LETTER

Age-independent and age-dependent decreases in reproduction of females

Julien G. A. Martin[1,2]* and Marco Festa-Bianchet[1,2]

[1]Département de biologie, Université de Sherbrooke, Sherbrooke, Québec, Canada

[2]Centre d'études nordiques, Université Laval, Québec, Canada

*Correspondence: E-mail: julien.martin2@usherbrooke.ca

Abstract

The terminal allocation and senescence hypotheses make opposite predictions about how age-specific reproductive effort should vary during old age. There is empirical support for both hypotheses, although reports on senescence are more numerous. Individual heterogeneity and selective mortality, however, decrease our ability to measure how reproductive effort varies during late life. The damage accumulation model proposes that terminal allocation and senescence could be partly age-independent. Using a reverse-age approach, we analysed an unusually complete record of annual reproductive success for 90 bighorn ewes that died between 7 and 18 years of age. We estimated age-specific and age-independent variation of reproductive effort in late-life. Reproductive effort decreased in the two last reproductions, independently of age at death. Fecundity also decreased in the last 2 years of life, with a steeper decline for older individuals. Our study reveals that reproductive senescence includes both age-dependent and age-independent components.

INTRODUCTION

Age-specific variation in reproductive effort, the proportion of available energy that is devoted to reproduction (Clutton-Brock 1991), can affect population dynamics, and is a key component of the evolution of reproductive tactics. The identification of the causes of that variation is therefore fundamental to our understanding of the ecology and evolution of iteroparous species (Rose 1991; Roff 2002). Life-history theory predicts that mothers should invest more in reproduction as they age, because the fitness costs of reproduction decrease as residual reproductive value decreases (Hirshfield & Tinkle 1975; Pianka & Parker 1975). However, empirical support for this 'terminal investment' hypothesis is limited (Clutton-Brock 1984; Ericsson *et al.* 2001; Morrow *et al.* 2003; Velando *et al.* 2006). Reproductive senescence could mask the increase in reproductive effort that is expected with terminal investment (Hirshfield & Tinkle 1975). According to the senescence hypothesis, older females have fewer resources to allocate to reproduction due to physiological deterioration with ageing (Rose 1991; Kirkwood & Austad 2000). Although decreases in survival probability with age, known as actuarial senescence, are well documented, we know little about changes in reproductive effort at the end of life (Monaghan *et al.* 2008).

The terminal investment hypothesis predicts an increase in reproductive effort with age, leading to higher fitness costs of reproduction (Pianka & Parker 1975). Behavioural changes with age (Cameron *et al.* 2000) or reproductive experience (Weladji *et al.* 2008), however, may allow females to increase reproductive effort as they age without increasing fitness costs. Following Weladji *et al.* (2010), we refer to an increase of reproductive effort in late-life as terminal allocation.

The senescence and terminal allocation hypotheses have been mostly evaluated using an age-specific approach (Pianka & Parker 1975; Kirkwood & Austad 2000). Ricklefs (2000, 2008) and McNamara *et al.* (2009), however, proposed that lifespan is not limited by time *per se*, but by physical deterioration over time, which can vary among individuals. An individual dies when accumulated damage attains a threshold. Therefore, senescence and terminal allocation processes could depend upon the rate of damage accumulation and not upon age. 'Time to death' (age at death minus age) is more informative than age itself as a metric that considers variability in damage accumulation among individuals. Instead of considering how reproductive effort varies with age, senescence and terminal allocation can be quantified according to an individual's 'time to death'. The model developed by McNamara *et al.* (2009) predicts either age-independent senescence (decreasing reproductive effort in late-life), age-independent terminal allocation (increasing reproductive effort in late-life) or no variation in reproductive effort depending on the relationships between reproductive effort, damage accumulation, and instantaneous mortality.

The 'damage accumulation' hypothesis (Ricklefs 2000; McNamara *et al.* 2009) predicts that both senescence and terminal allocation are age-independent, so that all individuals should show similar changes in reproductive effort in late-life. In contrast, both the 'mutation accumulation' (Medawar 1952) and the 'antagonistic pleiotropy' (Williams 1957) theories of senescence predict an age effect, at least at older ages. The mutation accumulation theory suggests that senescence is induced by an accumulation of deleterious mutations over time due to a decrease of selection pressure at older ages. Senescence could thus involve both age-dependent and age-independent processes.

The reverse-age approach offers several advantages in the study of late-life variation in reproductive effort. In addition to assessing how damage accumulation may affect changes in effort, it can also partly account for individual heterogeneity in reproductive potential and changes in the composition of successive age-classes through selective disappearance of individuals with greater frailty (Forslund & Pärt 1995; Service 2000). If reproductive potential is correlated with age at death, poor reproducers will progressively disappear from a cohort

over time, such that the oldest age classes will contain more individuals with high reproductive potential. As selective mortality would lead to an increase in average reproductive success with age, to evaluate terminal allocation or senescence, one cannot simply compare the average reproductive output of females of different ages (Nussey *et al.* 2008). The reverse-age approach partly avoids the problem of selective disappearance because all individuals, independently of their phenotype, have a last year of life.

On the basis of a long-term study of marked bighorn sheep (*Ovis canadensis*), we examined variation in both female reproductive effort and female fecundity during late life. We did not evaluate fitness costs and thus tested for senescence and terminal allocation, but not for terminal investment. Using a reverse-age approach, we estimated both age-dependent and age-independent variation in late-life reproduction. To assess changes in reproductive effort, we investigated variation in summer mass gain of mothers and lambs. We considered that maternal mass gain reflected energy allocation to maintenance and survival, and lamb summer mass gain corrected for maternal mass at birth and maternal summer mass gain estimated reproductive effort (Martin & Festa-Bianchet 2010). On the basis of previous studies of senescence (Bérubé *et al.* 1999; Festa-Bianchet & King 2007) and reproductive tactics (Martin & Festa-Bianchet 2010) in bighorn sheep, we predicted that ewes would maintain their mass gain in summer, but decrease reproductive effort as they approach death. As reproductive senescence at the population level had not been reported before 13 years of age (Bérubé *et al.* 1999), we also predicted that senescence would vary with age at death: individuals dying before 13 years should show little decline in either reproductive effort or fecundity in late life, whereas older ones should show a steep decline.

MATERIAL AND METHODS

Since 1971, bighorn sheep on Ram Mountain (52°8′ N, 115°8′ W, elevation 1082–2173 m), Alberta, Canada, have been captured several times each summer in a corral trap baited with salt (Jorgenson *et al.* 1993b). Most sheep are first caught as lambs, and marked with collars and ear tags. Over 97% of ewes born since 1975 were first captured as lambs or yearlings. At each capture, we recorded body mass (kg), and examined the udder to classify ewes as lactating or not and to determine yearly fecundity. Lamb–ewe matches were established through repeated observations of suckling. Yearly individual reproductive success was measured by lamb survival till September 15th, the approximate time of weaning (Festa-Bianchet 1988). As resighting rate of adult females at Ram Mountain is over 99%, estimates of age at death based on last year of observation are accurate. Females that were culled (*n* = 36; Jorgenson *et al.* 1993a) or died during trapping (*n* = 2) were not considered in the analysis. Age at last reproduction was defined as the oldest age at which a female weaned a lamb. Years to last reproduction and years before death were then backdated, with year zero indicating last reproduction or last year of life depending on the analysis.

Bighorn sheep gain mass during summer and lose mass during winter (Festa-Bianchet *et al.* 1996). Using repeated measurements of the same individual each summer, we adjusted body mass to spring (June 5 for adults, June 15 for lambs because some lambs were born in early June) and fall (September 15) for each sheep. We used linear mixed models with a REML method to adjust mass by fitting it as a function of date, with 25 May as day 1 (Pelletier *et al.* 2007; Martin and Pelletier 2011). Lambs gained mass linearly during summer. A square

root transformation of date linearized the relationship between mass and date for adult ewes (Festa-Bianchet *et al.* 1996). We included individual identity and the interaction between identity and date as random effects. We fitted separate linear mixed models for each year and used the predicted values of individual intercepts and slopes (provided by BLUPs) to adjust individual mass (Martin & Pelletier 2011). Summer mass gain was the difference between mass in September and in June. On average, ewes and lambs weighed 3.8 (range: 2–6 because we excluded the few individuals that were only caught once) times per summer, providing accurate mass estimates for each individual (Martin & Pelletier 2011). Variance around mass estimates was similar for all individuals with at least three measures of mass over summer, but was higher for individuals with only two observations. Each year, less than 20% of individuals (range 0–20%) were only weighed twice. No individuals were consistently trapped only twice per year, and number of trapping events per individual was independent of age and of years to death.

Following Martin & Festa-Bianchet (2010), reproductive effort was measured as lamb summer mass gain corrected for maternal mass in June and maternal mass gain during summer. For a given mass in June and a given mass gain in summer, a female with a fast-growing lamb would allocate more energy to reproduction than one with a slow-growing lamb. Reproductive effort is positively related to lamb survival for 1 year, but does not affect maternal survival (Martin & Festa-Bianchet 2010). We used the number of adult females (≥ 2 years old) in June each year as an index of density (Festa-Bianchet & Jorgenson 1998). Similar to Pelletier *et al.* (2007), we also considered two periods of contrasting environment, defined according to population trajectory and lamb survival. Until 1989, the population was increasing and lamb survival was high and stable. After 1989, the population declined and lamb survival was low and variable, following an apparent deterioration of environmental conditions.

To avoid the problem of selective disappearance, we included only ewes born before 1998, for which the cohort was totally extinct except for three 13 years old females in 2009. To avoid problems associated with selective appearance, as primiparity varies from 2 to 6 years, and with trade-offs between growth and reproduction among young ewes, we excluded individuals younger than 7 years. Age at death of ewes included in the analysis varied between 7 and 19 years with a mean of 12 years. For all analyses, we used mixed models, which correct for pseudoreplication problems due to repeated measures and measure the amount of individual variation.

To evaluate how maternal summer mass gain and reproductive effort vary at the end of reproductive life, we fitted number of years to last reproduction, age and their interactions as fixed effects. A significant effect of number of years to last reproduction would indicate an age-independent effect at the end of life. A significant interaction between number of years to last reproduction and age would indicate that the age-independent effect varies with age. Following Martin & Festa-Bianchet (2010), we also included as fixed effects maternal mass in June in analyses of maternal summer mass gain, and lamb sex, study period, density, maternal mass gain, maternal mass in June and maternal previous reproductive success when analysing lamb summer mass gain. We fitted year, individual identity and individual identity * years to last reproduction as random effects. The interaction between identity and years to last reproduction allows testing for individual differences in trait variation in late-life. Models of summer mass gain and of reproductive effort used the same dataset to allow comparison between models.

To assess how fecundity varied at the end of life and with age, we fitted a logistic mixed model with fecundity (a binomial variable as litter size is fixed at one) as a function of years before death, age and their interactions. To correct for potential environmental effects, we also included as fixed effects ewe mass in June, study period and density. We included year, ewe identity and identity * years before death interaction as random effects.

Following Whittingham *et al.* (2006), we reported full models including non significant fixed effects terms, but excluding non significant interactions. Models limited to significant effects provided similar results. Significance of random effects was assessed by a log-likelihood ratio test comparing models with and without random effects (Pinheiro & Bates 2000). Statistical analyses used R 2.10.0 (R Development Core Team, 2010). Mixed models were fitted using an REML maximization with the 'lmer' function from 'lme4' package that allows for unbalanced dataset (Bates *et al.* 2008).

RESULTS

Maternal summer mass gain was independent of the number of years before last reproduction, age (Table 1) or their interaction ($F_{3,90} = 1.03$, $P = 0.38$; Fig. 1a–d). Reproductive effort was independent of both age and its interaction with years to last reproduction ($F_{3,90} = 1.76$, $P = 0.16$), but decreased with years to last reproduction (Table 2, Fig. 1e–f), suggesting age-independent senescence. Ewes decreased reproductive effort by 3% (0.5 kg of lamb mass gain) during their penultimate reproduction and by 7% (1.2 kg of lamb mass gain) in their last reproduction (Table 2). Others significant effects (Tables 1 and 2) were as reported by Martin & Festa-Bianchet (2010): females that were heavy in June gained less mass over the summer (Table 1), male lambs gained more mass than female lambs, maternal and lamb mass gain were positively correlated, and previous reproductive success decreased lamb mass gain (Table 2).

Year explained some variation in summer mass gain and reproductive effort, but maternal identity had a significant effect only on reproductive effort (Tables 1 and 2). The interaction between years before last reproduction and ewe identity affected neither maternal mass gain ($\chi^2_9 = 8.29$, $P = 0.505$) nor reproductive effort ($\chi^2_9 = 13.86$, $P = 0.127$).

Table 1 Estimates of effects on summer mass gain of bighorn ewes aged 7 years and older at Ram Mountain, Alberta. Parameters with a significant effect are in bold. Mixed model analysis was based on 195 lamb–mother pairs from 90 ewes over 30 years

Fixed effects	Estimate	95% CI		*P*-value
(Intercept)	24.587	20.647 to 29.118		< 0.001
Mass in June	−0.166	−0.255 to −0.101		< 0.001
Years before last reproduction*				
1	−0.240	−1.446 to 0.300		0.518
2	0.102	−0.809 to 0.934		0.787
3	0.153	−1.050 to 0.927		0.725
Age	−0.037	−0.166 to 0.149		0.639

Random effects	Variance	%†	χ^2 (d.f.)	*P*-value
Identity	0.88	0.08	3.70	0.054
Year	6.74	0.64	115.86	< 0.001
Residual	2.90			

*'Last reproduction' was considered as reference.
†Proportion of variance.

Fecundity was independent of mass in June, study period and density, but was affected by age, years before death and their interaction (Table 3), revealing both age-independent and age-dependent senescence. Both year and maternal identity explained significant variation in fecundity (Table 3). Regardless of age at death, over 85% of ewes were lactating three and 2 years before death (Fig. 2a,b). One year before death and in the year of death, fecundity remained high for ewes that died young, but declined steeply for older ones (Fig. 2c,d). About 40% of ewes (55 of 129) survived 1–4 years after their last successful reproduction without weaning any more lambs. Among these 138 ewe-years, for 42% there were no signs of lactation, 38% involved neonatal losses (the udder had milk in May but no lamb was seen), and for 20% the lamb died before mid-September.

DISCUSSION

Our data provide clear evidence of both age-dependent and age-independent senescence in a long-lived mammal, and do not support the terminal allocation hypothesis. Bighorn ewes decreased reproductive effort during their last two reproductions independently of age. Fecundity also declined during the last 2 years of life, with a steeper decline for individuals that lived longer. These results suggest that ewes undergo a physiological deterioration in late life, independently of their age, which increases energy requirements for maintenance. Possibly to avoid compromising their own survival, ewes then reduce energy allocation to reproduction.

A mostly age-independent drop in physiological condition and reproductive effort at the end of life could result from illness rather than conventional senescence. Terminal illness, however, would probably involve a collapse in the last year of life (Coulson & Fairweather 2001), whereas senescence is a progressive decline in performance over several years (Rose 1991; Monaghan *et al.* 2008). We found that the decline in reproductive effort began 1 year before the last successful reproduction and steepened during the last reproduction. Over half (58%) of the ewes that survived after their last successful reproduction, produced lambs that died before weaning, suggesting a continuing decrease in reproductive effort during their final years. Our results therefore suggest progressive senescence rather than terminal illness. In addition, fecundity decreased in the last 2 years of life, suggesting a decline in both reproductive effort and performance over the last 3–5 years of life. A progressive decrease in reproductive performance at the end of life independent of individual age lends support to the damage accumulation model of senescence (McNamara *et al.* 2009). This model predicts that senescence would be manifested when the ratio of instantaneous mortality over damage accumulation decreases as reproductive effort increases. In other words, if an increase in reproductive effort led to a greater increase in damage than in instantaneous mortality, we would observe age-independent reproductive senescence.

Bighorn ewes adopt a conservative reproductive tactic, especially when facing harsh environments or high potential fitness costs of reproduction (Martin & Festa-Bianchet 2010). The decrease in reproductive effort in late life without a corresponding decrease in summer mass gain also suggests that females favour their own body condition over that of their lambs. This conservative tactic might lead to both low reproduction-induced mortality, and age-independent senescence. Similar to other ungulates (Gaillard *et al.* 1998), survival of juvenile bighorn sheep from birth to 1 year is much lower than survival of adult ewes and is highly variable from year to year (Portier
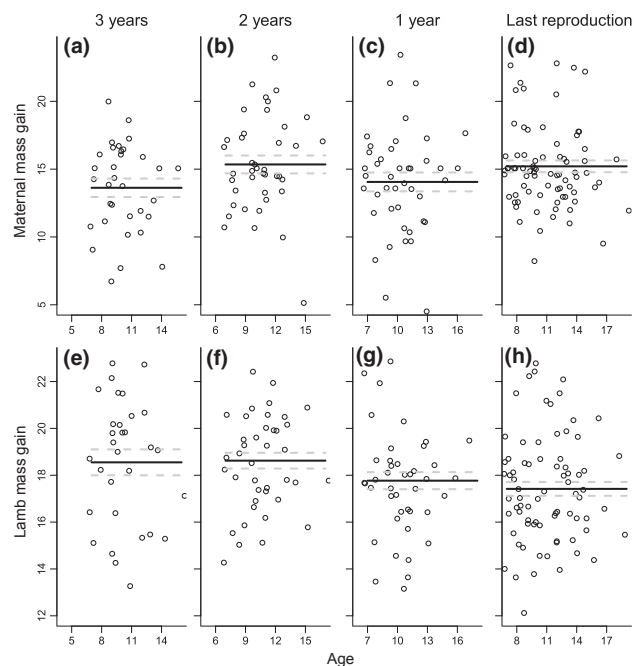
Figure 1 Variation in maternal (a–d) and lamb (e–h) summer mass gain as a function of age for the 4 years before last reproduction (a, e. 3 years before last reproduction; b, f. 2 years, c, g. 1 year; d, h. last reproduction) for bighorn ewes aged 7 years and older at Ram Mountain Alberta. Bold lines indicate the mean mass gain for all ages and dashed grey lines indicate the standard error.

Table 3 Estimates of effects on fecundity for bighorn ewes aged 7 years and older at Ram Mountain, Alberta. Mixed model analysis used 405 observations from 129 ewes over 33 years. Parameters with a significant effect are in bold

Fixed effects	Estimate	Standard error	Z	P-value
(Intercept)	7.004	2.072	3.380	0.001
Mass in June	−0.062	0.074	−0.837	0.403
Study period[After 1989]*	0.119	0.696	0.171	0.864
Population density	−0.007	0.011	−0.600	0.549
Years before death (YD)*				
1	1.904	2.226	0.855	0.392
2	−1.835	1.917	−0.957	0.338
3	−5.091	2.397	−2.124	0.034
Age	−0.345	0.120	−2.885	0.004
Age * Years before death*				
Age * 1 YD	−0.075	0.186	−0.402	0.688
Age * 2 YD	0.269	0.181	1.484	0.138
Age * 3 YD	0.662	0.279	2.369	0.018

Random effects	Variance	χ^2 (d.f.)	P-value
Identity	2.20	7.83 (1)	< 0.001
Year	0.14	0.34 (1)	0.574

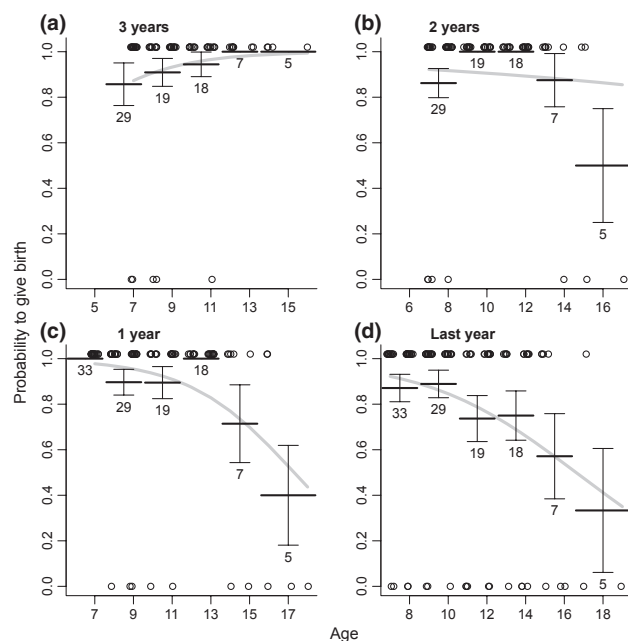*'First period of the study' and 'last year' were considered as references in analyses.

Table 2 Estimates of effects on summer mass gain by bighorn lambs born to ewes aged 7 years and older at Ram Mountain, Alberta. Mixed model analysis used 195 lamb–mother pairs from 90 ewes over 30 years. Parameters with a significant effect are in bold

Fixed effects	Estimate	95% CI	P-value
(Intercept)	16.710	9.553 to 19.706	< 0.001
Maternal mass gain	0.132	0.033 to 0.278	0.035
Maternal mass in June	0.036	−0.007 to 0.139	0.382
Lamb sex [Male]*	1.691	1.058 to 2.279	< 0.001
Previous reproductive success*			
Weaned a female	−0.597	−1.225 to 0.273	0.095
Weaned a male	−1.414	−1.943 to −0.432	< 0.001
Study period[After 1989]*	−2.239	−3.417 to −1.173	0.001
Population density	−0.025	−0.041 to −0.006	0.016
Years before last reproduction*			
1	0.627	−0.265 to 1.317	0.069
2	1.134	0.469 to 2.046	0.002
3	0.802	−0.211 to 1.593	0.060
Age	−0.005	−0.157 to 0.127	0.955

Random effects	Variance	%†	χ^2 (d.f.)	P-value
Maternal identity	1.49	0.31	12.92 (1)	< 0.001
Year	0.92	0.19	23.88 (1)	< 0.001
Residual	2.47			

*'Female lamb', 'not lactating', 'first period of the study' and 'last reproduction' were considered as references in analyses.
†Proportion of variance.

Figure 2 Variation in fecundity (mean and standard error) as a function of age for the last 4 year of life (a. 3 years before death, b. 2 years, c. 1 year, d. last year of life) for bighorn ewes aged 7 years and older at Ram Mountain, Alberta. Bold grey lines are the fit from the model on Table 3. Black horizontal line represents the mean probability to give birth (with standard error and sample size) estimated from raw data over 2-year age classes.

et al. 1998). A persistent conservative reproductive tactic in late life without terminal effort could arise if lamb reproductive potential was lower than maternal residual reproductive potential even for old ewes,

inducing no selection for increased effort. As lamb mass gain is an indirect measure of reproductive effort, its decrease might not be entirely due to an allocation tactic, but could partly be induced by genetic, physiological or pathological problems associated with damage accumulation (Ricklefs 2008).

Senescence has classically been reported as a decrease in both survival and reproductive performance with increasing age (Bérubé

et al. 1999; Monaghan *et al.* 2008). If senescence was considered as a within-individual process, however, two different scenarios appear possible. First, individuals may senesce in similar ways, but begin the process at different ages. Alternatively, senescence could be stronger for individuals dying at an older age because of additive effects of within-individual and age-specific processes. Considering years to death rather than age, Reed *et al.* (2008) reported that common guillemots (*Uria aalge*) with longer life showed a stronger decrease in reproductive performance in their last few years of life compared with birds that died when relatively young. In bighorn sheep, population-level data indicate a decrease in lactation rate beginning at 13 years (Bérubé *et al.* 1999). Our analysis of individual-level data, however, revealed a senescence-related decrease in reproductive effort similar for all individuals and independent of age. Fecundity also decreased in the last 2 years of life, but that decrease was more pronounced in older individuals. Therefore, some reproductive traits appear to show age-independent senescence, whereas others show both age-dependent and independent senescence. Age-independent senescence strongly suggests that individual variation affects its onset. Mechanisms underlying each type of senescence differ and should be under different selective pressures. Age-independent senescence might be induced by damage accumulation (Ricklefs 2008), whereas age-dependent senescence is more likely to be induced by a decrease of selection pressure at older ages.

Our results have important implications for our understanding of senescence and age-specific reproductive effort. Using a reverse-age approach, we found no evidence of terminal allocation and strong support for both age-independent and age-dependent senescence. For certain traits, individuals senesce at a similar rate, but starting at different ages. For others traits, senescence is mostly age-specific. Age-specific senescence has been widely reported. Few cases of age-independent senescence have been published, possibly because its detection requires detailed monitoring of individuals. An age-independent decrease in reproduction in late-life has been reported in mute swans (*Cygnus olor*; McCleery *et al.* 2008); a decline in horn growth in the last 2 years of life independently of age has been shown in Alpine ibex (*Capra ibex*; von Hardenberg *et al.* 2004); a decrease in reproduction during the last year of life has been reported in reindeer (*Rangifer tarandus*; Weladji *et al.* 2006); and terminal illness leading to a steep decrease in reproduction in the last year of life has been shown in some species of birds (Coulson & Fairweather 2001; Rattiste 2004) suggesting that age-independent senescence might be widespread. Age-dependent and age-independent senescence are not mutually exclusive and likely to co-occur frequently. We suggest that a combination of both forward and reverse-age approaches would provide important new insights on late-life variation in life-history traits.

ACKNOWLEDGEMENTS

REFERENCES

Bates, D.M., Maechler, M. & Dai, B. (2008). lme4: Linear mixed-effects models using S4 classes. Available at: http://lme4.r-forge.r-project.org/. Last accessed 26 February 2010.

Bérubé, C., Festa-Bianchet, M. & Jorgenson, J.T. (1999). Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology*, 80, 2555–2565.

Cameron, E.Z., Linklater, W.L., Stafford, K.J. & Minot, E.O. (2000). Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav. Ecol. Sociobiol.*, 47, 243–249.

Clutton-Brock, T.H. (1984). Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.*, 123, 212–229.

Clutton-Brock, T.H. (1991). *The Evolution of Parental Care*. Princeton University Press, Princeton.

Coulson, J.C. & Fairweather, J.A. (2001). Reduced reproductive performance prior to death in the black-legged kittiwake: senescence or terminal illness? *J. Avian Biol.*, 32, 146–152.

Ericsson, G., Wallin, K., Ball, J.P. & Broberg, M. (2001). Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology*, 82, 1613–1620.

Festa-Bianchet, M. (1988). Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. *Anim. Behav.*, 36, 1445–1454.

Festa-Bianchet, M. & Jorgenson, J.T. (1998). Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. *Behav. Ecol.*, 9, 144–150.

Festa-Bianchet, M. & King, W.J. (2007). Age-related reproductive effort in bighorn sheep ewes. *Écoscience*, 14, 318–322.

Festa-Bianchet, M., Jorgenson, J.T., King, W.J., Smith, K.G. & Wishart, W.D. (1996). The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. *Can. J. Zool.*, 74, 330–342.

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds – hypotheses and tests. *Trends Ecol. Evol.*, 10, 374–378.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.*, 13, 58–63.

von Hardenberg, A., Bassano, B., Arranz, M.P.Z. & Bogliani, G. (2004). Horn growth but not asymmetry heralds the onset of senescence in male Alpine ibex (*Capra ibex*). *J. Zool.*, 263, 425–432.

Hirshfield, M.F. & Tinkle, D.W. (1975). Natural selection and the evolution of reproductive effort. *Proc. Natl Acad. Sci. USA*, 72, 2227–2231.

Jorgenson, J.T., Festa-Bianchet, M. & Wishart, W.D. (1993a). Harvesting bighorn ewes: consequences for population size and trophy ram production. *J. Wildl. Manage.*, 57, 429–435.

Jorgenson, J.T., Festa-Bianchet, M., Lucherini, M. & Wishart, W.D. (1993b). Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. *Can. J. Zool.*, 71, 2509–2517.

Kirkwood, T.B.L. & Austad, S.N. (2000). Why do we age? *Nature*, 408, 233–238.

Martin, J.G.A. & Festa-Bianchet, M. (2010). Bighorn ewes transfer the costs of reproduction to their lambs. *Am. Nat.*, 176, 414–423.

Martin, J.G.A. & Pelletier, F. 2011. Measuring growth patterns in the field: Effects of sampling regime and methods on standardized estimates. *Can. J. Zool.*, In press (accepted).

McCleery, R.H., Perrins, C.M., Sheldon, B.C. & Charmantier, A. (2008). Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proc. R. Soc. Lond. Biol. Sci.*, 275, 963–970.

McNamara, J.M., Houston, A.I., Barta, Z., Scheuerlein, A. & Fromhage, L. (2009). Deterioration, death and the evolution of reproductive restraint in late life. *Proc. R. Soc. Lond. Biol. Sci.*, 276, 4061–4066.

Medawar, P.B. (1952). *An Unsolved Problem in Biology*. H. K. Lewis, London.

Monaghan, P., Charmantier, A., Nussey, D.H. & Ricklefs, R.E. (2008). The evolutionary ecology of senescence. *Func. Ecol.*, 22, 371–378.

Morrow, E.H., Arnqvist, G. & Pitnick, S. (2003). Adaptation versus pleiotropy: why do males harm their mates? *Behav. Ecol.*, 14, 802–806.

Nussey, D.H., Coulson, T., Festa-Bianchet, M. & Gaillard, J. (2008). Measuring senescence in wild animal populations: towards a longitudinal approach. *Func. Ecol.*, 22, 393–406.

Pelletier, F., Réale, D., Garant, D., Coltman, D.W. & Festa-Bianchet, M. (2007). Selection on heritable seasonal plasticity of body mass. *Evolution*, 61, 1969–1979.

Pianka, E.R. & Parker, W.S. (1975). Age-specific reproductive tactics. *Am. Nat.*, 109, 453–464.

Pinheiro, J.C. & Bates, D.M. (2000). *Mixed-Effects Models in S and S-Plus*. Springer-Verlag, New-York.

Portier, C., Festa-Bianchet, M., Gaillard, J.M., Jorgenson, J.T. & Yoccoz, N.G. (1998). Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool.*, 245, 271–278.

R Development Core Team (2010). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rattiste, K. (2004). Reproductive success in presenescent common gulls (Larus canus): the importance of the last year of life. *Proc. R. Soc. Lond. Biol. Sci.*, 271, 2059–2064.

Reed, T., Kruuk, L.E.B., Wanless, S., Frederiksen, M., Cunningham, E.J.A. & Harris, M. (2008). Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *Am. Nat.*, 171, E89–E101.

Ricklefs, R.E. (2000). Intrinsic aging-related mortality in birds. *J. Avian Biol.*, 31, 103–111.

Ricklefs, R.E. (2008). The evolution of senescence from a comparative perspective. *Funct. Ecol.*, 22, 379–392.

Roff, D.A. (2002). *Life History Evolution*. Sinauer Associates, Sunderland.

Rose, M.R. (1991). *Evolutionary Biology of Aging*. Oxford University Press, New York.

Service, P.M. (2000). Heterogeneity in individual mortality risk and its importance for evolutionary studies of senescence. *Am. Nat.*, 156, 1–13.

Velando, A., Drummond, H. & Torres, R. (2006). Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *Proc. R. Soc. Lond. Biol. Sci.*, 273, 1443–1448.

Weladji, R.B., Gaillard, J.M., Yoccoz, N.G., Holand, O., Mysterud, A., Loison, A. et al. (2006). Good reindeer mothers live longer and become better in raising offspring. *Proc. R. Soc. Lond. Biol. Sci.*, 273, 1239–1244.

Weladji, R.B., Loison, A., Gaillard, J., Holand, O., Mysterud, A., Yoccoz, N.G. et al. (2008). Heterogeneity in individual quality overrides costs of reproduction in female reindeer. *Oecologia*, 156, 237–247.

Weladji, R.B., Holand, Ø., Gaillard, J.M., Yoccoz, N., Mysterud, A., Nieminen, M. et al. (2010). Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence? *Oecologia*, 162, 261–271.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.*, 75, 1182–1189.

Williams, G.C. (1957). Pleiotropy, natural-selection, and the evolution of senescence. *Evolution*, 11, 398–411.