LETTER

The rate of senescence in maternal performance increases with early-life fecundity in red deer

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Abstract

Tradeoffs between reproduction and somatic maintenance are a frequently cited explanation for reproductive senescence in long-lived vertebrates. Between-individual variation in quality makes such tradeoffs difficult to detect and evidence for their presence from wild populations remains scarce. Here, we examine the factors affecting rates of senescence in maternal breeding performance in a natural population of red deer (*Cervus elaphus*), using a mixed model framework to control for between-individual variance. Senescence began at 9 years of age in two maternal performance traits. In both traits, females that produced more offspring in early life had faster rates of senescence. This tradeoff is evident alongside significant effects of individual quality on late life breeding performance. These results present rare evidence in support of the disposable soma and antagonistic pleiotropy theories of senescence from a wild vertebrate population and highlight the utility of mixed models for testing theories of ageing.

INTRODUCTION

There is now compelling evidence that senescence, defined as the decline in an individual's physiological and cellular function with age, occurs in many vertebrate taxa (Loison *et al.* 1999; Robertson & Rendell 2001; Hendry *et al.* 2004; Reznick *et al.* 2004). Despite this, we still have only a limited understanding of the causes of these patterns. Investment of limited physiological resources in reproduction at the expense of investment in somatic maintenance and an extended lifespan is expected where extrinsic mortality limits longevity (Williams 1957; Kirkwood 1977). The disposable soma and antagonistic pleiotropy theories of ageing predict tradeoffs between early- and late-life reproductive performance and, more specifically, that increases in reproductive effort in early life should be associated with reduced longevity and accelerated reproductive senescence in later life (Williams 1957; Kirkwood & Rose 1991). Although reproduction is known to reduce breeding performance and survival probability in the subsequent breeding season in many mammals (Clutton-Brock *et al.* 1983; Boyd *et al.* 1995), tests for tradeoffs between early-life reproduction and either survival or late life performance are rare. Where undertaken

they often reveal positive, rather than the predicted negative correlations, suggesting that increased early-reproductive investment incurs no later cost (Bérubé *et al.* 1999; McElligott *et al.* 2002; Beauplet *et al.* 2006; Moyes *et al.* 2006). Tests for tradeoffs between early-reproductive investment and rates of senescence in reproductive performance are currently lacking for wild bird and mammal populations.

Senescence theory refers to within-individual changes in reproductive performance with age. Between-individual variation in quality is common in vertebrate populations and can mask within-individual ageing patterns in cross-sectional analyses (Nol & Smith 1987; Forslund & Part 1995). Problems estimating within individual changes with age arise when covariance exists between-individual quality and the age at maturity and/or longevity (Reid *et al.* 2003; van de Pol & Verhulst 2006). These so-called 'selective (dis)appearance' effects result in differences in the average quality of individuals in different age classes. For example, in many ungulates high-quality individuals also live the longest and thus come to predominate amongst older age classes (Bérubé *et al.* 1999; Weladji *et al.* 2006). At the population level this is expected to generate an increase in mean breeding performance amongst older age classes, which may

mask within-individual patterns of senescence. Separation of the effects of within- and between-individual variation on age-specific breeding performance at the population level therefore represents a major challenge to any study of senescence in the wild (Forslund & Part 1995; van de Pol & Verhulst 2006).

High-quality individuals are likely to have higher breeding performance across their lifespan and higher probabilities of survival than the population average. Tradeoffs between early-reproduction and absolute late-life reproductive performance or survival can therefore be difficult to detect where individual quality varies. Variation in individual quality has been cited as the principle reason why studies of long-lived mammal populations have failed to detect the long-term costs of reproduction that are predicted by senescence theory (Bérubé et al. 1999; Beauplet et al. 2006). Costs of early reproduction that affect rates of senescence will be apparent at the within-individual level and so, unlike tradeoffs affecting absolute breeding performance values or survival, they can be estimated independently of between-individual variation in quality. However, the difficulties involved in collecting enough longitudinal data on old individuals in natural settings and the problems associated with estimating ageing at the within-individual level from such data sets have meant that the effects of early-life reproduction on rates of reproductive senescence remain unexplored in wild vertebrates.

When longitudinal breeding performance data are available, linear mixed-effects models (LMMs) provide a means of controlling for selective (dis)appearance effects and thereby estimating interactions between within-individual ageing rates and early-reproductive investment. LMMs in which breeder's identity is fitted as a random effect have been used previously in analyses of ageing in wild vertebrates (Ericsson et al. 2001; Cam et al. 2002; Reid et al. 2003). van de Pol & Verhulst (2006) have recently shown within-individual changes in breeding performance with age may be poorly estimated in these 'standard' mixed models. This is because their estimates of ageing patterns may still be influenced by between-individual selective (dis)appearance effects. A simple extension of the standard mixed model, allowing potential covariance between individual quality and age at first or last breeding to be explicitly measured and controlled for, generated accurate estimates of the mean within-individual ageing rate (van de Pol & Verhulst 2006). This approach has yet to be applied to model within-individual senescence rates or to specifically test senescence theory. Here we use it to test for tradeoffs between early-life reproduction and within-individual senescence rates in maternal breeding performance in a wild population of red deer (Cervus elaphus).

The red deer in the North Block study area of the Isle of Rum, Scotland have been the subject of individual-based study for over 30 years. Survival probability of females in this population begins to decline at around 9 years of age (Catchpole et al. 2004). Two key maternal traits, offspring birth weight and calving date, have also been shown to increase with maternal age through early life, peaking in prime-aged individuals, and declining amongst animals older than 9 years of age (Guinness et al. 1978; Clutton-Brock et al. 1982). Both traits vary between females, with heavy- and early-born calves associated with increased maternal quality and juvenile survival (Clutton-Brock et al. 1987). Calves that are heavier at birth have increased lifetime reproductive success (Kruuk et al. 1999). Delayed costs of reproduction, in the form of reduced survival and fecundity in the subsequent breeding season, have been documented amongst female deer on Rum (Clutton-Brock et al. 1983). A recent study showed that measures of cumulative maternal investment were positively associated with survival probability and ascribed this result to variation in maternal quality (Moyes et al. 2006). Here, we use longitudinal maternal data for offspring birth weights and calving dates from this population to: (i) examine the roles of within-female and between-female variation in overall patterns of changes with maternal age in these two traits; and (ii) test for tradeoffs between early-life reproduction and rates of maternal senescence.

MATERIALS AND METHODS

The study population and data collection

Red deer in the North Block of the Isle of Rum, Scotland, have been studied since the early 1970s. Individual deer are recognizable as a result of artificial markings and natural idiosyncrasies. Regular censusing of the population and mortality searching during winter mean that complete life-history data are available for most deer resident to the North Block (Clutton-Brock et al. 1982). Red deer on Rum typically give birth from late May to June. Females can begin breeding at 3 years of age, giving birth to a maximum of a single calf per year. Observation of females and their newborn offspring during the calving season allows calving dates to be accurately estimated and enables capture of around 80% of calves born to resident females within a few days of birth. Calves are weighed, sexed and artificially marked at capture. Further details of data collection can be found in Clutton-Brock et al. (1982); here we used data collected on red deer born in the North Block population between 1971 and 2002.

We examined age-dependent variation in two important maternal traits: (i) calving date, which was measured as the estimated date of parturition expressed in number of days

after 1st May; and (ii) offspring birth weight, which was calculated using data on calf weight at capture and estimated time of birth following Clutton-Brock *et al.* (1982) as:

$$\text{Birth weight} = \text{weight at capture (kg)}$$
$$- (0.01539 \times \text{age at capture (h))}.$$

This equation for the calculation of birth weight was validated using all capture weight records from the North Block study area collected between 1971 and 2002. We fitted a linear model of capture weight including age at capture, sex and year and their interactions as explanatory variables. The estimated increase in weight per hour in a model containing the only significant terms, sex and age at capture, was identical to the one above ($b_{(\text{Age at capture})} = 0.0153 \pm 0.001$ SE, $r^2 = 0.31$).

We analysed the effects of the following variables pertaining to maternal age, age of appearance and disappearance from the breeding population, and early-life reproduction on these two maternal traits:

Female's age: the age of female in years at a given breeding event, determined either through knowledge of the individual's year of birth or, for cases where females were born before monitoring began (*c.* 2% of individuals), by counting cementum annuli from jaws collected postmortem (Clutton-Brock *et al.* 1982). Only 5.7% of females reproduced at older than 17 years, and none of the females in our data set had more than one breeding record beyond 17 years of age. To avoid biasing our analyses by including female age classes greater than 17 for which only very small samples sizes were available, we grouped females aged 17 years or older into the same age class.

Female's age at first reproduction (AFR): a female's age in her first recorded breeding year. Thorough monitoring of the population began in 1971 and the earliest recorded AFR was 3 years (see Fig. 1 for distribution). Recorded ages of first reproduction for a few females born before 1968 were unusually high. This is likely to be because their first calf was born before 1971 and died as a neonate or juvenile and therefore may not have been recorded. Restricting the data set to include only females born in 1968 or later did not affect any of our results. We therefore present analysis excluding only data on females born before 1968 with first reproduction recorded at age 5 or more from our analyses, which may have been inaccurate.

Female's age at last reproduction (ALR): a female's age in her last recorded breeding year. Females that were still alive in 2002, those with an unknown year of death, and females that were shot (whilst venturing outside the study area) were excluded from analyses as these individuals may have continued to breed after their latest recorded attempt or may not have reached the natural end of their reproductive lives (following Kruuk *et al.* 1999; see Fig. 1 for distribution).
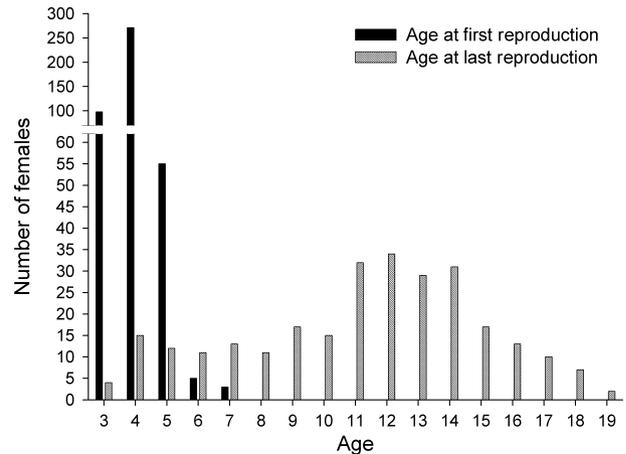
Figure 1 The frequencies of different ages at first (black bars) and last (grey bars) reproduction amongst female red deer with at least one offspring birth weight record. Females that were still alive in 2002 or that were shot were excluded for age at last reproduction.

Female's early-life fecundity (ELF): 'Early life' was defined as prior to 9 years of age, which was when senescence in maternal performance began (see *Results*). ELF was defined as the proportion of years in which a female produced a calf between AFR and 9 years old.

Female's mean early life offspring birth weight/calving date (ELBW/ELCD): a female's average offspring birth weight or calving date (depending on the response variable in the model in question) whilst she was between the ages of 3 and 8 years of age.

Statistical analysis

All models were run in S-PLUS version 6 (Insightful Inc., Seattle, VA, USA). We ran two types of LMMs on each of the maternal performance traits: (i) initial models using all data were used to explore overall ageing patterns; and (ii) subsequent models, using a subset of data on older females (aged 9 years and older), were used to specifically explore factors influencing reproductive senescence. LMMs run on longitudinal data with female's identity as a random effect control for the non-independence of repeated measures on the same female (Milner *et al.* 1999; Nussey *et al.* 2005). Inclusion of a female's AFR and ALR as fixed effects, where significant, controls for variation in appearance or disappearance from the breeding population that is associated with between-individual differences in quality (van de Pol & Verhulst 2006).

In all models, variables that had previously been shown to influence these maternal traits were included as fixed effects. For offspring birth weight these variables were: offspring sex (unsexed offspring were excluded from the models),

female reproductive status (defined based on a female's reproduction in year previous to a breeding event as a five-level factor, as described in Coulson *et al.* 2003), and date of birth. For calving dates the variables were: female reproductive status and population density in the breeding year (measured as the number of adult females appearing in ≥ 10% of January to May study area censuses in that given year; see Coulson *et al.* 1997).

Previous analysis of the red deer population in the North Block of Rum suggested a curvilinear change in offspring birth weight and calving date with maternal age at the population level (Guinness *et al.* 1978; Coulson *et al.* 2003). To test the appropriateness of a quadratic function for modelling the change in performance with female age we ran additive models for both offspring birth weight and calving date including the fixed effects described above and a smoothing function for maternal age. The explanatory power of these additive models were compared with linear models in which the smoothed age term was replaced by female's age and its square (Venables & Ripley 1996). As there was no significant difference between the additive and linear models (see *Results*), the following analyses included female's age and its square as fixed effects.

Prior to running LMMs offspring birth weights and calving dates were standardized by subtracting annual mean values from each value to control for environmental differences associated with the year of breeding (as in van de Pol & Verhulst 2006). All models included female identity as a random effect. Additional fixed effects included in the two types of LMM are discussed below:

(1) Maternal ageing models: female AFR and ALR were included as covariates. Curvilinear relationships between ALR and breeding performance, suggesting tradeoffs between reproduction and survival, have been documented in wild vertebrates (Reid *et al.* 2003) and so we included a quadratic term for ALR in our models. For comparison, we also ran cross-sectional models of offspring birth weight and calving date which were as above but excluding a random term for female identity and fixed effects of AFR or ALR.

(2) Maternal senescence models: the data set for the senescence LMMs was restricted to offspring birth weights and calving dates from females aged 9 years or more, which was after the estimated peak in age-related maternal performance (see *Results*). Initial LMMs included the same fixed effects as in the maternal ageing models. Since few females with AFR of 5 years or more survived to 9 years ($n = 28$), we collapsed AFR to a three-level factor in our senescence models (3, 4 or 5 or more years old at first breeding attempt). We fitted an additional fixed effect term for ELF in LMMs of both performance traits. ELBW and ELCD

were included as fixed effects in birth weight and calving date LMMs respectively. Significant main effects for ELF and ELBW/ELCD would indicate relationships between early-life reproductive parameters (fecundity or breeding performance respectively) and a female's average maternal performance in late life. Significant interactions between these terms and age and its quadratic would indicate relationships between early-life reproduction and within-individual rates of senescence. In order to examine which terms influenced rates of maternal senescence, first-order interactions between female's age and age[2] with all other fixed effects terms were fitted.

Linear mixed-effects models described in (1) and (2) were fitted for offspring birth weight and calving date using a maximum-likelihood algorithm and then simplified by dropping the term with the lowest marginal *F*-value (based on Wald-type statistics), and testing the significance of the removal of the term by comparing models using a likelihood-ratio test (Crawley 2002). This reverse stepwise model simplification method proceeded until only terms significant at the $P < 0.05$ level remained in the model, leaving minimum adequate LMMs which were then re-run using restricted maximum-likelihood methods (Pinheiro & Bates 2000; Crawley 2002). The influence of breeding in extreme old age (aged 17 years or more) on our results was examined by excluding breeding records from females aged 17 years or over and re-running these analyses.

RESULTS

Maternal ageing patterns

Maternal performance initially increased with female age, peaking at around 8 years and then declining until death. A quadratic function of female age adequately explained changes in both maternal performance traits with age (comparison of linear and additive models of both offspring birth weight and calving date: $F_{(d.f.=2)} < 2.2$, $P > 0.05$). Figure 2a,b shows this trend using mean standardized offspring birth weights and calving dates at each female age, and Table 1 gives details of the significance and estimated effect sizes in the minimum adequate maternal ageing LMMs. The final LMMs for offspring birth weight and calving date both contained a significant quadratic effect of female's age (Table 1). The estimated age effects reveal that offspring birth weights increased initially with age, peaking at 8.24 years of age, and showing an accelerating decline thereafter. A similar, although inverted, pattern occurs in calving dates which advanced with female's age until 8.34 years, and then showed an accelerating delay with age.
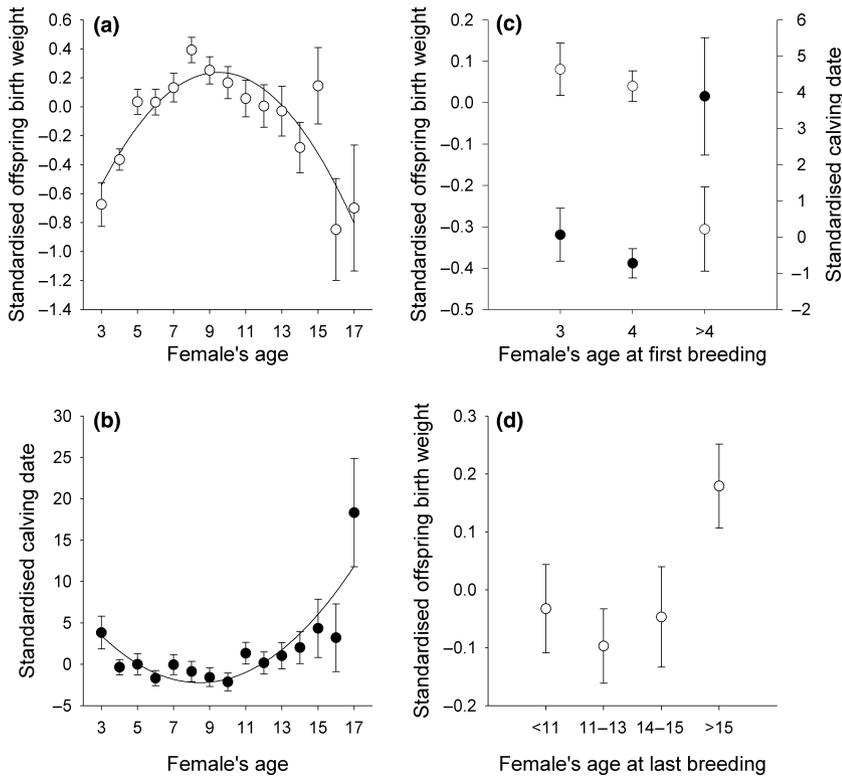
Figure 2 Senescence and selective (dis)appearance effects influence age-dependent breeding performance. Panels (a) and (b) show the average standardized trait value for each maternal age with standard error bars and quadratic regression line fitted to these means for offspring birth weights and calving dates, respectively. Panel (c) shows mean offspring birth weights (open circles, left *y*-axis) and calving dates (filled circles, right *y*-axis) of females first breeding at 3, 4 and > 4 years of age. Panel (d) shows mean offspring birth weights of females which last bred at < 11, 11–13, 14–15 and > 15 years of age.

Table 1 Linear mixed models of offspring birth weight (left, 1123 offspring from 261 females) and calving date (right, 2120 measures from 471 females) using data from all maternal ages

	Random effects				
	Offspring birth weight			Calving date	
	SD	95% CI		SD	95% CI
Female identity	0.768	0.678–0.871		5.259	4.280–6.463
Residual	0.951	0.907–0.997		15.701	15.183–16.128

	Fixed effects					
	Estimate	SE	*F*	Estimate	SE	*F*
Offspring sex			35.95*	N/A		
Female reproductive status			18.90*			23.86*
Date of birth	0.013	0.002	29.23*	N/A		
Female's age	0.313	0.068	21.12*	−3.468	0.775	20.00*
Female's age^2	−0.019	0.004	30.75*	0.208	0.040	26.92*
AFR	−0.260	0.091	8.20**	2.469	0.698	12.50*
ALR	−0.172	0.094	3.35****	N/S		
ALR^2	0.009	0.004	4.22***	N/S		

Estimated effect sizes and their standard errors are shown for all fixed covariates, along with significance based on marginal Wald-type statistics. Abbreviations are explained in *Materials and methods* section.
*$P < 0.001$; **$P < 0.01$; ***$P < 0.05$; ****$P < 0.1$; $^{N/S}P > 0.05$ and term dropped from model; N/A, term not fitted to the model.

Linear mixed-effects models revealed considerable variation between females in offspring birth weights and calving dates, and these individual differences in maternal quality were significantly associated with age at first and last reproduction (Table 1, Fig. 2c,d). Female identity accounted for 39.5% and 10.1% of the total variance (calculated as the

sum of the female variance component and the residual variance) in offspring birth weight and calving date respectively. The significant effect of AFR on both maternal traits (Table 1) appeared to result from the fact that females that reproduced for the first time aged 5 years or more produced offspring that were both lighter and later than average (Fig. 2c). ALR and its square were significant predictors of offspring birth weight only (Table 1). The quadratic effect of ALR predicts an accelerating increase in offspring birth weights with maternal longevity from around 9.6 years of age. This pattern appeared to be driven by an increase of the mean offspring birth weight relative to the population average amongst females that lived to reproduce beyond 15 years of age (Fig. 2d).

Other factors, including offspring sex, female reproductive status and date of birth that were previously shown to predict offspring birth weights and calving dates, were also significant in the final LMMs (Table 1). In the calving date LMM, a previously documented effect of population density was not significant and was dropped from the final model. Previous analyses had not standardized calving dates by their annual mean, which may explain this difference. Excluding females aged 17 years or more from our analysis did not alter our findings, but did reduce the magnitude of the estimated age effects for calving date (estimated age effects from LMM: offspring birth weight: age $= 0.317 \pm 0.072$ SE, age$^2 = -0.020 \pm 0.004$ SE; calving date:

age $= -2.352 \pm 0.829$ SE, age$^2 = 0.142 \pm 0.044$ SE). The magnitude of the estimated effects of age and its quadratic were reduced in the cross-sectional analysis of maternal ageing (offspring birth weight: age $= 0.214 \pm 0.063$ SE, age$^2 = -0.013 \pm 0.003$ SE; calving date: age $= -2.383 \pm 0.731$ SE, age$^2 = 0.152 \pm 0.038$ SE).

Maternal senescence

The only significant interaction in both birth weight and calving date minimum adequate LMMs was between female's age and ELF (Table 2, Fig. 3). Females which reproduced most frequently between maturity and 8 years of age showed the strongest declines in offspring birth weight and delays in offspring calving date in old age (Fig. 3). This tradeoff between ELF and the rate of reproductive senescence was present in the minimum models alongside significant main effects of female's ELBW or ELCD (Table 2). The positive direction of these main effects shows that females that gave birth to the heaviest, earliest calves whilst aged 3–8 years of age also had the heaviest, earliest calves in later life.

Visual examination of Fig. 3b suggests that the effect of ELF on the rate of maternal senescence in calving dates may have been driven by severely delayed calving amongst females aged 17 years or more. Dropping data from females aged 17 or more from these models produced no change in

Table 2 Mimimum adequate linear mixed models of offspring birth weight (left, 472 offspring from 171 females) and calving date (right, 633 offspring from 193 females), including only data from females aged 9 years or older

	Random effects				
	Offspring birth weight			Calving date	
	SD	95% CI		SD	95% CI
Female identity	0.44	0.30–0.64		6.194	4.690–8.181
Residual	1.03	0.95–1.11		13.327	12.473–14.240
	Fixed effects					
	Estimate	SE	F	Estimate	SE	F
Offspring sex			6.90**	N/A		
Reproductive status			10.20*			15.82*
Date of birth	0.017	0.004	19.65*	N/A		
Age	0.765	0.296	6.69***	−9.971	3.056	10.65**
Age^2	−0.026	0.011	5.21***	0.312	0.115	7.38**
ALR	0.116	0.031	14.16*	−1.427	0.360	15.76*
ELBW/ELCD	0.643	0.060	114.10*	0.211	0.058	13.21*
ELF	4.320	1.659	6.78***	−67.239	18.432	13.31**
ELF × age	−0.432	0.144	9.03**	5.956	1.587	14.09**

Estimated effect sizes and their standard errors are shown for all fixed covariates, along with significance based on marginal Wald-type statistics. Abbreviations are explained in *Materials and methods* section.
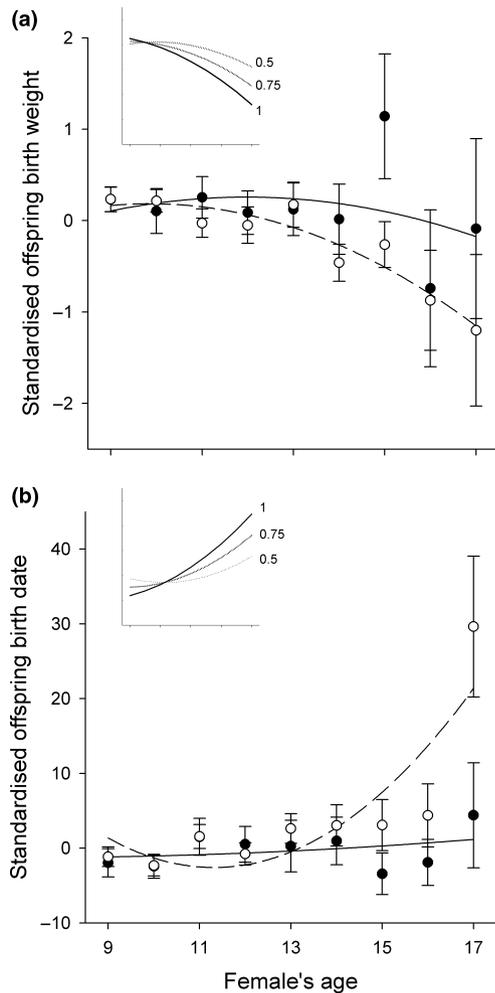*$P < 0.001$; **$P < 0.01$; ***$P < 0.05$; N/A, term not fitted to the model.

Figure 3 Investment in reproduction early in a female's life increases her rate of senescence. The plots show mean offspring birth weights for each maternal age with standard error bars and a least squares quadratic regression line fitted through the mean values for females with an early-life fecundity of less than the median value of 0.8 (filled circles, unbroken line) and of 0.8 or greater (open circles, broken line) for: (a) offspring birth weight (note that the mean and error bars for age 9 overlap completely for the two groups); and (b) birth date. Inset in both plots are the predicted age curves from the senescence mixed models for females with early fecundities of 0.5, 0.75 and 1. The predicted curves are plotted across the same *y*-axis range as the main figure.

the predicted effects of ELF and its interaction with age for offspring birth weight. However, in the calving date LMM using this restricted data set, the quadratic term for age was no longer significant although the interaction between ELF and the linear age term remained highly significant ($F = 9.41$, $P < 0.01$). The estimated effects were in the same direction and of similar magnitude to those in Table 2. This implies that the curvature in the senescent decline for

calving date is driven by breeding records from these very old females, but that the effect of ELF on the rate of senescence was not restricted to females in the eldest age class.

Age at last reproduction was a significant predictor of both a female's late-life offspring birth weights and calving dates (Table 2). Longer-lived females had heavier, earlier calves in late life (Table 2). This effect of ALR on calving dates had not been detected in the overall maternal ageing models (Table 1). There were no significant main effects or interactions with AFR in the models of offspring birth weight and calving date.

DISCUSSION

The decline in offspring birth weights and the delay in calving dates amongst females from 9 years of age onwards are both evidences of senescence in reproductive performance. The mixed model approach utilized here controls both for between-female variation in quality and for possible covariance between female quality and age at first or last breeding, which can obscure within-individual ageing patterns (van de Pol & Verhulst 2006). Poorer quality females, with lower average breeding performance, matured later and had shorter reproductive life spans (Fig. 2c,d). High-quality females would therefore be over-represented in the youngest and oldest age classes, inflating the mean breeding performances at either end of the age range. This effect would explain the reduction in the magnitude of the age effects estimated in a cross-sectional analysis of the data, which did not control for these selective (dis)appearance effects, relative to the age effects estimated in the mixed models. The cross-sectional age trends (Fig. 2a,b) are therefore conservative illustrations of the pattern of senescence in this population. Although, in this case, controlling for between-individual effects did not affect the qualitative nature of our results, this is certainly a possibility (see van de Pol & Verhulst 2006). The estimated age effects in Tables 1 and 2 more accurately reflect within-individual ageing patterns, and the use of mixed models to account for between-individual effects represents a considerable step forward in our ability to investigate the patterns and causes of ageing in natural populations.

Evidence for early- and late-life tradeoffs that would support the disposable soma theory of senescence remain scare, particularly for mammals. In our study population, female deer that bred more regularly between maturity and prime age (high ELF females) showed accelerated declines in maternal performance in old age, independent of their longevity and average breeding performance (Fig. 3; Table 2). There are examples of tradeoffs between early-reproduction and both late-life reproductive performance and future survival in birds (Gustafsson & Part 1990;

McCleery *et al.* 1996; Orrell & Belda 2002; Reid *et al.* 2003) and humans (Pettay *et al.* 2005). For example, Reid *et al.* (2003) found that female red-billed choughs (*Pyrrhocorax pyrrhocorax*) that produced the largest clutches in early life suffered reduced longevity relative to those laying intermediate early clutches. However, many studies of wild vertebrates have found positive, rather than the predicted negative, correlations between female's early-life breeding performance and later life performance or survival and have attributed this to effects of variation in female quality (Bérubé *et al.* 1999; McElligott *et al.* 2002; Beauplet *et al.* 2006). Our results represent, to our knowledge, the first demonstration of a tradeoff between early reproduction and the rate of reproductive senescence in a wild vertebrate population.

A remaining question is whether these tradeoffs are present at the genetic level. Antagonistic pleiotropy is a frequently cited mechanism for the evolution of senescence, and the disposable soma hypothesis has been described as a particular case of antagonistic pleiotropy (Kirkwood & Rose 1991). The declining force of natural selection with age means that genes with advantageous effects in early life but deleterious effects in late life could ultimately be favoured by selection (Williams 1957). Genetic correlations suggesting that increases in early reproduction are associated with increases in the rate of survival or reproductive senescence would support this hypothesis. Most evidence to date comes from laboratory studies of *Drosophila* on longevity (Rose 1991), although such effects have been also demonstrated in pedigreed populations using quantitative genetic 'animal model' analyses (Pettay *et al.* 2005; Charmantier *et al.* 2006). Here, we have assessed senescence in maternal reproductive performance at the phenotypic level. Both offspring birth weight and calving dates are heritable traits at the maternal level in our study population (Coulson *et al.* 2003; L.E.B. Kruuk, unpublished results). The presence of negative genetic correlations between ELF and rates of senescence would represent evidence that reproductive senescence was the result of antagonistic effects of pleiotropic genes expressed in early and late life. However, tests for genetic correlations involving rates of change in a trait would involve complex random regression analyses (Wilson *et al.* 2005) and have yet to be undertaken in any wild population using 'animal model' techniques. The results presented here support the disposable soma hypothesis, but until such analyses can corroborate the findings at the genetic level they do not necessarily support the antagonistic pleiotropy theory. Establishing these trends at the phenotypic level represents an important first step towards our understanding of processes governing senescence in nature at the genetic level.

The importance of testing for tradeoffs predicted by senescence theory at the within-individual level are brought home strongly by our results. Only when interactions between early-life reproduction and within-individual rates of ageing were examined did tradeoffs become apparent in our study population. Mixed-effects models allow us to correct for between-individual variance, but tradeoffs with either survival or absolute late life reproductive performance may still be difficult to detect where there is much variation in individual quality. Our results demonstrate the within-individual tradeoffs predicted by senescence theory can occur alongside effects of between-individual variation in quality, and highlight the importance of considering between- and within-individual variation as non-exclusive mechanisms driving ageing patterns in wild populations.

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