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Citation for published version:

Nussey, DH, Coulson, T, Delorme, D, Clutton-Brock, TH, Pemberton, JM, Festa-Bianchet, M & Gaillard, J-M 2011, 'Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates' *Ecology*, vol. 92, no. 10, pp. 1936-1947. DOI: 10.1890/11-0308.1

Digital Object Identifier (DOI):

[10.1890/11-0308.1](https://doi.org/10.1890/11-0308.1)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Ecology

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Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates

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Abstract. Declines in survival and reproduction with age are prevalent in wild vertebrates, but we know little about longitudinal changes in behavioral, morphological, or physiological variables that may explain these demographic declines. We compared age-related variation in body mass of adult females in three free-living ungulate populations that have been the focus of long-term, individual-based research: bighorn sheep (*Ovis canadensis*) at Ram Mountain, Canada; roe deer (*Capreolus capreolus*) at Trois Fontaines, France; and Soay sheep (*Ovis aries*) on St. Kilda, Scotland. We use two recently proposed approaches to separate contributions to age-dependent variation at the population level from within-individual changes and between-individual selective disappearance. Selective disappearance of light individuals in all three populations was most evident at the youngest and oldest ages. In later adulthood, bighorn sheep and roe deer showed a continuous decline in body mass that accelerated with age while Soay sheep showed a precipitous decrease in mass in the two years preceding death. Our results highlight the importance of mass loss in explaining within-individual demographic declines in later adulthood in natural populations. They also reveal that the pattern of senescence, and potentially also the processes underlying demographic declines in late life, can differ markedly across related species with similar life histories.

Key words: aging; life history; mammal; selective disappearance; senescence; ungulates; wild populations.

INTRODUCTION

Understanding the influences of age structure and age-dependent variation in demographic rates within natural populations is a central challenge within population ecology and evolutionary biology (Charlesworth 1980, Stearns 1992, Caswell 2001, Coulson et al. 2001). In long-lived iteroparous vertebrates, survival and reproduction typically improve through early life, plateau in prime age, and then decline (Caughley 1966, Clutton-Brock 1988, Forslund and Part 1995, Gaillard et al. 2000b). The processes responsible for increased performance through early life, such as growth, sexual maturation, experience, and changes in resource allocation with age, are well studied in free-living populations (Curio 1983, Clutton-Brock 1988, Forslund and Part 1995). Over the last decade, the prevalence of demographic declines in old age in wild vertebrate populations has also become clear (Loison et al. 1999, Bennett

and Owens 2002, Brunet-Rossinni and Austad 2006, Nussey et al. 2008). It is typically assumed that senescence, the deterioration of physiological function in old age, is responsible for observed declines in survival and reproductive performance in natural populations (Ricklefs 1998, 2010, Jones et al. 2008). However, few studies of natural populations have examined longitudinal changes in morphological or physiological measures in old age that may underpin these demographic declines. Body mass is an important predictor of survival and reproductive success in wild mammals (Gaillard et al. 2000a, b, Pelletier et al. 2007), and may decline through senescence of physiological function and foraging ability (Brunet-Rossinni and Austad 2006). Here, we use longitudinal data from long-term studies of three ungulate populations to test for within-individual declines in adult female mass in old age and compare patterns of senescence across species.

Studies of several wild mammals have documented age-related declines in adult body mass and have ascribed these declines to senescence in physiological function and condition (Derocher and Stirling 1994, Bérubé et al. 1999, Mysterud et al. 2001, 2005, Yoccoz et

Manuscript received 19 February 2011; revised 5 May 2011; accepted 13 May 2011. Corresponding Editor: H. U. Wittmer.

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al. 2002, Reimers et al. 2005, Proffitt et al. 2007, Weladji et al. 2010). However, most of these were cross-sectional studies that could not partition within-individual changes with age from compositional differences between age classes. A major challenge in the study of aging is to accurately dissect the role of these two processes (Vaupel et al. 1979, van de Pol and Verhulst 2006, Coulson and Tuljapurkar 2008, Rebke et al. 2010). Individual heterogeneity in demographic rates, and in the phenotypic traits underpinning them, is ubiquitous in wild vertebrates, where the longest-lived individuals frequently show higher reproductive performance and body mass (Bérubé et al. 1999, Cam et al. 2002, Weladji et al. 2006). If phenotypically inferior individuals die younger, older age classes will be composed of a nonrandom subset of “high-quality” individuals. If the selective disappearance of inferior individuals is not accounted for, within-individual declines associated with senescence will be underestimated (Vaupel et al. 1979, van de Pol and Verhulst 2006). Furthermore, declines in performance measures with age at the cross-sectional level may be entirely the result of more subtle forms of selective mortality (e.g., Reid et al. 2010).

Two previous longitudinal studies of wild mammals found within-individual declines in mass in old age (Bérubé et al. 1999, Weladji et al. 2010). Both studies showed declines in individual mass across consecutive years among old individuals (Bérubé et al. 1999, Weladji et al. 2010). However, the relative contributions of within-individual aging and compositional change across age classes to population-level variation in body mass have not been addressed in wild mammal populations. Various analytical approaches have recently been advocated to dissect within- and between-individual contributions to aging patterns (e.g., Cam et al. 2002, van de Pol and Verhulst 2006, Rebke et al. 2010, Reid et al. 2010). These have yet to be applied in the context of age-dependent variation in body mass. Furthermore, most studies to date have assumed that declines in body mass in later adulthood would follow a continuous and accelerating trend with chronological age (Fig. 1A and B). This need not be the case: senescence is an extremely variable and plastic process (Walker and Herndon 2010), while chronological age is biologically invariant (Aviv 2002, McNamara et al. 2009). An individual’s onset and rate of senescence may be partly independent of age and depend instead on previous experiences, life history, and rates of accumulation of physiological damage (Aviv 2002, Monaghan et al. 2008, McNamara et al. 2009). If this were the case, the number of years of life remaining would predict variation in an individual’s body mass better than age (Fig. 1C and D). Finally, studies of long-lived birds suggest that reproductive traits might decline rather suddenly prior to death, independently of age (so-called “terminal declines”; Coulson and Fairweather 2001, Rattiste 2004). The possibility that body mass may show sudden declines prior to death, either alone or following

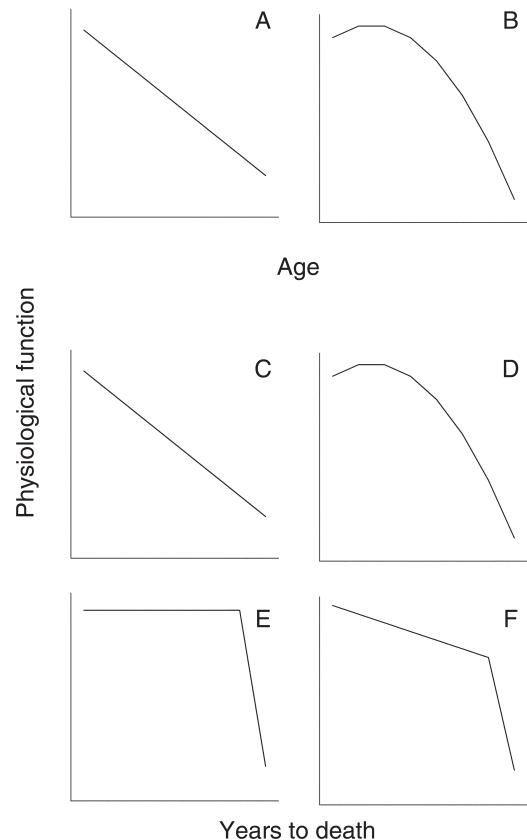


FIG. 1. A schematic illustration of different patterns of senescence. Declines in function in old age may be entirely chronological and either (A) linear or (B) accelerating in form, or they could be age-independent and be predicted by years to death rather than age (C–F). Age-independent declines prior to death might be (C) linear, (D) accelerating, (E) sudden (decline over years prior to death), or (F) a combination of gradual and sudden declines.

more gradual, age-independent declines (Fig. 1E and F), has received little attention in wild vertebrates (but see Weladji et al. [2006] for an example of terminal decline in reproductive performance). More generally, despite mounting evidence for individual differences in aging rates in wild animals (Nussey et al. 2007, Reed et al. 2008, Hayward et al. 2009, Bouwhuis et al. 2010), very few studies have explicitly sought to test for the different patterns of age-dependent and -independent senescence illustrated in Fig. 1.

Here we dissect within- and between-individual contributions to age-dependent variation in body mass among females in three related species with similar life histories. We use two recent statistical approaches: the decomposition approach of Rebke et al. (2010) and the within-individual centering approach of van de Pol and Verhulst (2006). We examine patterns across the entire adult lifespan and then focus specifically on later adulthood to test for within-individual declines in mass consistent with senescence and compare patterns of within-individual change across the three study systems.

METHODS

Study populations

We used data from three long-term studies of free-living ungulate populations: (1) bighorn sheep (*Ovis canadensis*; see Plate 1) on Ram Mountain, Canada; (2) roe deer (*Capreolus capreolus*) at Trois Fontaines in France; and (3) Soay sheep (*Ovis aries*) on the island of Hirta in the St Kilda archipelago off North-West Scotland. In all three systems, individuals are first captured near birth and marked for future identification. Around 95%, 50%, and 60% of the individuals in each population, respectively, are captured annually and weighed. We used body mass data collected on females of known year of birth.

Bighorn sheep are medium-sized bovids, widely distributed across mountainous regions of western North America. Bighorn sheep on Ram Mountain (Alberta, Canada) have been individually monitored since 1971. Sheep in the study population are caught in a corral trap each year between May and October (Jorgenson et al. 1997). Since body mass varies markedly across the trapping period, measures are adjusted to 15 September (Festa-Bianchet et al. 1996). Bighorn ewes give birth to a single lamb in May–June. Females can be primiparous when aged 2–4 years and the oldest recorded female in the population died at 19. The very high resighting rate of ewes in this population (0.99) means that last recorded sighting is a reliable indicator of age at death (Gaillard et al. 2000a). We used data collected between 1973 and 2001, including individuals born up to and including 1998.

Roe deer are small, forest-dwelling cervids with a pan-European distribution. The Territoire d'Etude et d'Expérimentation of Trois Fontaines (Champagne-Ardenne, France) is an enclosed 1360-ha area composed principally of oak (*Quercus* spp.) and beech (*Fagus sylvatica*) forest. Since 1976, roe deer in the reserve have been individually monitored through a capture–mark–recapture program. Deer are captured using net drives in January–February and around 50% of females are caught each year (Gaillard et al. 1993). As body mass is relatively stable across seasons in adult roe deer (Andersen et al. 2000), we simply used measures taken at trapping (Gaillard et al. 2000a). Female roe deer give birth to litters of between one and three in May. Females usually are primiparous at two years of age (Gaillard et al. 1998) and the oldest recorded female survived to 17. Combining winter captures and intensive observations from March to December, resighting rates of female roe deer are 0.84 (Gaillard et al. 2000a). The date of last recapture or resighting was therefore used as a reasonably reliable indicator of age at death (Gaillard et al. 2000a). We used data collected between 1975 and 2008, including individuals born up to and including 2003.

Soay sheep are descendants of domestic sheep that were present throughout northwest Europe during the

Bronze Age and probably reached the St. Kilda archipelago 3000–4000 years ago. The largest island of the archipelago, Hirta, was evacuated of humans and their modern domestic stock in 1930. In 1932, 107 Soay sheep were reintroduced to the island from the neighboring island of Soay, and have since remained as an unmanaged population. The population in the Village Bay area of Hirta has been subject to individual-based study since 1985 (Clutton-Brock and Pemberton 2004). Each August, as many sheep from the study population as possible are rounded up in a series of temporary traps, caught, and weighed. Soay ewes produce litters of one or two in March–April. They can be primiparous in their first year, but most first successfully reproduce as two-year olds. The oldest recorded female survived to 16 years. Regular summer censuses of the study area undertaken throughout the year and mortality searches in winter lead to recapture or resighting rates of 0.93 for females (Catchpole et al. 2000). We estimated age at death either through carcass recovery or based on date of last sighting. We used data collected between 1985 and 2008, including individuals born up to and including 2003.

Analysis

We used a recently developed approach to decompose observed changes in average body mass between ages (Fig. 2A–C) into contributions from within-individual changes and compositional change at each age through selective disappearance (Rebke et al. 2010). We also applied a linear mixed-effects model (LMM) approach, which statistically separates the contribution of within-individual changes with age and selective disappearance effects to variation in body mass (van de Pol and Verhulst 2006). In each system, we analyzed age-dependent variation in body mass beginning at the measurement taken closest to the age of one year (around 8.5 months in roe deer, 15.5 months in bighorn sheep, and 17 months in Soay sheep). Successive age-specific mass measurements were collected at intervals of 12 months in each population. Only one female roe deer and Soay sheep were measured at 15 years or older, so in both systems the last age class analyzed was 14. All analyses were conducted in the R statistical package, using library lme4 (R Development Core Team 2009).

Decomposing changes in average mass among ages.—We applied the method described by Rebke et al. (2010) which is a version of the Price equation (Price 1970) applied to phenotypes (Coulson and Tuljapurkar 2008) to estimate the contribution of within-individual change and selective disappearance to changes in body mass across ages at the population level. Assuming no migration and that all surviving individuals are measured, the change in mean phenotype of the population between ages (P) can be exactly decomposed into an average within-individual change across ages (I) plus a compositional change due to selective disappearance (D ; see Rebke et al. [2010] for details). We also calculated

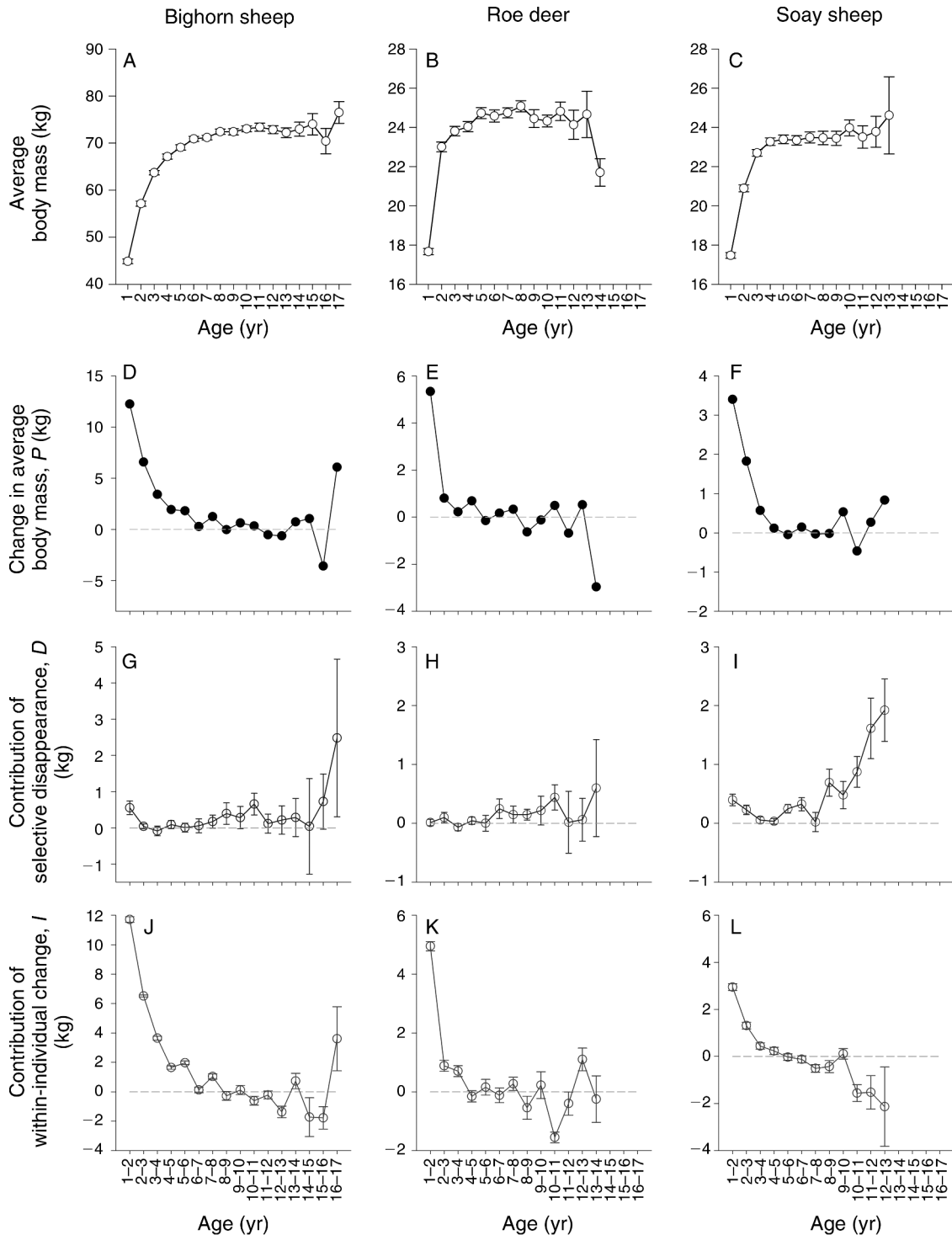


FIG. 2. Age-specific variation in average body mass (error bars show SE) for (A) bighorn sheep, (B) roe deer, and (C) Soay sheep and a decomposition of the change in mean body mass across age classes in bighorn sheep (D, G, J), roe deer (E, H, K) and Soay sheep (F, I, L). (D–F) The change in average body mass across each age. (G–I) Selective disappearance across each age step (with SE; positive values indicate selection against survival of light individuals from one age to another). (J–L) Average within-individual changes in mass across each age step (with SE; negative values indicate mass loss).

measures of variance around values of I and D across each age group, using individual values $i_{j,x}$ and $d_{j,x}$, respectively, calculated as follows:

$$i_{j,x} = \text{mass}_{j,x+1} - \text{mass}_{j,x}$$

where $i_{j,x}$ is the within-individual change in body mass i for an individual j measured at both age x and age $x + 1$. This is simply an individual's change in body mass over consecutive measurements (Rebke et al. 2010). The selective disappearance term is the difference between the trait mean (measured at age t) of individuals that survived and of the entire population. It can also be written as the covariance between the trait and survival divided by mean survival. This means that an individual's contribution to change in the trait mean due to selective disappearance can be written as

$$d_{j,x} = (\text{mass}_{j,x} - \text{mean}[\text{mass}_{j,x}]) \\ \times ([s_{j,x} - \text{mean}(s_{j,x})] / \text{mean}[s_{j,x}])$$

where $s_{j,x}$ and $\text{mean}(s_{j,x})$ are whether or not individual j survived from x to $x + 1$ (scored as zero or one) and the average of this value across individuals of age x , respectively (Coulson et al. 2006). We calculated I and D as well as the variance and standard error in i and d at each age for each population.

Immigration and emigration of females in all three study populations was extremely rare and our focus was on senescence in later life, where selective disappearance, rather than selective appearance, should be the main driver of compositional change across ages. We therefore did not calculate the contribution of selective appearance to changes in body mass across ages, as this was likely to be of minimal relevance in the context of senescence (Rebke et al. 2010). Furthermore, our calculations of D and d considered only whether an individual either survived or died between age x and $x + 1$. Given a recapture rate < 1 , a proportion of the average change in phenotype (P) across ages can be attributed to both death and failure to recapture living individuals at age $x + 1$. In light of this, we adopted a slightly different approach to that used by Rebke et al. (2010) and calculated D using information on an individual's year of death rather than simply whether or not they were recaptured at the next age class. Our measure of selective disappearance (D) is therefore the difference in average mass between all individuals measured at age x and individuals measured at age x that were dead by $x + 1$. Therefore, D incorporates only selective disappearance due to mortality, and not that due to failure to recapture individuals. A further potential bias could arise if there were differences in age-specific mean mass between surviving individuals that were and were not recaptured at time $x + 1$. High recapture rates in bighorn sheep preclude this problem. In Soay sheep and roe deer, where recapture rates are less than 1, we compared mean mass in each age class for individuals measured at x and at $x + 1$ (recaptured)

vs. mean mass for individuals that survived from x to $x + 1$ but were only measured at age x . In the Soay sheep, out of 11 possible comparisons, none were significant ($t < 1.2$, $P > 0.24$). In the roe deer, out of 12 possible comparisons, only one was significant (ages 2–3, $t_{(81)} = 2.24$, $P = 0.03$), all others were nonsignificant ($t < 1.3$, $P > 0.18$). Therefore, any effects on age-related changes in mass associated with recapture failure and immigration were likely very small. However, these considerations mean that $I + D$ does not represent an exact decomposition of P here.

In order to measure the relative contribution of selective disappearance and growth among survivors to the observed body mass at each age, we calculated the cumulative sum of absolute D values across all ages in each population, expressed in both absolute terms (in kilograms) and in relative terms (as a proportion of the average mass in prime adulthood, taken to be seven years, in each species). Under the strong assumption that the mean growth rates of individuals that died would have been equivalent to the mean growth rates of those that survived, we can interpret the cumulative sum of selective disappearance from birth to a given age as the difference in mean weight of individuals expected in the absence of viability selection on body mass. We also calculated the proportion of observed population level fluctuations in mass with age that was due to selective removal overall and in early and later adulthood in each species. We did this by taking the cumulative sum of absolute D values and dividing by the cumulative sum of absolute D plus the cumulative sum of absolute I values first across all ages, then through to prime adulthood (1–7 years) and finally from prime adulthood to old age (from 8 years to the oldest age class).

Mixed-effects models of age-specific variation in body mass.—We also examined age-specific variation in body mass using linear mixed-effects models (LMMs), following the within-group centering approach described by van de Pol and Verhulst (2006). This approach involves fitting LMMs including individual as a random effect and age as a fixed effect (typically as a linear or polynomial covariate) and then splitting the population-level estimate of the age effect into contributions from within-individual and selective disappearance effects by including both age and longevity (or age at last measurement) as fixed covariates (van de Pol and Verhulst 2006, Nussey et al. 2008).

We used this approach to examine age-dependent changes in body mass across all ages and then, separately, among a subset of “elderly” individuals measured after the onset of actuarial senescence. We included capture year as a fixed factor in all models to account for between-year variation in mass associated with annual environmental conditions. All mixed-effects models were initially run and compared using maximum likelihood algorithms, but parameters were estimated from models run using restricted maximum likelihood (Pinheiro and Bates 2000).

We began by examining the form of age-dependent variation in body mass and selective disappearance effects across all ages in each population. We compared LMMs with age fitted either as a factor or as linear or polynomial functions (up to fourth order). We selected the model with the lowest AIC and then tested for selective disappearance effects by adding individual longevity, as either a linear or quadratic function, and examining whether this decreased AIC.

To focus more specifically on senescence in body mass using the LMM-based approach, we ran analyses as above but restricted the datasets to include only observations at ages after the onset of actuarial senescence (8 years in roe deer and bighorn sheep [Festa-Bianchet et al. 2003] and 7 years in Soay sheep [Catchpole et al. 2000]). We fitted LMMs of “elderly” individuals including different functions of age or years to death to compare the six scenarios described in Fig. 1. Age was fitted as a linear or quadratic function to model gradual or accelerating changes with chronological age (Fig. 1A and B). Years to death was fitted as a linear or quadratic function to model gradual or accelerating declines independent of chronological age (Fig. 1C and D). A terminal decline in mass prior to death was modeled by fitting a two-level factor for whether or not the individual was in its last year of life or not (Fig. 1E). A threshold model was fitted with a linear function of years to death up to the second-to-last year of life and an independent intercept for the last year of life to capture a combination of continuous and terminal declines (Fig. 1F).

These models do not account for selective disappearance effects; doing so within this LMM framework would require incorporation of longevity as a fixed covariate (van de Pol and Verhulst 2006). However, models including either age or years to death as a covariate along with longevity are statistically exactly equivalent (van de Pol and Verhulst 2006). We therefore compared the six models described above with models including additive combinations of age (linear and quadratic), longevity (linear and quadratic), and whether or not it was an individual’s last year of life, selecting the model with the lowest AIC (see Table 2 for a full list of models compared).

To verify the within-individual effects from the LMMs, we additionally modeled within-individual changes in body mass across years (i , as described above) for individuals weighed in consecutive years. Since individuals can have multiple measures of i , we followed Rebke et al. (2010) and modeled i in a LMM with individual identity as a random factor. We compared the six scenarios in Fig. 1 with respect to within-individual changes in body mass, by comparing AIC values from LMMs of i fitted with age (as linear and quadratic), years to death (as linear and quadratic), a terminal effect, and a threshold effect. We also separately tested whether there was any evidence of associations between i and individual longevity in these

LMMs. These analyses were restricted to females aged 8 or more (bighorn sheep and roe deer) or 7 or more (Soay sheep) and with 6 or fewer years until death (as very few observations were available for these older females with >6 years to death).

RESULTS

Decomposition of change in average body mass between ages

Age-specific variation in average body mass across all three ungulate species was characterized by marked increases over the first few years of life and smaller increases through early adulthood (Fig. 2A–F). Average mass continued to increase until six years of age in bighorn sheep and until four years in roe deer and Soay sheep (Fig. 2D–F). In later adulthood, neither cross-sectional average mass nor changes in average mass across ages revealed consistent age-related patterns of variation (Fig. 2A–F). The contributions of selective disappearance effects (D) to between-age changes in mass were almost invariably positive: lighter individuals were generally less likely to survive and this effect was most pronounced at the oldest ages (Fig. 2G–I). The cumulative sum of D across ages was 6.01 kg in bighorn sheep, 1.95 kg in roe deer, and 6.98 kg in Soay sheep, or 8.4%, 6.0%, and 29.3% of the average body mass at age seven, respectively. Within-individual increases (high, positive I values) were responsible for the population-level increases in average mass in early adulthood (Fig. 2J–L). Beyond prime age (7 or 8 years), within-individual mass loss across some ages was evident in all species. Only in the Soay sheep, however, was there evidence for consistently and increasingly negative contributions of I with age (Fig. 2L). In both bighorn sheep and roe deer, within-individual declines in mass were predominant in later adulthood, but were followed by average mass gains in the few individuals that survived to the very oldest age classes (Fig. 2J and K).

Across all ages, the proportion of observed population-level fluctuations in mass with age due to selective mortality was 14.3% in bighorn sheep, 11.9% in roe deer, and 37.7% in Soay sheep. This proportion was notably higher in later adulthood (≥ 8 years) compared to early adulthood (1–7 years) in bighorn sheep (31.9% vs. 3.1%, respectively), Soay sheep (47.2% vs. 20.1%), and roe deer (20.0% vs. 6.3%).

Linear mixed-effects models of body mass across all ages

In all three populations, linear mixed-effects models fitted with age as a factor outperformed models with polynomial functions of age (up to fourth order; Table 1). This suggests a complex pattern of age-specific variation in body mass across the lifespan, in keeping with results of our decomposition analysis (see above, Fig. 2). Adding longevity as a between-individual covariate to LMMs of body mass, to account for selective disappearances, improved model fit in all three populations (Table 1). In all three populations the best

TABLE 1. Comparison of linear mixed-effects models of body mass with different age functions and effects of longevity included for three wild ungulate populations.

Model	Bighorn sheep			Roe deer			Soay sheep		
	Terms	AIC	Δ AIC	Terms	AIC	Δ AIC	Terms	AIC	Δ AIC
Age (factor)	<i>45</i>	<i>6487.52</i>	<i>7.39</i>	<i>48</i>	<i>3191.95</i>	<i>4.70</i>	<i>37</i>	<i>5245.97</i>	<i>21.56</i>
Age (linear)	30	7919.06	1438.94	36	3957.01	769.76	26	6002.67	778.25
Age (quadratic)	31	7065.30	585.18	37	3539.27	352.03	27	5516.06	291.65
Age (cubic)	32	6676.10	195.98	38	3372.51	185.26	28	5287.5	63.09
Age (quadratic)	33	6524.14	44.01	39	3241.87	54.62	29	5248.98	24.57
Age (factor) + longevity (linear)	46	6480.13	0.00	49	3187.25	0.00	38	5224.41	0.00
Age (factor) + longevity (quadratic)	47	6481.66	1.53	50	3187.41	0.16	39	5226.14	1.73

Notes: “Terms” is the number of terms in the model. All models included individual identity as a random effect and year of measurement as a fixed factor. Models were compared based on AIC values; the best-fitting model of age alone is shown in italic type. In all cases, the best model included age as a factor, and we subsequently tested whether additional effects of longevity (selective disappearance) were present by adding either a linear or quadratic function of longevity and comparing the model fit. In all cases it did, and the best model overall is shown in boldface type. The total number of body mass measures, N , is 1170 (181 females) for bighorn sheep; 786 (225 females) for roe deer; and 1309 (411 females) for Soay sheep.

model overall included a positive linear effect of longevity, showing selective disappearance of lighter females (bighorn sheep, $b = 0.27 \pm 0.09$ [mean \pm SE]; roe deer, $b = 0.09 \pm 0.04$; Soay sheep, $b = 0.16 \pm 0.03$). The LMMs provided evidence for further, substantial between-individual variation in body mass over the lifespan. In the best fitting models (Table 1) of bighorn sheep, roe deer, and Soay sheep, between-individual variance accounted for 62%, 58%, and 67% of the total variance in body mass in the random effects structure of each model, respectively.

Analyses of senescence

In bighorn ewes, the best-fitting LMM of body mass in old age included a quadratic effect of age (slope of

linear term in model = 1.64 ± 0.73 [mean \pm SE]; slope of quadratic term = -0.08 ± 0.03) and a positive linear effect of longevity (slope = 0.41 ± 0.19 ; Table 2). Within individuals, the decline in mass accelerated with age; between individuals, heavy females were, on average, longer lived (Fig. 3A). There was no evidence for an additional decline in mass in the year before death (adding “last year” to best-fitting model, $b = 0.17 \pm 0.52$ kg lighter in last year, $P = 0.77$). In the best model, between-individual variation explained 70% of the variation in mass (calculated by dividing the individual variance component by the sum of individual and residual variances).

The best-fitting model of body mass in old age for roe deer included quadratic effects of age (linear, $2.00 \pm$

TABLE 2. A comparison of senescence models using data from elderly females (≥ 8 years old for bighorn sheep and roe deer, ≥ 7 years old for Soay sheep).

Model	Bighorn sheep			Roe deer			Soay sheep		
	Terms	AIC	Δ AIC	Terms	AIC	Δ AIC	Terms	AIC	Δ AIC
Null	23	1874.45	6.81	27	659.99	17.97	19	1072.99	21.45
Years to death	24	1872.70	5.06	28	647.08	5.06	20	1069.17	17.62
Age	24	1876.22	8.58	28	652.92	10.90	20	1074.97	23.43
Longevity	24	1873.07	5.44	28	660.30	18.28	20	1064.42	12.87
Last year	24	1874.56	6.93	28	651.72	9.70	20	1059.42	7.87
Years to death ²	25	1872.97	5.34	29	647.78	5.75	21	1052.10	0.55
Age ²	25	1870.08	2.45	29	650.38	8.36	21	1076.82	25.28
Longevity ²	25	1875.06	7.42	29	659.22	17.20	21	1062.22	10.68
Threshold	25	1874.22	6.59	29	645.89	3.87	21	1061.35	9.81
Age + Longevity	25	1872.83	5.19	29	648.51	6.49	21	1064.97	13.42
Age + Last	25	1876.52	8.89	29	650.21	8.18	21	1059.09	7.55
Longevity + Last year	25	1874.04	6.40	29	653.59	11.57	21	1055.94	4.40
Age ² + Longevity	26	1867.63	0.00	30	646.03	4.01	22	1066.94	15.39
Age ² + Last year	26	1870.85	3.21	30	648.41	6.38	22	1060.83	9.29
Longevity ² + Age	26	1874.8	7.17	30	646.56	4.54	22	1062.47	10.93
Longevity ² + Last year	26	1876.02	8.39	30	649.49	7.47	22	1051.54	0.00
Age + Longevity + Last year	26	1874.55	6.91	30	649.45	7.43	22	1057.63	6.08
Longevity ² + Age ²	27	1869.35	1.72	31	642.03	0.01	23	1064.24	12.69
Age ² + Longevity + Last year	27	1869.46	1.83	31	647.28	5.25	23	1059.44	7.90
Longevity ² + Age + Last year	27	1876.48	8.85	31	646.24	4.22	23	1053.19	1.65
Longevity ² + Age ² + Last year	28	1871.09	3.46	32	642.02	0.00	24	1055.17	3.63

Notes: “Terms” is the number of terms in the model. All models included individual identity as a random effect and year of measurement as a fixed factor. The model with the lowest AIC is shown in boldface italic type; models with very similar explanatory power (Δ AIC < 2.0), which included fewer terms, are shown in boldface type. The total number of body mass measures (N) is 346 (92 females) for bighorn sheep; 150 (80 females) for roe deer; and 256 (137 females) for Soay sheep.

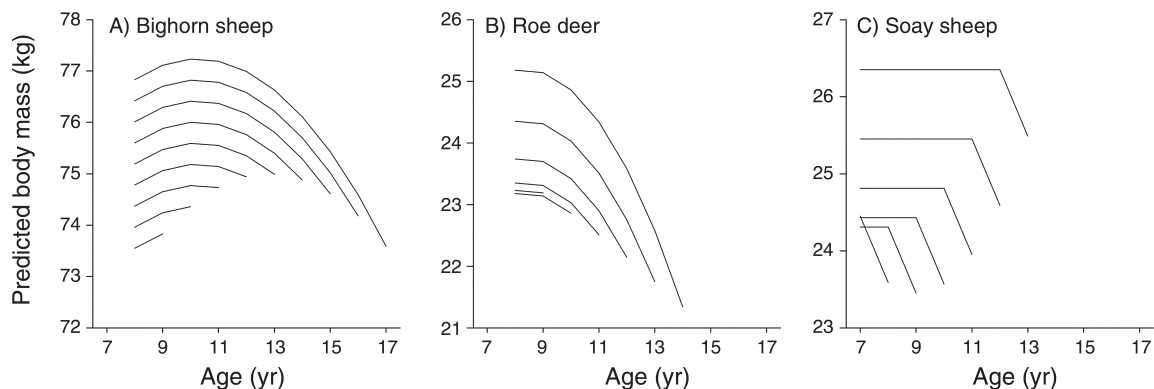


FIG. 3. Predicted changes in body mass with age and longevity in elderly females in each of the three study populations. Plots are based on predicted effects from the selected model for each system (see Table 2). Each line is a predicted age curve for an individual with a different longevity.

1.07; quadratic, -0.12 ± 0.05) and longevity (linear, -2.14 ± 1.05 ; quadratic, 0.11 ± 0.05) and whether or not it was the last year of life (0.66 ± 0.49 kg lighter in last year; Table 2). However, there was very little difference between models including or excluding last year of life and the “last year” effect was not significant when assessed using a likelihood ratio test ($\Delta\text{AIC} = 0.01$; $\chi^2_{(1)} = 2.01$, $P = 0.16$). Within individuals, body mass declined in an accelerating fashion with age; between individuals, particularly heavy females were longer lived (Fig. 3B). In the best-fitting model, between-individual differences explained 42% of the variation in body mass.

The best-fitting model of body mass in old age for Soay ewes included an effect of whether or not it was the last year of life (0.86 ± 0.25 kg lighter in last year) and a quadratic effect of longevity (linear, -2.35 ± 1.07 ; quadratic, 0.13 ± 0.05 ; Table 2). Within individuals, mass was not predicted by age but rather declined between the two measurements before death; at the between-individual level particularly heavy individuals were, on average, longer lived (Fig. 3C). A model including a quadratic term for years to death performed almost as well as the best model ($\Delta\text{AIC} = 0.55$; linear, 0.82 ± 0.17 ; quadratic, -0.14 ± 0.03 ; Table 2). This suggests that declines in body mass in old age were independent of age in Soay sheep and that mass declined suddenly one year prior to death. However, as with age terms, years to death terms fitted alone in a model without longevity will incorporate both within-individual age effects and between-individual selective disappearance effects. In light of this, and since both models suggest a sudden decline in mass just before death, we retained the model including longevity. In the best fitting model, between-individual differences explained 76% of the variation in body mass. LMMs of within-individual changes in mass across consecutive measurements (*i*) confirmed that within-individual declines prior to death were evident in Soay sheep but not the other two species (see Appendix).

DISCUSSION

Senescence in body mass was evident in all three study ungulate species, although the pattern varied. In roe deer and bighorn sheep, mass declined in an accelerating fashion with age, while in Soay sheep, a sudden decline in mass between the two measurements prior to death was evident (Fig. 3). Our findings provide empirical support for the hypothesis that mass loss is an important driver of the late-life declines in survival and reproductive performance widely observed in wild vertebrates (Brunet-Rossini and Austad 2006). Selective disappearance of light individuals explained a substantial proportion of age-dependent variation in mass, a result that is consistent with previous reports that body mass frequently correlates with survival in vertebrates (Gailard et al. 2000a, b). The relative importance of selective mortality was much stronger in Soay sheep, accounting for around 38% of the overall age-dependent variation in mass and 47% of the variation in later life, compared to either bighorn sheep or roe deer (14% and 12% overall, 32% and 20% in later life, respectively). Below we discuss potential explanations and implications of the different patterns of senescence among the three populations, and the strengths and weaknesses of the two analytical methods applied in this study.

Different patterns of senescence between species

Very few studies have explicitly compared the patterns of senescence illustrated in Fig. 1 across populations or species. It remains unclear why we observed gradual declines in body mass in two study species, but more sudden age-independent declines in a third. Evidence for such “terminal” declines in fitness-correlated traits from wild vertebrates remains limited (Coulson and Fairweather 2001, Rattiste 2004, Weladji et al. 2006). Studies that simultaneously tested for both gradual and terminal declines, as we have here, found either only gradual or a combination of both patterns (Rattiste 2004, Reed et al. 2008, Bouwhuis et al. 2009, Weladji et al. 2006).



PLATE 1. A bighorn ewe and lamb in our study site on Ram Mountain, Canada. Photo credit: Fanie Pelletier.

The difference among populations could be due to differences in the mechanisms underpinning mass loss in old age. Body mass is a complex, composite phenotypic trait, and the mechanisms responsible for declines in body mass in later adulthood in wild mammals have very rarely been explored. Declines in body mass in later life could result from sarcopenia, the loss of muscle mass with age, which is widely observed in humans and lab rodents but has also recently been shown to occur in wild seals and shrews (Hindle et al. 2009*a, b*). Skeletal mass loss is another possible explanation, and one recent study does suggest osteo-arthritis may play a role in age-specific mortality in wild ungulates under predation pressure (Peterson et al. 2010). Tooth wear may also limit individuals' ability to obtain and process food, resulting in reduced fat stores and lean mass (Carranza et al. 2004, Brunet-Rossinni and Austad 2006) and declines in physiological function associated with reduced foraging ability or efficiency could also contribute to gradual mass loss. Direct support for this possibility is currently lacking but changes in hunting efficiency in wolves (*Canis lupus*; MacNulty et al. 2009) and in foraging behaviour in Albatrosses (*Diomedea exulans*; Catry et al. 2006, Lecomte et al. 2010) in later life have recently been documented. Further investigation into the contributions of foraging behaviour and changes in protein, fat and muscle structure and mass through adulthood, although challenging to conduct in wild animals, is clearly required to better understand the processes driving variation in age-related declines in body mass.

Differences in the environment and its interactions with intrinsic processes responsible for mass loss in old age could also account for interspecific variation.

Selective predation on older individuals in poor condition could have a profound effect on the relationship between mass loss in old age and mortality risk. The only population subject to predation on adults, bighorn sheep, showed similar patterns to predator-free roe deer, suggesting that predation per se is unlikely to explain the differences we observed. Soay sheep do experience a highly variable environment and undergo population "crashes" during which, due to a combination of high sheep density and poor winter weather, over half of the population can perish (Clutton-Brock and Pemberton 2004). Most adult mortality occurs during these crashes, and the sudden declines in body mass may reflect very strong mortality selection against females in the early stages of senescence. The clear association between mass declines and death in adult Soay sheep also implies that senescence in mass in this population has important consequences for demography and population dynamics (Pelletier et al. 2007). An important next step will be to develop our understanding of the links between environmental conditions, within-individual mass change and demographic rates in species showing both sudden and gradual declines in performance measures during adulthood.

Separating within-individual aging and selective disappearance

Our results obtained with two different methods for analyzing age-dependent variation were broadly consistent, but their side-by-side application does highlight some strengths and weaknesses. Rebke et al.'s (2010) method yields an exact decomposition of the change in trait mean between age classes, providing unambiguous insight into the relative roles of within-individual aging and selection at different ages (Fig. 2). However, investigation of within-individual aging using this method, as we have applied it, remains restricted to measurements at consecutive ages. Incomplete longitudinal data are typical in field studies and this approach may therefore discard large amounts of potentially informative data, reducing the power to test hypotheses related to aging. Furthermore, as originally framed by Rebke et al. (2010), the approach addresses only trait changes across ages and not the potential for more subtle, age-independent changes that are nevertheless relevant to our understanding of senescence. For example, the increasingly negative measures of I (mean within-individual change) from age nine in the Soay sheep would have been interpreted as evidence for progressive senescent declines in body mass in old age. However, mixed-effects models revealed this to be the result of age-independent declines among elderly female sheep (Table 2). That said, the approach is flexible and can readily be adapted to investigate changes in relation to years to death rather than age (see Appendix). Our results suggest it is important to do this in any decompositional analysis focused on changes in traits during adulthood.

The linear mixed-effects modeling approach, first advocated by van de Pol and Verhulst (2006), is another relatively simple method that can readily be adapted to estimate contributions to age-related trait variation from gradual within-individual changes, selective disappearance and terminal declines (Nussey et al. 2008, Bouwhuis et al. 2009). However, unlike Rebke et al.'s (2010) approach, it does not provide an exact decomposition of such effects. Thus, while this model can utilize all available data on a trait to estimate within-individual changes with age, its capacity to reliably separate within-individual aging from selective effects will be limited by the amount of longitudinal data available and the degree to which age and longevity are confounded. Furthermore, the approach does not account for uncertainty or error associated with survival data, unlike the multivariate approach used by Cam et al. (2002). This more complex and rigorous approach has not been widely applied to study aging in natural systems, and it remains unclear whether the relatively small data sets typically available for the elderly component of wild populations are sufficient for such models to provide much biological insight. Simulation-based studies comparing the reliability and efficiency of different approaches in different contexts (sample size, data structure, and so on) could provide further useful insight into the limitations and strengths of each of the methods. Ultimately, while the best method for analyzing aging in ecological studies may depend on the system used and the specific question or hypothesis being addressed, our results suggest that applying more than one approach can provide important complementary insights.

Conclusions

We have provided compelling evidence for within-individual declines in body mass in old age using long-term longitudinal data from three free-living ungulate populations. Our analyses also provide strong evidence for terminal declines in body mass and further support for selection for increased body mass, particularly among the oldest age classes, in wild mammals. The importance of applying methods capable of dissecting within- and between-individual components of age-dependent trait variation to longitudinal data is very clearly illustrated: little can be discerned of the complex patterns of age-specific selection and within-individual aging occurring in our study populations (Fig. 1G–L) from the cross-sectional patterns presented in Fig. 1A–C. Furthermore, the evident system-specific differences in the pattern of within-individual change in body mass with age provides stark warning against making unsupported generalizations with respect to aging rates or patterns across populations or species. It also represents a clear demonstration that patterns of senescence in body mass vary among related species with similar life histories, in support of the “mosaic aging” view recently proposed by Walker and Herndon (2010). The terminal declines in body mass evident in the

Soay sheep system and the prevalence of selective disappearance of light individuals in all three systems point to important demographic consequences of variation in body mass in later adulthood in wild ungulates. Further work is now required to understand how changes in different physiological, morphological, and life history traits in old age are linked with demographic rates and, ultimately, how important senescence is for population dynamics.

ACKNOWLEDGMENTS

We are grateful to Jon Jorgenson for keeping the Ram Mountain project going for 32 years and to NSERC for financial support for the project. The Soay sheep project is supported by NERC, and we thank the National Trust for Scotland and Scottish National Heritage for permission to work on St. Kilda and the Ministry of Defense, QinetiQ, Amey, and Eurest Support Services staff on St. Kilda and Benbecula for logistical support. We are especially grateful to Jill Pilkington, Andrew MacColl, Tony Robertson, Jerry Kinsley, and many other field volunteers for collection and management of the Soay sheep data. Financial support for the roe deer study was provided by the Office National de la Chasse et de la Faune Sauvage and the CNRS, and we thank François Klein for organizing the winter captures of roe deer, and all volunteers who participated to the roe deer captures. T. N. Coulson thanks the Royal Society and Wolfson foundation. D. H. Nussey was supported by a NERC postdoctoral fellowship and a BBSRC David Phillips fellowship and is grateful to members of the Wild Evolution Group in Edinburgh and the Scottish Ecological Ageing Research Group for useful discussions and comments. We are also grateful to Peter Korsten, Atle Mysterud, and one anonymous referee for their constructive comments on an earlier draft of the manuscript.

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APPENDIX

Results of linear mixed-effects models of within-individual changes in mass (*Ecological Archives* E092-165-A1).