followed a slight decrease in body mass, which began at ~11 yr of age. Reproductive senescence in this species appears to begin 6–7 yr after the onset of survival senescence. Longevity was positively related to late-summer body mass at 6 yr. Contrary to reproductive cost theories, there was no negative relationship between early and late reproductive success or between early reproductive success and longevity; instead, those relationships tended to be weakly positive. Longevity had a strong positive influence on lifetime reproductive success in both populations. Since the longest lived ewes were among the heaviest as young adults and had high reproductive success throughout their lifetime, longevity appears to be state-dependent: only ewes of higher phenotypic quality survived long enough to reach reproductive senescence. Models that assume that survival to old age is random with respect to phenotype are therefore not applicable to reproductive senescence in bighorn sheep.

Key words: bighorn sheep; life history theory; longevity; *Ovis canadensis*; population density; reproductive success; senescence; trade-offs; early reproductive success.

INTRODUCTION

The effects of aging on survival and reproductive success are key elements of life history theory. Senescence is an age-related decrease of an organism's survivorship and fecundity (Williams 1957, Rose 1991), where fecundity is measured through reproductive potential or capacity (Fisher 1958). Although reproductive senescence has been shown in some short-lived mammals (Hoogland 1995, Wauters and Dhondt 1995) as well as long-lived ones (Clutton-Brock et al. 1982, Green 1990), particularly primates (Wolfe and Noyes 1981, Paul et al. 1993, Sugiyama 1994), it has not been shown in others (Sæther and Haagenrud 1983, Gaillard et al. 1992). Williams (1957) suggested that reproduction and survival should steadily decrease after sexual maturity because of senescence effects. The survival and reproductive patterns of many long-lived mammals and birds, however, tend to follow a bell-shaped curve (Gaillard et al. 1994, Lunn et al. 1994,

Komdeur 1996, Jorgenson et al. 1997, Newton and Rothery 1997); survival and reproduction increase after sexual maturity, stabilize in prime-aged individuals, then decrease until death. Contrary to suggestions by Williams (1957) and Promislow (1991) (see also Promislow and Harvey 1990), senescence does not usually begin at sexual maturity or with the first reproduction (Gaillard et al. 1994).

Senescence is sometimes attributed to cellular breakdown or to long-term effects of accumulated toxins and mutation-causing radiations (Adelman and Roth 1982, Rose 1991). The evolutionary approach, however, explains senescence as a consequence of age-specific selective pressures and reproductive costs (Williams 1957, Hamilton 1966, Stearns 1992, Charlesworth 1993), relying on the assumption that reproduction early in life has a stronger impact on fitness than reproduction later in life (Williams 1957, Rose 1991). Antagonistic pleiotropy could thus be involved in the evolution of senescence (Rose 1983, Lessels 1991); pleiotropic genes could be selected for, if the benefits they confer to early reproduction influence a large number of young individuals, so that on average they surpass the detriment caused to old individuals. Negative life history correlations could therefore arise from antagonistic pleiotropy (Williams 1957).

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Female reproductive success increases with body mass in many mammals (Albon et al. 1983, King et al. 1991, Iverson et al. 1993). Reproductive costs could therefore include decreased growth or seasonal mass accumulation (Mitchell et al. 1976, Green 1990) that could limit future reproductive potential. If the increase in fecundity early in the life-span of long-lived mammals is due to body growth, then a decrease at the end of the life-span could be due to a decrease in body mass. However, little is known about patterns of mass change at the end of life (Skogland 1988, Nelson and Mech 1990), partly because data on repeated mass measurements and individual reproductive success are very difficult to obtain. Ungulates are often considered to be "capital breeders": investment in reproduction at one point in life is expected to decrease their long-term reproductive ability by affecting their body condition (Stearns 1992). It is therefore reasonable to expect that reproductive senescence in ungulates could follow a decrease in body mass.

Few studies have tested the cumulative costs of reproduction over several reproductive seasons (Sydeman et al. 1991, Byers 1997) and little is known about the effects of early reproductive output on reproductive output late in life and on longevity in long-lived mammals. Information on lifetime reproduction from individually marked animals is essential for assessing trade-offs between life history components, and for assessing the relationship between individual phenotypic quality and reproduction proposed by state-dependent life history theory (Marlow et al. 1996, McNamara and Houston 1996). There is clear evidence that individual phenotype affects reproduction (van Noordwijk and de Jong 1986, Morris 1996) and individual parameters such as body mass must be accounted for when considering reproductive costs (Festa-Bianchet et al. 1998). Given that the age of first reproduction and patterns of reproduction vary among individuals, it is possible that patterns of senescence also vary according to phenotype, yet no study to date has been able to identify phenotypic correlates of longevity beyond survival to sexual maturity.

The objectives of this paper were to test whether or not reproductive senescence and trade-offs between reproduction early in life and late in life exist in bighorn ewes. Analyses were performed using 24 and 18 yr of data on individually marked ewes from two populations. Jorgenson et al. (1997) reported that yearly survival was ~95% for ewes aged 2–7 yr, decreasing to ~85% for older ewes. We therefore expected reproductive senescence to also begin at ~8 yr of age. Ewes attain >90% of their adult mass by age 4, with small increases until age 7 (Festa-Bianchet et al. 1996), but the relationship between mass and age is unknown for older ewes. Accordingly, we tested whether body mass decreased at the end of the life-span and whether a possible decrease in mass coincided with reproductive senescence.

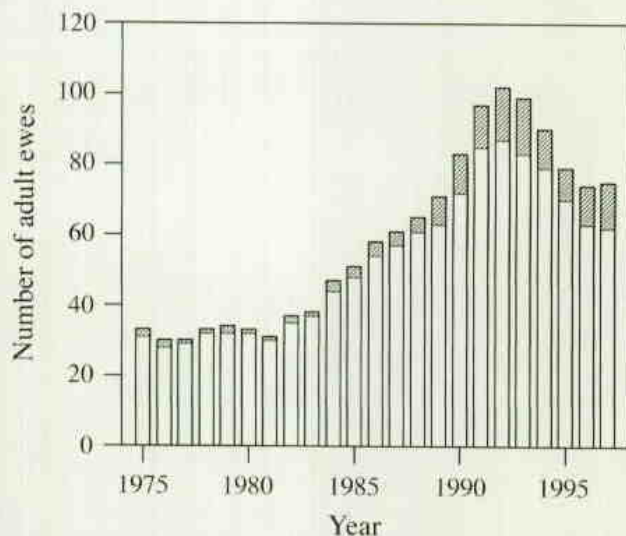


FIG. 1. Number of bighorn ewes aged 2–10 yr (empty bars) and ≥ 11 yr (hatched bars) at Ram Mountain, 1975–1997.

We attempted to identify correlates of longevity. Interspecifically, body mass influences potential life-span (Prothero and Jürgens 1987); therefore we tested the prediction that individual longevity was positively related to adult mass in ewes. We also tested hypotheses predicting an inverse relationship between reproductive output early in life and reproductive output late in life, and between reproductive output early in life and longevity. Because high population density can increase reproductive costs (Bérubé et al. 1996, Festa-Bianchet et al. 1998) and decrease lamb survival (Portier et al. 1998), we included population density in the analyses.

METHODS

Bighorn ewes first give birth at 2–4 yr of age (Jorgenson et al. 1993a). In Alberta, most births occur between mid-May and mid-June. The birth peak is normally the last week of May (Festa-Bianchet 1988, Bérubé 1997). Litter size is fixed at one lamb. Maximum known ewe longevity in our study populations is 19 yr. In both study areas, the very high proportion of marked sheep, ease of access, and the sheep's habituation to human observers allowed us to collect precise data on individual survival and reproductive success (Festa-Bianchet et al. 1995, Jorgenson et al. 1997).

Ram Mountain

Ram Mountain, Alberta, Canada (52° N, 115° W), includes ~38 km² of alpine and subalpine habitat, at elevations of 1082–2173 m. Bighorn sheep on Ram Mountain have been studied since 1972. Between 1972 and 1981, density was kept low by annual removals of 12–24% of adult ewes (Jorgenson et al. 1993b). After 1981 the population increased, more than doubled by 1992, and then decreased (Fig. 1).

Sheep were captured in a corral trap baited with salt, from late May to early October. All ewes have been

marked since 1976 and >90% were captured at least twice each summer. Lactation status and mass (measured to the nearest 0.25 kg with a spring scale) were recorded for captured ewes. Lamb-ewe pairs were identified through field observations of nursing behavior. Lamb and ewe survival were monitored through field observations from May to October. Because reproductive data are incomplete for many ewes before 1975, we used data collected from 1975 to 1998.

Sheep River

Ewes from the Sheep River population winter in the foothills of southwestern Alberta (50° N, 114° W, elevation 1450–1700 m) and in summer migrate 10–16 km to the Rocky Mountains (elevation 1500–2450 m). The population has been studied since 1981 and all ewes have been marked since 1987. Sheep were only captured once, mostly as lambs; therefore data on mass were not available. Data on survival and reproductive success were gathered through field observations in 1981–1996 (see Festa-Bianchet 1989 for more details).

Definitions

Ewes were classified as having died from natural mortality factors such as predation or disease if they disappeared or were found dead. Predators such as wolves (*Canis lupus*), coyotes (*C. latrans*), and cougars (*Puma concolor*) were present in both study areas, but cause of death was seldom known (Jorgenson et al. 1997). Ewes removed from Ram Mountain ($n = 63$), and those that died from trapping injuries at Ram Mountain ($n = 3$), or were shot by hunters at Sheep River ($n = 5$) were excluded from analyses of natural mortality.

Categories for ewe reproductive status were "barren" (no evidence of lactation), "lamb lost neonatally" (the ewe was lactating in late spring, but never seen with a lamb), and "lactating" (ewe seen nursing a lamb) (Bérubé et al. 1996). Lamb survival categories were "neonatal death," "summer death" (before October), "survival to weaning" (to October; survival to weaning could be monitored also for unmarked lambs through ewe-lamb associations) and "survival to 1 yr," which was only known for lambs that were marked.

Data analyses

The proportion of ewes reproducing according to age was calculated including all ewes. The proportion of ewes weaning a lamb was calculated excluding barren ewes. Standard deviations reported for proportions (p) were calculated as the square root of $pq/(n - 1)$, where $q = 1 - p$ and $n =$ the number of ewes per age group (Zar 1984).

Backward stepwise logistic regression models were constructed and the likelihood ratio statistic was used to remove variables with insignificant effects (P set at 0.10). Categorical factors (reproductive success) in lo-

gistic models were evaluated using deviation contrasts (Norusis 1994).

Ewes can lamb at 2 yr, and survival decreases after 7 yr of age (Jorgenson et al. 1997). Reproduction early in life was therefore defined as occurring between 2 and 7 yr inclusively, and reproduction late in life was defined as occurring after 7 yr of age. Accordingly, only ewes surviving ≥ 8 yr were included in analyses relating to reproduction early in life. Some analyses included only ewes born up to 1986, to avoid biasing the sample towards short-lived ewes, as many ewes born after 1986 were still alive at the time of writing.

Analyses comparing reproduction early and late in life, or reproduction according to longevity, included only ewes with natural mortalities, to ensure that reproduction was measured throughout each ewe's natural life-span. Estimates of the number of lambs produced that survived to become yearlings excluded lambs whose survival was unknown after weaning.

Dates of capture were coded from 24 May as day 0. To calculate individual rates of mass gain, a linear regression was fitted to individual mass measurements plotted against the square root of the capture date. Each ewe's mass was adjusted to 5 June (day 12) and 15 September (day 114). More details of mass adjustment procedures are reported in Bérubé et al. (1996) and Festa-Bianchet et al. (1996).

Only ewes that died of natural causes were included in analyses comparing mean mass early and late in life. To determine whether longevity was affected by body mass in early adulthood, we used mid-September mass at age 6, which represented mass in mid-life, as >95% of adult mass is reached by that age (Festa-Bianchet et al. 1996). Although we report here results of analyses using mass at age 6, we obtained similar results using mass at age 5, or the average mass at ages 4–7. To take into account the potential effects of population density on ewe survival, we used the number of adult ewes in the population when each ewe was 6 yr old.

The significance level was set at $P = 0.05$ and all P values are two-tailed. Analyses were performed using SPSS (Norusis 1994). Means are reported with standard deviations, except where stated.

RESULTS

Age and ewe reproductive success

At Ram Mountain, reproductive senescence appeared at ~ 13 yr of age through a decrease in lamb production, but there were no apparent effects on lamb survival to weaning (Fig. 2). The increase in lamb production from 2 to 5 yr of age reflected density-dependent changes in age of primiparity (Jorgenson et al. 1993a). Logistic regression models for ewes aged ≥ 6 yr confirmed that when the effects of ewe mass, reproductive success the previous year, and the number of ewes in the population in the year considered were taken into account, old age had a negative effect on

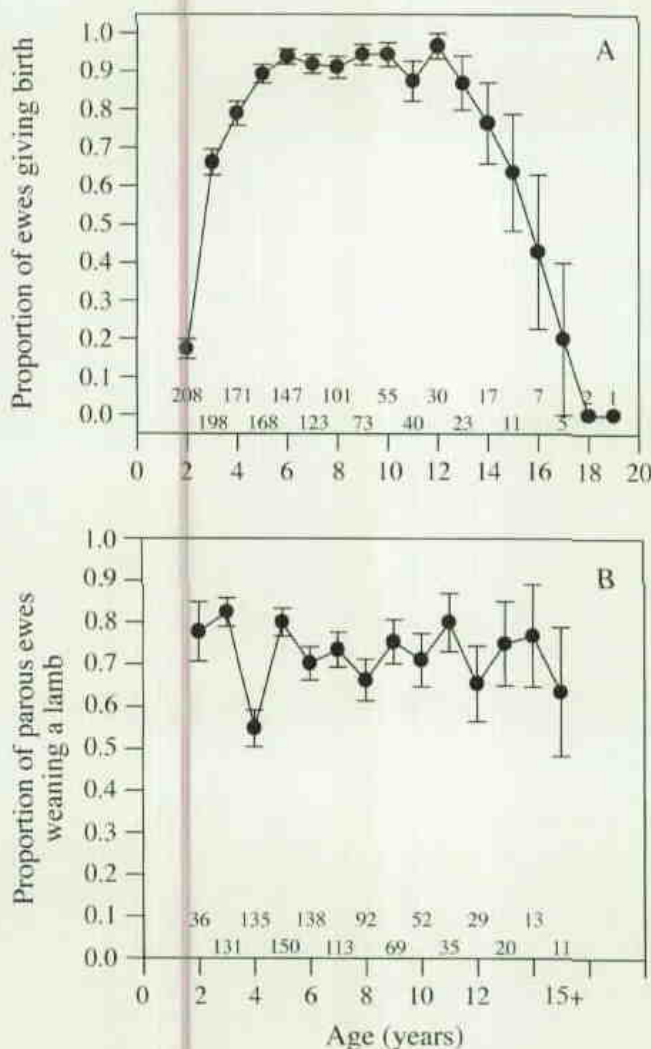


FIG. 2. Proportion (± 1 SD) of ewes giving birth (A) and weaning a lamb (B) according to age in the Ram Mountain population, 1975-1997. The number of ewes sampled for each age appears above the abscissa; the overall sample was 265 individual ewes.

lamb production, but not on weaning success (Table 1). At Sheep River, there are neither measurable phenotypic costs of reproduction (Festa-Bianchet 1989) nor density effects on lamb survival (Portier et al. 1998), and ewe mass data were not available. For this population, logistic regressions therefore only tested the effects of ewe age on lamb production and survival to weaning, for ewes ≥ 6 yr of age. Age had a negative effect on both lamb production ($\chi^2 = 9.25$, $P = 0.002$, $n = 330$ ewe-years) and survival to weaning ($\chi^2 = 6.65$, $P = 0.01$, $n = 303$). Lamb production at Sheep River decreased from 96.2% for ewes aged 6-13 yr to 64.7% for ewes aged 14-18 yr. Lamb survival to weaning declined from 68.9 to 54.5% for the same age classes.

Age-related changes in ewe mass

The existence of age-related changes in mass for old ewes was tested through analysis of seasonally adjusted mass. Mass on 15 September was examined first, since this variable affected overwinter survival of old ewes (Festa-Bianchet et al. 1997). The relationship between mass and age followed a quadratic function (mass = $a(\text{age}) + b(\text{age})^2 + c$); in order to calculate the age when mass started decreasing (the critical value), we first calculated the derivative of the quadratic function, then solved the equation for age when the slope equaled zero (see Skogland 1988).

Considering all ewes that survived to ≥ 2 yr of age, mass began declining at 11 yr ($F = 482.1$, $df = 2$, 1080, $P < 0.0001$, $r^2 = 0.47$; mass on 15 September = $4.16(\text{age}) - 0.19(\text{age}^2) + 52.0$; critical value = 11.0 yr). Mass adjusted to 5 June followed the same pattern ($F = 542.7$, $df = 2$, 1147, $P < 0.0001$, $r^2 = 0.49$; mass = $4.46(\text{age}) - 0.20(\text{age}^2) + 35.7$; critical value = 11.0 yr). We then considered only ewes with a longevity of ≥ 11 yr (based on the critical age reported above), and found that body mass began decreasing at 11.2 yr ($F = 100.3$, $df = 2$, 395, $P < 0.0001$, $r^2 = 0.34$; mass on 15 September = $2.98(\text{age}) - 0.13(\text{age}^2) + 57.9$), consistent with the previous result. In all cases both

TABLE 1. Logistic regression models comparing ewe reproductive success in year 2 to reproductive success in year 1, body mass the preceding fall (year 1), population density, and age for Ram Mountain ewes aged ≥ 6 yr.

Year 2 reproductive success	Variables	B^\dagger	P^\ddagger	R^\S
Year 2 lamb production ($n = 472$)	Lamb production (year 1)	1.17	<0.0001	0.27
	Mass (year 1)	0.09	0.007	0.14
	Density		NS	
	Age	-0.27	<0.0001	-0.25
Year 2 weaning ($n = 423$)	Weaning (year 1)	-0.54	<0.0001	-0.17
	Mass (year 1)		NS	
	Density	-0.03	<0.0001	-0.17
	Age		NS	

Note: All models are significant ($P < 0.0001$) and exclude nonsignificant variables.

† Regression coefficient.

‡ P value for B .

§ Partial correlation.

|| Reproductive success in year 1 was treated as a binary categorical variable.

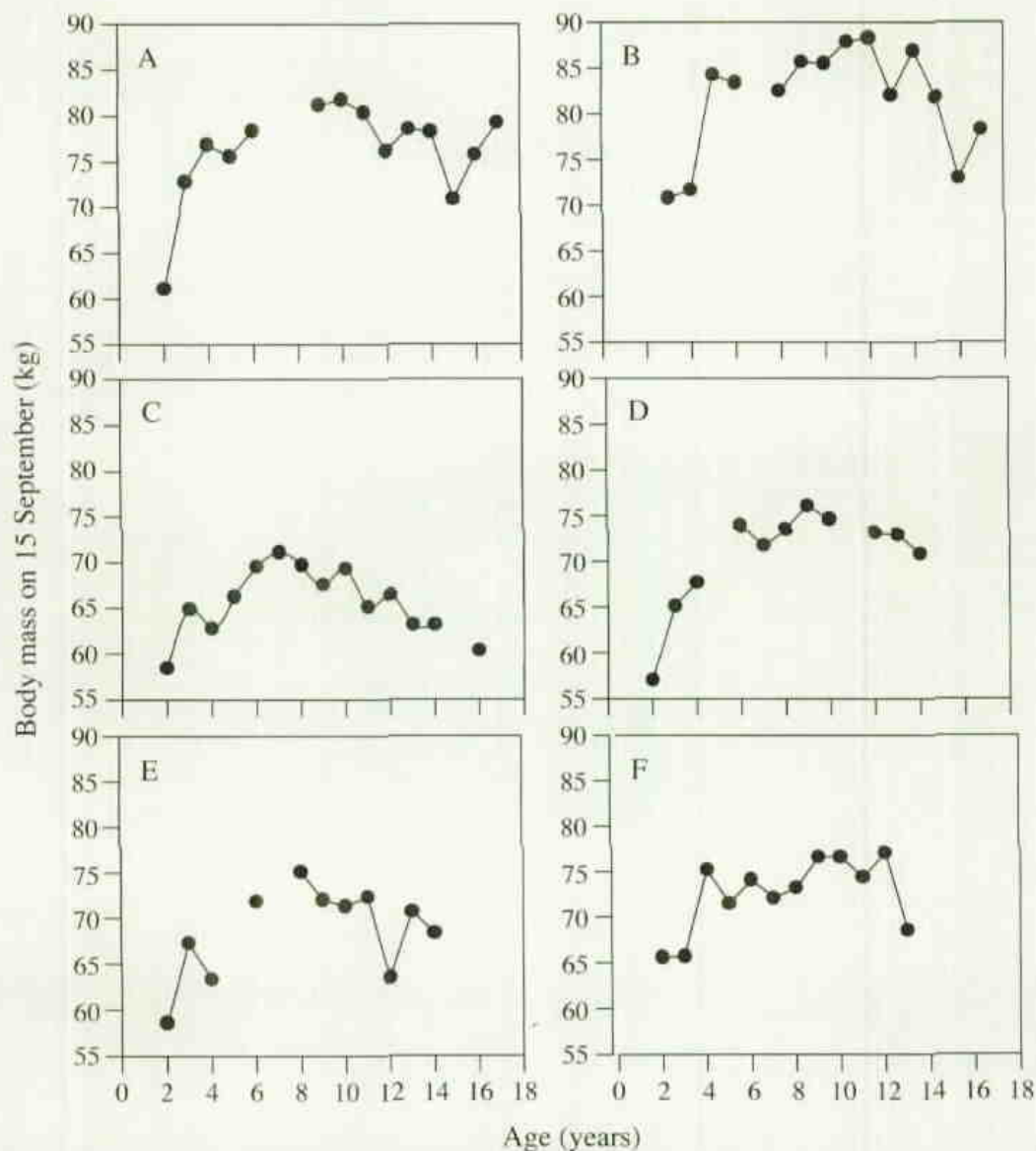


FIG. 3. Individual changes in mass on 15 September according to age: (A) ewe 21i, alive at 17 yr; (B) ewe 7g, died at 17 yr; (C) ewe 7i, died at 16 yr; (D) ewe 22j, died at 15 yr; (E) ewe 11i, died at 14 yr; (F) ewe 16m, still alive at 13 yr. Individual data are missing for some years. In (A) the increase in mass for 16 and 17 yr is associated with neonatal lamb loss and barren status, and in (B) the increase in mass at age 17 is associated with neonatal loss.

the linear and the quadratic terms were highly significant ($P < 0.001$)

Individual analyses of 15 September mass according to age (Fig. 3) revealed that the age at which September mass began decreasing did not vary according to age at death ($F = 0.0004$, $df = 1, 26$, $P = 0.98$). "Old" ewes, for the purpose of mass analysis, were therefore defined as being ≥ 11 yr old.

Ewes displayed a clear tendency for mass loss after age 10 when measured in September (Figs. 3 and 4). Non-lactating ewes gain mass (Festa-Bianchet et al. 1998), and the increase in mass between 16 and 17 yr (Fig. 4A) was associated with barren status at age 17 for all three ewes. Paired t tests comparing mean September mass between 7 and 11 yr of age with mean September mass starting at 12 yr of age confirmed that ewes surviving ≥ 12 yr lost mass after age 10 (mean

$[\pm 1$ SD] mass difference: -1.0 ± 2.7 kg, $n = 27$, $t = 2.01$, $P = 0.055$). There was no apparent mass decrease when comparing mean June mass for the same age ranges (mean difference: -0.8 ± 3.9 kg, $n = 26$, $t = 1.05$, $P = 0.3$) (Fig. 4B).

Body mass and longevity

For females that survived ≥ 8 yr, longevity was positively related to 15 September mass at 6 yr of age ($F = 19.8$, $df = 1, 62$, $P < 0.0001$, $r^2 = 0.24$) (Fig. 5). To control for any potential effects of population density, we performed a multiple regression including the number of adult ewes in the population at 6 yr of age for each ewe. For this analysis, however, we included seven ewes that were still alive in 1998 (four 12-yr-olds and three 13-yr-olds), using their age in 1998 as their age at death. Excluding these seven ewes, the

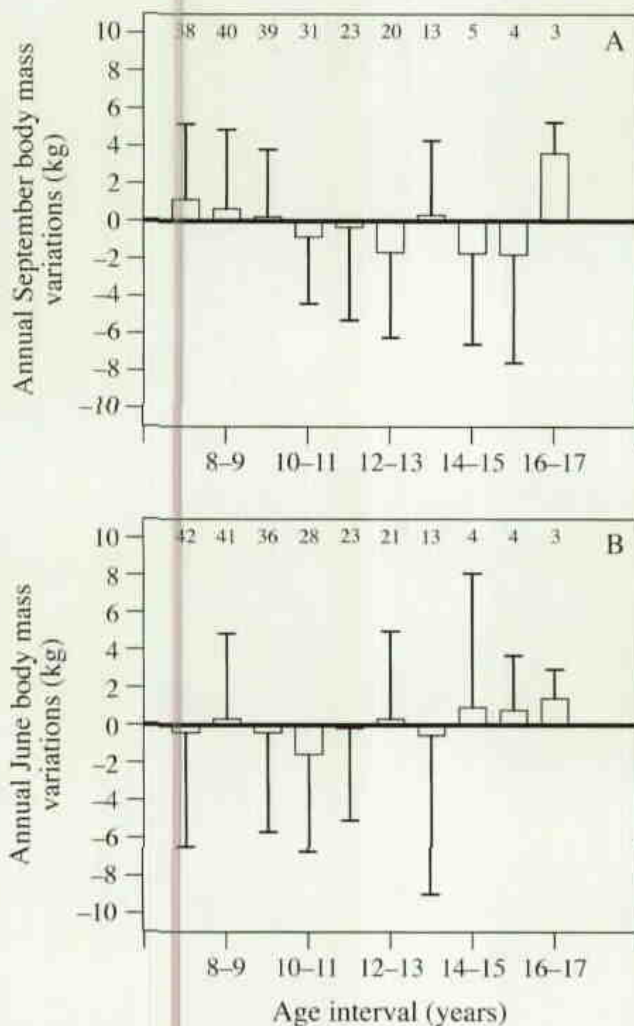


FIG. 4. Changes in body mass (± 1 SD) adjusted to 15 September (A) and to 5 June (B) in consecutive years for ewes with a longevity of ≥ 12 yr. Sample sizes for each age interval appear above columns.

multiple regression suggested a negative effect of population size on longevity (partial correlation controlling for mass: $r = -0.34$, $n = 50$, $P = 0.017$), but this result was likely due to a temporal bias, as the analysis included mostly short-lived ewes that were adults, at very high density (in 1990–1992). When we included the seven surviving ewes aged 12 or 13 yr, the negative effect of population density was no longer significant (Table 2). Ewes born before 1987 with a life-span of between 6 and 10 yr were $\sim 6\%$ lighter at age 6 (mean = 69.4 ± 5.2 kg, $n = 28$) than ewes with a longevity of ≥ 11 yr (mean = 73.5 ± 4.7 kg, $n = 30$) ($t = 3.22$, $df = 56$, $P = 0.002$).

Reproduction early and late in life

We expected that the cost of high reproductive success early in life would lead to decreased reproductive success late in life. For Ram Mountain ewes, however, we found no evidence of such a relationship; on the contrary, there appeared to be positive relationships between reproductive success up to 7 yr of age and

reproductive success starting at 8 yr. Both the number of lambs produced and the number of lambs weaned between 2 and 7 yr of age were positively correlated with the number of lambs weaned by the same ewe after 7 yr of age (for ewes born before 1987, $r = 0.30$ and $r = 0.29$; $n = 63$ and $P < 0.025$ in both cases). However, when population density (measured as the number of ewes in the population when each ewe was 6 yr old) was included in a multiple regression, the relationship between individual reproductive success before and after 8 yr became not significant ($P = 0.13$ for lambs born, $P = 0.92$ for lambs weaned), apparently because of the overriding effects of population density on lamb survival (Festa-Bianchet et al. 1998).

At Sheep River, there was a generally weak but positive relationship between individual reproductive success before and after age 7. The numbers of lambs weaned were correlated ($r = 0.38$, $n = 30$, $P = 0.03$) and of the nine possible correlations among early and late reproductive success (measured as the number of lambs produced, weaned, or surviving to 1 yr), seven were positive, including three that were significant. Therefore, results from Sheep River confirmed the lack of a negative relationship between early and late reproductive success during a ewe's lifetime.

Longevity and reproduction early in life

At Ram Mountain, longevity was positively correlated with the number of lambs produced between the ages of 2 and 7 by ewes born before 1987 ($r = 0.32$, $n = 64$, $P = 0.01$) and with the number of lambs weaned between the ages of 2 and 7 ($r = 0.25$, $n = 64$, $P = 0.05$). However, when the effects of population

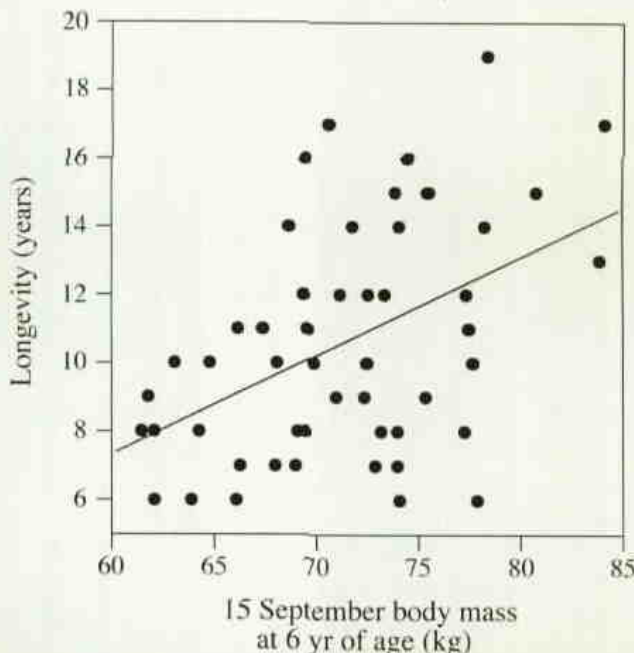


FIG. 5. Ewe longevity according to 15 September body mass at age 6, for Ram Mountain ewes living ≥ 6 yr, born before 1987 and with natural deaths.

TABLE 2. Multiple regression of the effects of population size and 15 September body mass at 6 yr of age on longevity of Ram Mountain ewes surviving ≥ 6 yr and born before 1987.

Factor	B	F	t	df	P	R ²	Partial correlation
Regression†	...	9.3	...	2.56	0.0003	0.25	...
Mass at age 6	0.25		3.40		0.001		0.41
Number of ewes	-0.03		1.53		0.13		-0.20

† Seven ewes still alive in 1998 (aged 12–14 yr) are included.

density were accounted for by partial correlation, only the relationship between longevity and the number of lambs produced from 2 to 7 yr of age approached significance (partial $r = 0.23$, $P = 0.07$).

Results from Sheep River agreed with those from Ram Mountain: the relationships between longevity and the number of lambs weaned and surviving to 1 yr between the ages of 2 and 7 were positive although not significant (weaning: $r = 0.34$, $P = 0.06$; survival to 1 yr: $r = 0.24$, $P = 0.19$), while there was no relationship between longevity and the number of lambs produced between ages 2 and 7 ($r = 0.001$, $n = 30$ in all cases). Therefore we did not find evidence of a negative effect of early reproduction on longevity in either study area.

Longevity and lifetime reproductive success

There was a strong relationship between lifetime reproductive success and longevity for Ram Mountain ewes, whether reproductive success was measured as the number of offspring born ($F = 1612.5$, $df = 1$, 117 , $P < 0.0001$, $r^2 = 0.93$) (Fig. 6A), weaned ($F = 581.2$, $df = 1$, 117 , $P < 0.0001$, $r^2 = 0.83$) (Fig. 6B), or surviving to 1 yr of age ($F = 187.8$, $df = 1$, 117 , $P < 0.0001$, $r^2 = 0.62$) (Fig. 6C). In multiple regressions including the effect of September mass and population density at 6 yr of age (for ewes surviving to ≥ 6 yr), population density always had a significant negative effect on reproductive success (partial correlations controlling for density: $r = -0.22$, $P = 0.047$ for number of lambs born, $r = -0.39$, $P < 0.001$ for lambs weaned and $r = -0.31$, $P = 0.004$ for lambs raised to 1 yr of age, $n = 81$ in all cases), while mass at 6 yr of age had no significant effects. Even when population density was controlled through partial correlation, longevity remained a very strong factor affecting lifetime reproductive success (partial correlations: $r = 0.93$ for number of lambs born, 0.81 for lambs weaned and 0.58 for lambs raised to 1 yr of age, $P < 0.001$ and $n = 81$ in all cases).

Sheep River data also revealed a strong relationship between ewe longevity and the number of lambs produced ($F = 550.3$, $df = 1$, 65 , $P < 0.0001$, $r^2 = 0.89$) (Fig. 6D), weaned ($F = 222.0$, $df = 1$, 65 , $P < 0.0001$, $r^2 = 0.77$) (Fig. 6E), and surviving to 1 yr ($F = 75.6$, $df = 1$, 65 , $P < 0.0001$, $r^2 = 0.54$) (Fig. 6F).

DISCUSSION

The most important result of our long-term study is that longevity in bighorn ewes is not random, but is

correlated with body mass in midlife. Mass therefore appears to be a useful phenotypic indicator of individual quality, confirming earlier work showing that the fitness costs of reproduction decrease with increasing body mass (Festa-Bianchet et al. 1998). Although some of the individual variations in mass were due to year-to-year changes in body condition, most of the variation in body mass between individuals appears to reflect differences in skeletal size (Festa-Bianchet 1998). Contrary to trade-off hypotheses, the association between reproduction early and late in life tended to be positive, and there was no trade-off between longevity and early reproductive success. Reproductive senescence did not coincide with survival senescence nor with senescent mass loss. Instead, reproductive senescence was only evident 6 yr after the onset of survival senescence (Jorgenson et al. 1997) and 3 yr after the onset of senescence-related mass loss. It appears likely that the onset of survival senescence at ~ 7 – 8 yr of age is due to increased mortality of low-quality individuals, while mass loss for old ewes presumably reflects a decrease in condition. The time differences in age-related changes in survival, reproduction, and mass underline the need to account for individual phenotypic characteristics to understand the evolution of senescence.

Phenotypic differences within a population, such as the positive association of mass and longevity that we found for bighorn ewes, can lead to heterogeneity in reproductive potential and in the expression of reproductive costs. Heterogeneity must be considered in life history studies when individual patterns vary from population patterns, because the latter may overlook individual differences in quality (Vaupel and Yashin 1985, Pemberton et al. 1991, Burnham and Rexstad 1993, Forslund and Pärt 1995, McDonald et al. 1996). These differences are particularly important when they vary with age, as shown by our results; ewes that reached old age were not a random sample of the population. A positive relationship between mass and longevity has also been reported for female red squirrels *Sciurus vulgaris* (Wauters and Dhondt 1989). There is clearly a need to determine whether phenotypic characteristics affect longevity in other mammals.

In mammals that undergo seasonal mass changes, the physiological impact of mass loss may depend on initial mass. For example, in grey seals (*Halichoerus grypus*), heavier females undergo more rapid mass loss during lactation, and their offspring are heavier and fatter at weaning, compared to females that are lighter (Iverson

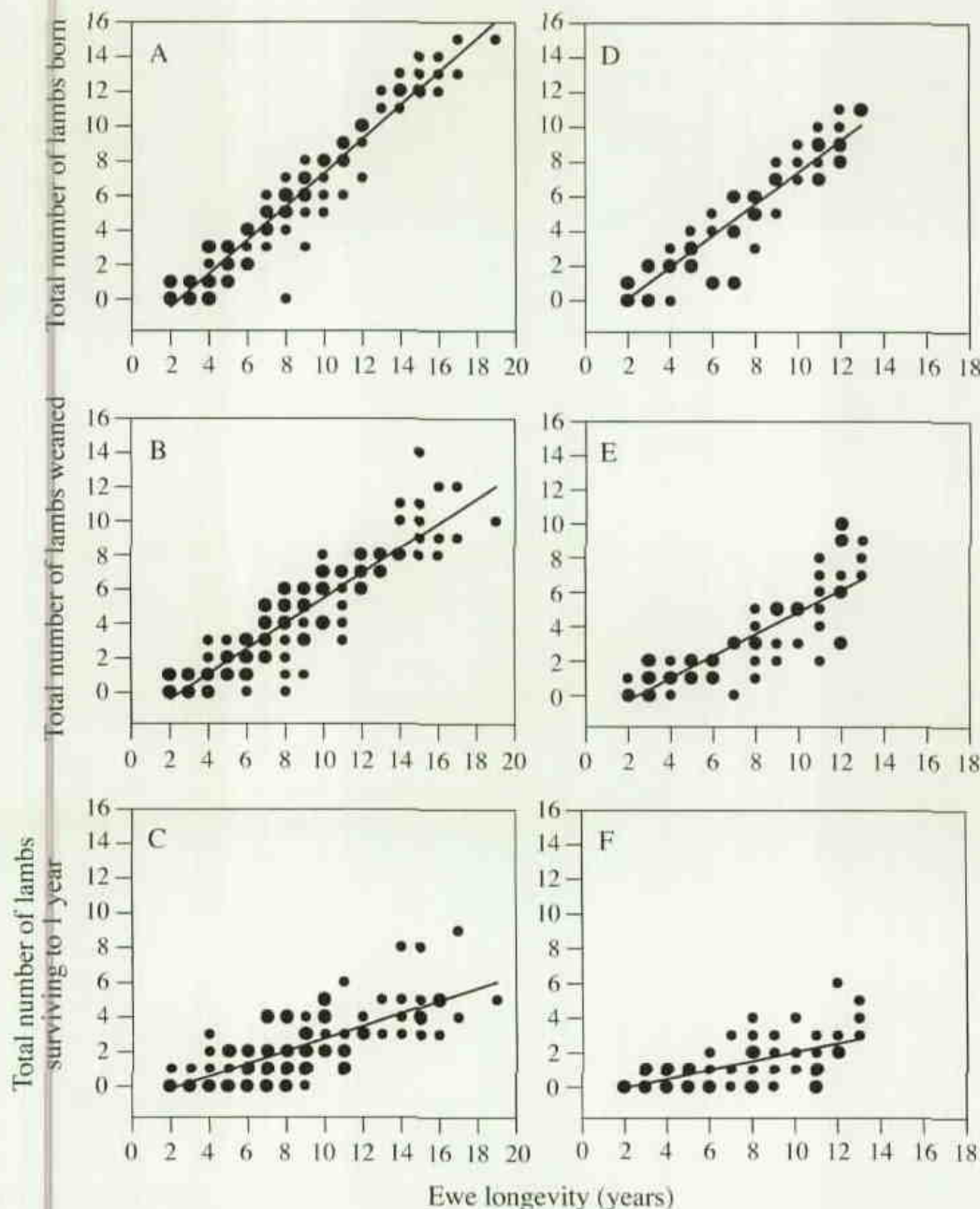


FIG. 6. Lifetime reproductive success for Ram Mountain ewes (A–C) and Sheep River ewes (D–F), measured as the number of offspring produced, weaned, and surviving to 1 yr of age, according to longevity. Small points refer to single observations, large points to two or more overlapping observations: 118 ewes were sampled for graphs A–C, and 66 ewes for D–F.

et al. 1993). If the capacity to absorb mass fluctuations varies according to size, mass loss (during winter or during reproduction) may be more taxing for light than for heavy ewes. If heavier ewes were more capable of absorbing fluctuations in body fat stores, this could partly explain their longer life-spans.

Not only were long-lived ewes the only ones to show reproductive senescence, they also had superior reproductive success between the ages of 2 and 7 yr and higher lifetime success. Longevity is an important predictor of lifetime reproductive success in other large mammals (Clutton-Brock 1988, Le Boeuf and Reiter 1988). The potential therefore exists for natural selec-

tion to act on differences in individual quality through the inheritance of genetic factors that affect mass and life-span (Edney and Gilt 1968).

For both bighorn populations, long-lived ewes had been "good" rather than "poor" reproducers when young, and they were also reproductively successful when old. Positive phenotypic correlations between early and late reproduction have been reported for some insects and birds (Stearns 1992). The data on individual mass point to why we found positive correlations between life history traits; body mass is a useful measure of individual quality in this species. Mass by itself, however, is unlikely to fully explain the positive cor-

relations of reproductive success and longevity. The expression of individual quality could therefore depend on genotypes that code simultaneously for reproductive and longevity potential, in addition to a phenotypic association between mass and life-span (Dobson et al. 1999).

Compensatory selection, comparable to antagonistic pleiotropy, could explain the maintenance of polymorphism in a population of red deer (Pemberton et al. 1991). In bighorn ewes, body mass was associated with longevity, better survival of old ewes (Festa-Bianchet et al. 1997) and lower fitness costs of reproduction (Festa-Bianchet et al. 1998). Therefore, the considerable variation in individual body mass may suggest that there could be countervailing costs of heavy mass. So far, however, we have been unable to demonstrate any negative effects of mass for any sex-age class of bighorn sheep (Festa-Bianchet et al. 1995, 1997, 1998, Jorgenson et al. 1993a). For this species, it appears that large adult body mass, within the limits encountered in our study, always tends to confer a reproductive advantage. Although the survival of adult females in large mammals tends to be high and stable from year to year (Gaillard et al. 1998), populations of wild and feral sheep occasionally experience massive die-offs due to disease or starvation (Clutton-Brock et al. 1996, Jorgenson et al. 1997). It is possible that countervailing selection against large body mass may manifest itself under these circumstances, but no die-off occurred at Ram Mountain during our 27-yr study, and evidence from domestic sheep suggests that body mass increases the probability of survival during die-offs (Clutton-Brock et al. 1996). It is likely that much of the variation in individual body mass is environmental in origin; there is only a weak correlation between maternal mass and lamb mass at weaning (Festa-Bianchet and Jorgenson 1998), and the long period of mass gain (Festa-Bianchet et al. 1996) provides ample opportunities for factors such as food availability, parasites, and injuries to affect individual mass.

Our study revealed clear evidence of reproductive senescence, which appeared in Ram Mountain ewes aged ≥ 14 yr, through a decrease in lamb production that was significant also when body mass, population density, and previous reproductive success were accounted for. Senescent ewes, however, showed weaning success similar to that of younger ewes. At Sheep River, both lamb production and weaning success decreased for older ewes. Mass loss of old ewes appeared to be a consequence of continued investment in reproduction; these phenotypically superior individuals apparently used their superior mass as a buffer that allowed them to both continue reproducing and survive into old age. The loss of mass after age 10 likely reflected a decrease in lipid stores, although senescent ewes could also show some muscular mass loss, due to degenerative physiological processes (Medina 1996). For old ewes, a senescence-related mass decrease in June was

less obvious than the decrease in September mass. Ewes that lose much mass during winter could die and therefore not be present in samples of June mass; for senescent ewes, September mass affected the probability of overwinter survival (Festa-Bianchet et al. 1997). September mass estimates therefore seem to have more predictive power over variation in individual age-related condition than June mass estimates.

Body condition can influence several aspects of female reproduction. It acts notably on ovulation (Leader-Williams and Rosser 1983), the ability to conceive (Boyd 1984), and on offspring mass (Iverson et al. 1993, Atkinson and Ramsay 1995). For example, lamb production was positively related to maternal mass the preceding September, which is comparable to results found in other ungulates (Cameron et al. 1993). A reduction in body mass in senescent ewes could therefore contribute either to a disturbance in their hormonal cycles during the rut in autumn (decreasing their chances of conceiving) or to a reduction in their ability to complete gestation, bringing about the decrease in lamb production observed in old ewes.

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LITERATURE CITED

- Adelman, R. C., and G. S. Roth. 1982. Testing the theories of aging. CRC Press, Boca Raton, Florida, USA.
- Albon, S. D., B. Mitchell, and B. W. Staines. 1983. Fertility and body weight in female red deer: a density-dependent relationship. *Journal of Animal Ecology* 52:969-980.
- Atkinson, S. N., and M. A. Ramsay. 1995. The effects of prolonged fasting on the body composition and reproductive success of female Polar Bears (*Ursus maritimus*). *Functional Ecology* 9:559-567.
- Bérubé, C. H. 1997. Les stratégies d'adaptation vitale chez les brebis du mouflon d'Amérique (*Ovis canadensis*): la reproduction en fonction de l'âge. Dissertation, Université de Sherbrooke, Sherbrooke, Québec, Canada.
- Bérubé, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behavioral Ecology* 7:60-68.
- Boyd, I. L. 1984. The relationship between body condition and the timing of implantation in Grey seals (*Halichoerus grypus*). *Journal of Zoology* 203:113-123.

- Burnham, K. P., and E. A. Rexstad. 1993. Modeling heterogeneity in survival rates of banded waterfowl. *Biometrics* **49**:1194–1208.
- Byers, J. A. 1997. American Pronghorn. University of Chicago Press, Chicago, Illinois, USA.
- Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. *Canadian Journal of Zoology* **71**:480–486.
- Charlesworth, B. 1993. Evolutionary mechanisms of senescence. *Genetica* **91**:11–19.
- Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.
- Clutton-Brock, T. H., I. R. Stevenson, P. Marrow, A. D. MacColl, A. I. Houston, and J. M. McNamara. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. *Journal of Animal Ecology* **65**: 675–689.
- Dobson, F. S., T. S. Risch, and J. O. Murie. 1999. Increasing returns in the life history of Columbian ground squirrels. *Journal of Animal Ecology* **68**:73–86.
- Edney, E. B., and R. W. Gilt. 1968. Evolution of senescence and specific longevity. *Nature* **220**:281–282.
- Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* **214**:653–661.
- . 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). *Journal of Animal Ecology* **58**:785–795.
- . 1998. Condition-dependent reproductive success in bighorn ewes. *Ecology Letters* **1**:91–94.
- Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *American Naturalist* **152**:367–379.
- Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behavioral Ecology* **9**:144–150.
- Festa-Bianchet, M., J. T. Jorgenson, C. H. Bérubé, C. Portier, and W. D. Wishart. 1997. Body mass and survival of bighorn sheep. *Canadian Journal of Zoology* **75**:1372–1379.
- Festa-Bianchet, M., J. T. Jorgenson, W. J. King, K. G. Smith, and W. D. Wishart. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. *Canadian Journal of Zoology* **74**:330–342.
- Festa-Bianchet, M., J. T. Jorgenson, M. Lucherini, and W. D. Wishart. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. *Ecology* **76**:871–881.
- Fisher, R. A. 1958. The genetical theory of natural selection. Dover Publishing, New York, New York, USA.
- Forslund, P., and T. Pärt. 1995. Age and reproduction in birds. *Trends in Ecology and Evolution* **10**:374–378.
- Gaillard, J.-M., D. Allainé, D. Pontier, N. G. Yoccoz, and D. E. L. Promislow. 1994. Senescence in natural populations of mammals: a reanalysis. *Evolution* **48**:509–516.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* **13**:58–63.
- Gaillard, J.-M., A. J. Sempéré, J.-M. Boutin, G. Van Laere, and B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Canadian Journal of Zoology* **70**:1541–1545.
- Green, W. C. H. 1990. Reproductive effort and associated costs in bison (*Bison bison*): do older mothers try harder? *Behavioral Ecology* **1**:148–160.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* **12**:12–45.
- Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois, USA.
- Iverson, S. J., W. D. Bowen, D. J. Boness, and O. T. Oftedal. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiological Zoology* **66**:61–88.
- Jorgenson, J. T., M. Festa-Bianchet, J.-M. Gaillard, and W. D. Wishart. 1997. Effects of age, sex, disease and density on survival of bighorn sheep. *Ecology* **78**:1019–1032.
- Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993a. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. *Canadian Journal of Zoology* **71**:2509–2517.
- Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1993b. Harvesting bighorn ewes: consequences for population size and trophy ram production. *Journal of Wildlife Management* **57**:429–435.
- King, W. J., M. Festa-Bianchet, and S. E. Hatfield. 1991. Determinants of reproductive success in female Columbian ground squirrels. *Oecologia* **86**:528–534.
- Komdeur, J. 1996. Influence of age on reproductive performance in the Seychelles warbler. *Behavioral Ecology* **7**: 417–425.
- Leader-Williams, N., and A. M. Rosser. 1983. Ovarian characteristics and reproductive performance of reindeer, *Rangifer tarandus*. *Journal of Reproduction and Fertility* **67**: 247–256.
- Le Boeuf, B. J., and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. Pages 344–361 in T. H. Clutton-Brock, editor. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.
- Lessels, C. M. 1991. The evolution of life histories. Pages 32–68 in J. R. Krebs and N. B. Davies, editors. Behavioural ecology: an evolutionary approach. Blackwell Scientific Publications, Oxford, UK.
- Lunn, N. J., I. L. Boyd, and J. P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *Journal of Animal Ecology* **63**:827–840.
- Marrow, P., J. M. McNamara, A. I. Houston, I. R. Stevenson, and T. H. Clutton-Brock. 1996. State-dependent life history evolution in Soay sheep: dynamic modelling of reproductive scheduling. *Philosophical Transactions of the Royal Society of London B* **351**:17–32.
- McDonald, D. B., J. W. Fitzpatrick, and G. E. Woolfenden. 1996. Actuarial senescence and demographic heterogeneity in the Florida scrub jay. *Ecology* **77**:2373–2381.
- McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. *Nature* **380**:215–221.
- Medina, J. J. 1996. The clock of ages: why we age, how we age, winding back the clock. Cambridge University Press, Cambridge, UK.
- Mitchell, B., D. McCowan, and I. A. Nicholson. 1976. Annual cycles of body weight and condition in Scottish red deer. *Journal of Zoology* **180**:107–127.
- Morris, D. W. 1996. State-dependent life histories, Mountford's hypothesis, and the evolution of brood size. *Journal of Animal Ecology* **65**:43–51.
- Nelson, M. E., and L. D. Mech. 1990. Weights, productivity, and mortality of old white-tailed deer. *Journal of Mammalogy* **71**:689–691.
- Newton, I., and P. Rothery. 1997. Senescence and reproductive value in sparrowhawks. *Ecology* **78**:1000–1008.
- Norusis, M. J. 1994. SPSS Advanced statistics version 6.1. SPSS, Chicago, Illinois, USA.
- Paul, A., J. Kuester, and D. Podzuweit. 1993. Reproductive

- senescence and terminal investment in female barbary macaques (*Macaca sylvanus*) at Salem. *International Journal of Primatology* **14**:105-124.
- Pemberton, J. M., S. D. Albon, F. E. Guinness, and T. H. Clutton-Brock. 1991. Countervailing selection in different fitness components in female red deer. *Evolution* **45**:93-103.
- Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology* **245**:271-278.
- Promislow, D. E. L. 1991. Senescence in natural populations of mammals: a comparative study. *Evolution* **45**:1869-1887.
- Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology* **220**:417-437.
- Prothero, J., and K. D. Jürgens. 1987. Scaling of maximum life-span in mammals: a review. *Basic Life Sciences* **42**:49-74.
- Rose, M. R. 1983. Theories of life-history evolution. *American Zoologist* **23**:15-23.
- . 1991. *Evolutionary biology of aging*. Oxford University Press, New York, New York, USA.
- Sæther, B.-E., and H. Haagenrud. 1983. Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. *Journal of Mammalogy* **64**:226-237.
- Skogland, T. 1988. Tooth wear by food limitation and its life history consequences in wild reindeer. *Oikos* **51**:238-242.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Sugiyama, Y. 1994. Age-specific birth rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. *American Journal of Primatology* **32**:311-318.
- Sydeman, W. J., H. R. Huber, S. D. Emslie, C. A. Ribic, and N. Nur. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. *Ecology* **72**:2204-2217.
- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* **128**:137-142.
- Vaupel, J. M., and A. I. Yashin. 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. *The American Statistician* **39**:176-185.
- Wauters, L., and A. A. Dhondt. 1989. Body weight, longevity and reproductive success in red squirrels (*Sciurus vulgaris*). *Journal of Animal Ecology* **58**:637-651.
- Wauters, L. A., and A. A. Dhondt. 1995. Lifetime reproductive success and its correlates in female Eurasian red squirrels. *Oikos* **72**:402-410.
- Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**:398-411.
- Wolfe, L. D., and M. J. S. Noyes. 1981. Reproductive senescence among female Japanese macaques (*Macaca fuscata fuscata*). *Journal of Mammalogy* **62**:698-705.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.