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Age–related reproductive effort in bighorn sheep ewes[1]

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Abstract: The "terminal investment" hypothesis predicts that reproductive effort should increase with age as life expectancy, and therefore residual reproductive potential, decreases. Several studies, however, have found that reproductive success decreases with age because of senescence. We monitored the age–specific reproductive success of individually marked bighorn sheep ewes at Sheep River, Alberta, from 1982 to 2006. Lamb production increased from 2 to 4 y of age, then remained at approximately 88% until age 13 y, when it began to decline. Lamb survival was higher for ewes aged 4 to 12 y than for ewes aged 2 or 3 y. Reproductive senescence began at 13 y of age but was restricted to a decrease in lamb production. There were no differences in lamb survival between prime–aged and older ewes. The onset of reproductive senescence is about 5 y later than the onset of survival senescence. Positive correlations between reproductive success before 9 y of age and longevity, and between reproductive success before and after 9 y of age, suggest that ewes that survived to the onset of reproductive senescence were mostly of high phenotypic quality. Our data provide no clear support for the terminal investment hypothesis. Future tests of this hypothesis should account for individual heterogeneity in phenotypic quality.
Keywords: age–specific reproduction, bighorn sheep, recruitment, senescence, terminal investment.

Résumé : L'hypothèse de « l'investissement terminal » prédit que l'effort reproducteur devrait augmenter avec l'âge puisque l'espérance de vie et donc le potentiel reproductif résiduel diminuent. Plusieurs études ont cependant trouvé que le succès reproducteur diminue avec l'âge à cause de la sénescence. Nous avons suivi le succès reproducteur en fonction de l'âge chez des brebis du mouflon d'Amérique marquées individuellement à Sheep River en Alberta de 1982 à 2006. La production d'agneaux augmentait entre 2 et 4 ans et demeurait ensuite à approximativement 88% jusqu'à l'âge de 13 ans où elle commençait à décliner. La survie des agneaux était plus élevée pour les brebis âgées de 4 à 12 ans que pour celles âgées de 2 ou 3 ans. La sénescence reproductive commençait à 13 ans mais se limitait à une diminution de la production d'agneaux. Il n'y avait pas de différences dans la survie des agneaux entre les brebis dans la force de l'âge et celles plus vieilles. Le début de la sénescence reproductive se produit environ 5 ans après le début de la sénescence de la survie. Des corrélations positives entre le succès reproducteur avant l'âge de 9 ans et la longévité et entre le succès reproducteur avant et après l'âge de 9 ans suggèrent que les brebis qui ont survécu après le début de la sénescence reproductive était principalement de haute qualité phénotypique. Nos données ne supportent pas l'hypothèse de l'investissement terminal. Les tests futurs concernant cette hypothèse devrait tenir compte de l'hétérogénéité individuelle dans la qualité phénotypique.
Mots-clés : investissement terminal, mouflon d'Amérique, recrutement, reproduction en fonction de l'âge, sénescence.

Nomenclature: Bamfield, 1974.

Introduction

Life–history theory predicts that in iteroparous organisms, maternal effort should increase as residual reproductive value decreases, because the fitness cost of increased effort should decrease as effort–independent survival probability decreases (Pianka & Parker, 1975). Alternatively, older females may be unable to provide adequate maternal care due to the physiological deterioration brought about by senescence (Ericsson *et al.,* 2001). Female ungulates are highly iteroparous, have a long life expectancy after sexual maturity, and show clear evidence of survival senescence (Loison *et al.,* 1999; Gaillard *et al.,* 2000a). Ungulates, therefore, have frequently been used as model species to test evolutionary theories of senescence, with some studies supporting the "terminal investment" hypothesis of increased maternal effort as females age (Clutton–Brock, 1984; Ericsson *et al.,* 2001) and others providing evidence of a physiological decline in females' ability to reproduce (Bérubé, Festa–Bianchet & Jorgenson, 1999; Mysterud *et al.,* 2002). Recent studies have also shown that individuals of high phenotypic quality are more likely to survive to the age at which the effects of senescence become apparent (Bérubé, Festa–Bianchet & Jorgenson, 1999; Gaillard *et al.,* 2000b). It is therefore likely that the onset of senescence varies among individuals according to phenotypic quality and possibly genotype (von Hardenberg *et al.,* 2004).

Although survival senescence has been repeatedly documented in female ungulates (Loison *et al.,* 1999), fewer studies have obtained data on age–specific patterns of reproductive effort, particularly in terms of the ability of parturient mothers of different ages to ensure survival

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of offspring. In bighorn sheep (*Ovis canadensis*), Bérubé, Festa–Bianchet, and Jorgenson (1999) reported that ewe fecundity increased from 2 (the minimum age of primiparity) to 5 y of age, was stable from 5 to 12 y, then declined each year, such that ewes aged 18 y and older appeared no longer to be able to reproduce. Because of survival senescence, however, very few ewes survive past 15 y of age. In red deer (*Cervus elaphus*), calf production also follows a bell–shaped curve (Clutton–Brock, 1984). Bérubé, Festa–Bianchet, and Jorgenson (1999), however, found no maternal age effect on lamb survival, possibly due to a complex relationship between ewe age structure, population density, and age of primiparity in their study population (Festa–Bianchet *et al.,* 1995; Festa–Bianchet, Gaillard & Côté, 2003).

Here we examine age–specific reproduction of bighorn sheep ewes in a population that showed no clear density–dependence but was affected by pneumonia epizootics and cougar predation over a period of 26 y (Festa–Bianchet, 1988a; Festa–Bianchet *et al.,* 2006). We monitored both lamb production and survival according to maternal age to test for the occurrence of survival senescence and terminal reproductive effort. The terminal investment hypothesis predicts that as ewes become older and their survival probability decreases, lamb production should decline (because ewes are physically debilitated by senescence) and lamb survival should improve (because ewes make a greater maternal effort to ensure survival of what may be their last lamb). We also compared reproductive success early and later in life for individual ewes that survived to old age. A negative correlation would suggest a fitness trade–off (Sydeman *et al.,* 1991), while a positive correlation would suggest the occurrence of strong and consistent differences in individual phenotypic quality (Bérubé, 1997; Bérubé, Festa–Bianchet & Jorgenson, 1999; Gaillard *et al.,* 2000b).

For bighorn studied elsewhere, reproductive senescence began at 13 y of age (Bérubé, Festa–Bianchet & Jorgenson, 1999), even though survival senescence began at 8 y of age (Loison *et al.,* 1999) and senescence–related mass loss began at approximately 11 y of age (Bérubé, Festa–Bianchet & Jorgenson, 1999). We therefore expected to see evidence of reproductive senescence for ewes aged 13 y and older.

Study population and methods

We analyzed data collected from the Sheep River bighorn sheep population from 1982 to 2006. The study population is in southwestern Alberta, Canada, and by 1982 over 80% of the resident ewes were individually marked with ear tags. A few unmarked ewes were present in the first 3 y of this study, but all resident ewes have been identified since 1985. Between 1982 and 1988, approximately 70—80% of the lambs were caught and marked with ear tags in the autumn, in time to identify their mother through behavioural observations of suckling and close associations. From 1989 onward, all lambs surviving to weaning (October) have been captured and marked, with the exception of 1996 when capture operations were stopped when 60% of the lambs had been marked and 2002—2005 when a change in seasonal area use led to some lambs (about 10—20% a year) not being in the winter range (and therefore inaccessible for capture) in autumn.

Both ewes and lambs were captured by free–range darting using either xylazine (Rompun) or a mixture of ketamine and xylazine (Festa–Bianchet & Jorgenson, 1985; Jorgenson, Samson & Festa–Bianchet, 1990; 1991). After the first few years of the study, the vast majority of females were captured and tagged as lambs or yearlings. We monitored reproductive effort by first checking for lactation in the few days before ewes left the winter range to give birth in the alpine range approximately 12–15 km to the west (Festa–Bianchet, 1988b). We then searched both the winter and the alpine ranges from late May to September and determined which ewes were accompanied by lambs through behavioural observations of suckling.

Our measures of fecundity (the proportion of ewes known to be lactating) are likely conservative, because some ewes may have been pregnant without visibly swollen udders and could have given birth to lambs that died before we saw them. We believe this underestimate to be minimal, because we checked the lactation status of all ewes we saw in summer and in several cases, ewes whose lambs had died retained visibly swollen udders for several days or weeks. We also have no reason to believe that estimates of fecundity were biased according to ewe age. The calculation of fecundity excluded 40 ewe–y (3.8% of the 1046 ewe–y of available data) where ewes of unknown lactation status were not seen until October, when they were not accompanied by a lamb.

For calculations of age–specific reproduction, we used all ewes of known age (*i.e.,* first captured when aged 3 y or less) during all years of the study. We also created a group of ewes aged 13 y and older, including ewes of known age and ewes that were marked as adults older than 3 y, with minimum age estimated from horn annuli (Geist, 1966). This group of ewes aged at least 13 y provided us with an additional 66 ewe–y of monitoring. For comparisons of reproductive success early and late in life, we included only ewes of known age with complete lifetime reproductive histories that were born before 1995 and had either died or were aged 11 y and older by May 2006. This sample included 92 ewes, of which 39 survived to 10 y of age. These 92 ewes produced 569 offspring and weaned 382 lambs during our study.

Because we monitored unmarked lambs through associations with marked mothers, we had complete data on survival to weaning (October) for all ewes each year. To monitor lamb survival to 1 y, however, we needed to mark the lamb, since mother–lamb associations weakened during winter and yearlings generally did not associate with their mothers (Festa–Bianchet, 1991). In a few cases, mostly in the earlier years of the study, we knew the lamb had survived to weaning but we were unable to capture it. Simply removing those unmarked lambs from analyses would have negatively biased conclusions regarding lamb survival to 1 y, because they had survived to at least November (or later, as suckles were occasionally seen in winter), and their survival from birth to 1 y was therefore higher than the average for all lambs. Consequently, we assigned to ewes with unmarked lambs a fraction of reproductive success equal to the mean survival of all lambs in the population that year from the time of the last identification of her

lamb through behavioural association to the following May. This procedure decreased individual heterogeneity in lamb survival, but was only applied to 24 lambs for calculations of age–specific reproduction (3.1% of 771 lambs born) and to 13 lambs of ewes of known age with complete lifetime monitoring (2.3% of lambs born and 3.4% of lambs weaned).

We used nonparametric correlations to test whether the survival (to weaning and to 1 y) of lambs produced by the same ewe up to and after 9 y of age were correlated. We then tested whether each ewe's longevity was associated with the average survival to weaning of lambs she had produced up to 9 y of age. We first performed this test for ewes that had survived to at least 10 y, then for all ewes with known lifetime reproductive success. All probability values are two–tailed.

Results

There were strong age effects on lamb production, and somewhat weaker but similar effects of age on lamb survival. There were 3 age groups of ewes with differing levels of reproductive success: young ewes aged 2 or 3 y, prime–aged ewes aged 4–12 y, and senescent ewes aged 13 y and older. Ewes aged 2 or 3 y were less likely to be lactating than ewes aged 4 to 12 y (Figure 1; $\chi^2 = 170.05$, $P < 0.0001$), and the probability of lactation decreased after age 12 (Figure 1; $\chi^2 = 18.82$, $P = 0.0001$). Only one of three 17–y–old and none of two 18–y–old ewes produced lambs. An increase in lamb survival to both weaning and 1 y was evident as mothers aged from 2–3 y to prime age (comparing young and prime–aged ewes, survival to weaning: $\chi^2 = 12.62$, $P = 0.0004$; survival to 1 y: $\chi^2 = 6.55$, $P = 0.01$; 1 df in both cases). Lambs born to ewes older than 12 y had similar or higher survival than lambs born to prime–aged ewes (Figure 1 and Table I), but the difference was not significant (comparing old and prime–aged ewes, $\chi^2 < 0.9$, $P > 0.34$ for both survival to weaning and to 1 y). Because of their lower lamb production, ewes aged 13 y and older appeared slightly less likely than prime–aged ewes to recruit a yearling into the population the following year (Table I), but the difference was not significant ($\chi^2 = 0.22$, $P = 0.63$).

Comparisons of reproductive success early and late in life, and of reproductive success and longevity, generally suggested positive correlations between components of lifetime reproductive success. For ewes of known age that survived to at least 10 y, the average survival of lambs produced up to and after age 9 appeared to be weakly but positively correlated (lamb survival to weaning: $rs = 0.25$, $n = 37$, $P = 0.13$; survival to 1 y: $rs = 0.32$, $n = 38$, $P = 0.050$). The survival of lambs produced up to 9 y of age, however, was not significantly correlated with longevity for ewes surviving to at least 10 y of age (correlation of average lamb survival to weaning and ewe longevity: $rs = 0.032$, $n = 39$, $P = 0.85$; correlation of average lamb survival to 1 y and ewe longevity: $rs = 0.135$, $n = 39$, $P = 0.13$). For all ewes ($n = 92$) with known lifetime reproductive success, the correlations between average survival of lambs produced up to 9 y and longevity were positive and significant (survival to weaning: $rs = 0.26$, $P = 0.013$; survival to 1 y: $rs = 0.21$, $P = 0.042$). Although the results were not significant, comparing the average survival of lambs produced when aged 10 y and older to ewe longevity suggested that ewes that lived longer appeared to be better at weaning lambs as old adults ($rs = 0.31$, $n = 37$, $P = 0.064$) and the lambs they produced when aged 10 y or older seemed more likely to survive to 1 y of age ($rs = 0.29$, $n = 37$, $P = 0.078$).

Discussion

Bighorn sheep ewes in the Sheep River population underwent reproductive senescence beginning at about 13 y of age, but did not appear to increase maternal effort late in life as predicted by the terminal investment hypothesis. Instead, and similarly to results obtained in the Ram Mountain population of bighorn sheep and for roe deer

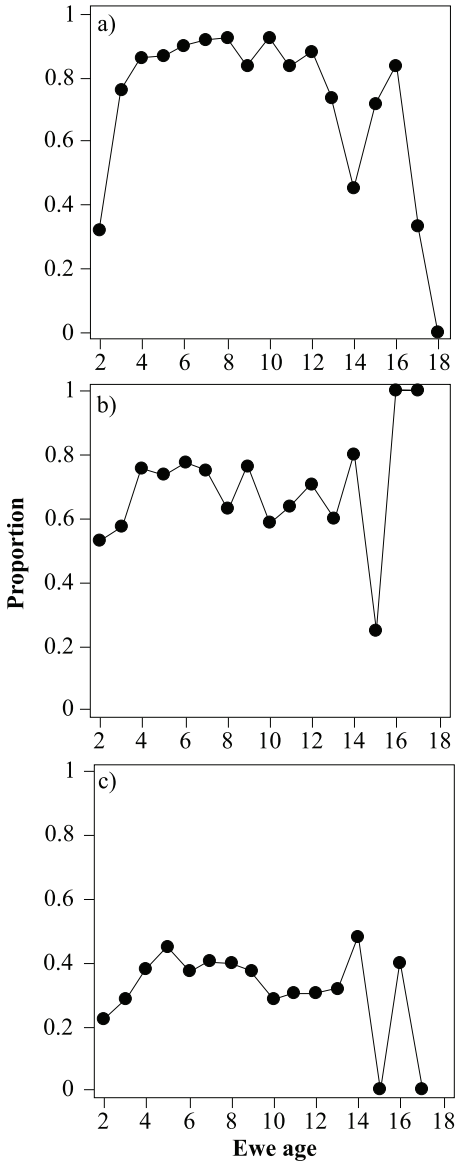

FIGURE 1. The proportion of ewes known to have produced a lamb (a), of lambs surviving to weaning (October) (b), and of lambs surviving to 1 y of age (c) at Sheep River, Alberta, Canada, according to ewe age in years, 1982 to 2006.

TABLE I. Age–specific reproduction by bighorn ewes at Sheep River, Alberta, Canada, from 1982 to 2006. Sample sizes (number of ewe–y) are in parentheses. "Lactation" refers to the proportion of ewes of each age class known to have given birth to a lamb. "Weaning" and "Lamb survival to 1 y" refer to the proportion of lambs born to mothers of each age group that survived to weaning (October) and to 1 y of age. "Yearling recruitment" refers to the proportion of ewes in each age class that led to a yearling sheep recruited into the population the following year. The category "13+" includes all ewes known to be aged at least 13 y, while the other 2 age groups include only ewes whose exact age (in years) was known.

Ewe age	Lactation	Weaning	Lamb survival to 1 y	Yearling recruitment
2–3	0.528 (260)	0.562 (137)	0.265 (141)	0.139 (268)
4–12	0.883 (640)	0.719 (572)	0.378 (464)	0.328 (650)
13+	0.758 (62)	0.725 (51)	0.437 (47)	0.294 (70)

(Bérubé, Festa–Bianchet & Jorgenson, 1999; Gaillard *et al.,* 2000b), it appears that only high–quality individuals survived to the age when reproductive senescence became evident. Consequently, we suggest that the terminal investment hypothesis can only be tested by accounting for individual differences in quality. One cannot simply compare the average reproductive output of ewes of different ages because the average quality of surviving females appears to increase with age.

Ewes aged 2 or 3 y were less likely to produce lambs than prime–aged ewes (aged 4 to 12 y), and their lambs suffered heavier mortality than those born to older ewes. These results were expected given the smaller mass of young ewes (especially 2–y–olds) compared to prime–aged ewes (Festa–Bianchet *et al.,* 1996). Ewes aged 2 or 3 y have not yet completed their own body growth, and it may be more difficult for them than for older ewes to provide sufficient resources for their lambs. In addition, prime–aged ewes may have higher reproductive success than young ewes due to their greater maternal experience (Ozoga & Verme, 1986; Cameron *et al.,* 2000; Georges & Guinet, 2000).

The overall pattern of age–specific reproduction that we documented was very similar to that reported for other female ungulates, with an increase in production following primiparity and a decline at the very advanced age of 13 y and older (Festa–Bianchet, Urquhart & Smith, 1994; Adams & Dale, 1998; Bérubé, Festa–Bianchet & Jorgenson, 1999; Ericsson *et al.,* 2001). It therefore appears that in most ungulates the onset of reproductive senescence occurs a few years later than survival senescence, which typically begins at 8–10 y of age (Loison *et al.,* 1999; Catchpole *et al.,* 2004). Similar patterns, with a strong "individual quality" effect, have also been reported for pinnipeds (Beauplet *et al.,* 2006) and sciurids (Broussard *et al.,* 2005).

Although we found little support for the terminal investment hypothesis, a proper test would require information on body condition of individual females and size of their offspring in addition to data on offspring production and survival. It is likely that the body condition of ewes older than 12 y was declining: by that age their survival rate is only about 60% (as opposed to about 92% for ewes aged 2–7 y; Loison *et al.,* 1999), and older ewes tend to lose mass from one year to the next (Bérubé, Festa–Bianchet & Jorgenson, 1999). Thus, the fact that the survival of lambs produced by ewes of this age was similar to that of lambs produced by prime–aged ewes could be evidence of increased maternal effort in the face of senescence in maternal quality. On the other hand, the positive correlation between reproductive success early in life and longevity strongly suggests that senescent ewes were not a random sample of all ewes, but that they were mostly of high phenotypic quality. Senescent ewes may therefore have been better mothers at any age, as also indicated by the positive correlation in individual reproductive success before and after age 9. Possibly, ewes for which senescence had strong effects were both less likely to reproduce and less likely to survive. This situation was reported for the Ram Mountain population, where old non–lactating ewes showed density–dependent survival, while the survival of old lactating ewes was independent of population density (Festa–Bianchet, Gaillard & Jorgenson, 1998). Clearly, the study of senescence as an evolutionary phenomenon and the study of the impact of senescence on population dynamics require different approaches.

If survival and reproductive success of old ewes are both correlated with individual quality, it would be very difficult to test the terminal investment hypothesis with observational data, since poor–quality ewes that make little reproductive effort (or none at all) would still suffer increased mortality because of physiological senescence. Ewes that are still in good body condition despite their advanced age, on the other hand, should not be selected to increase reproductive effort if that was to compromise their probability to survive to reproduce again. Even at 12–14 y of age, these ewes may have an additional 2 to 3 remaining reproductive opportunities. Because lamb survival is much lower and more variable than maternal survival (Gaillard *et al.,* 2000a), the reproductive value of high–quality old mothers may remain higher than that of their offspring.

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