

Age-specific changes in different components of reproductive output in female reindeer: terminal allocation or senescence?

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Abstract Two different processes can lead to a change in individual reproductive output with age in long-lived iteroparous vertebrates. The senescence hypothesis predicts a decline of performance in old age, whereas the terminal allocation hypothesis predicts an increase. Using long-term (>30 years) individually based data of female reindeer, we first assessed age-specific variation in body mass and different components of reproductive output. Then we investigated the contribution of senescence and terminal allocation (the increase in components of reproductive output) processes for shaping observed patterns. We found

that female reindeer body mass increased up to about 11.5 years of age, and decreased afterwards, supporting the senescence hypothesis. Calf birth mass, both in absolute terms or for a given female mass, first increased and then declined with female age, also supporting the senescence hypothesis. The female mass gain (June–September) decreased with increasing age, and female change in mass between 2 consecutive years decreased with female age, all patterns again supporting the senescence hypothesis. However, the autumn calf mass did not change with age. Calf body mass in autumn tended to be positively related to female mass gain, supporting a quality effect. Raising a calf had a marked negative effect on female mass gain, indicating energetic reproductive costs of raising a calf. Calf body mass in autumn did not influence yearly female mass change. Overall, our results provided consistent evidence for general effects of senescence on most components of reproductive output and highlighted that both individual heterogeneity and reproductive costs shape female reindeer reproductive tactics.

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Introduction

Understanding age-specific patterns of survival and reproduction remains a central issue in population ecology of iteroparous organisms (Stearns 1992). Recent comparative studies have provided clear evidence that patterns of survival and reproduction vary with age in large herbivores (Gaillard et al. 1998, 2000b; Loison et al. 1999). As a general rule, the performance is lower and more variable in young and old individuals than among prime-aged

individuals. While there is compelling evidence that the reproductive output increases with age over the first years of reproductive life in response to an increase in body condition and/or experience (Curio 1988), it is only in the last decade that convincing evidence of senescence in reproduction (Bérubé et al. 1999; Ericsson et al. 2001; Gaillard et al. 2003; Nussey et al. 2006) has been reported. Changes in reproductive output as females age is likely to be driven by the principle of energy allocation (Williams 1966).

Two different hypotheses can account for changes in reproductive output when animals age: (1) the terminal investment hypothesis predicts that mothers should invest more in reproduction when they age because their expected number of future offspring decreases markedly in old age (Gadgil and Bossert 1970; Trivers 1972; Pianka and Parker 1975), and (2) the senescence hypothesis predicts that mothers should have less resources to allocate to reproduction with increasing age because of general wear and a progressive loss of physiological functions when ageing (Kirkwood and Austad 2000; Myrsetrud et al. 2001). However, as the terminal investment involves an increased investment (i.e., an increase in the fitness costs sensu Trivers 1972), whereas the reproductive senescence involves a decreased allocation, the two processes are not mutually exclusive. Five major patterns of age-dependent reproductive output can result from the interplay of these processes (Fig. 1):

1. No change in either reproductive allocation or investment with age, providing either no support for both the senescence and the terminal investment processes, or support for both processes in a compensatory relationship.
2. A decrease in reproductive allocation but no change or a decrease in reproductive investment with age, providing support for the senescence process only.
3. A decrease in reproductive allocation and an increase in investment, providing support for both processes.
4. An increase in reproductive investment but no change or an increase in reproductive allocation with age, providing support for the terminal investment process only.
5. An increase in reproductive allocation in old age but with no associated age-specific changes (or a decrease) of fitness costs, providing no support for any process.

Indeed, increased allocation to reproduction in old age does not necessarily translate to fitness costs. Behavioral changes with age (i.e., females becoming wiser with age; Cameron et al. 2000) and/or increased experience of old females could allow them to allocate more to their offspring than younger ones without any detrimental effects on expected reproductive value: we will call this outcome the “terminal allocation process”.

In this paper we aim to assess whether the processes of terminal allocation or senescence shape age-related variation in reproductive output by using an exceptionally detailed and long-term dataset collected from an experimental population of reindeer (*Rangifer tarandus*). This data set is unique because most individuals are known and have been monitored from birth to death, with detailed information including birth mass, date of birth, calf sex, mother mass in spring and autumn, mother age, calving rate, reproductive status, and annual and neonatal survival. In contrast to some transversal studies of senescence previously performed on ungulates [reindeer (Weladji et al. 2002); red deer *Cervus elaphus* (Myrsetrud et al. 2001); domestic sheep *Ovis aries* (Myrsetrud et al. 2002)], the data analyzed here allowed us to account for individual heterogeneity that often confounds

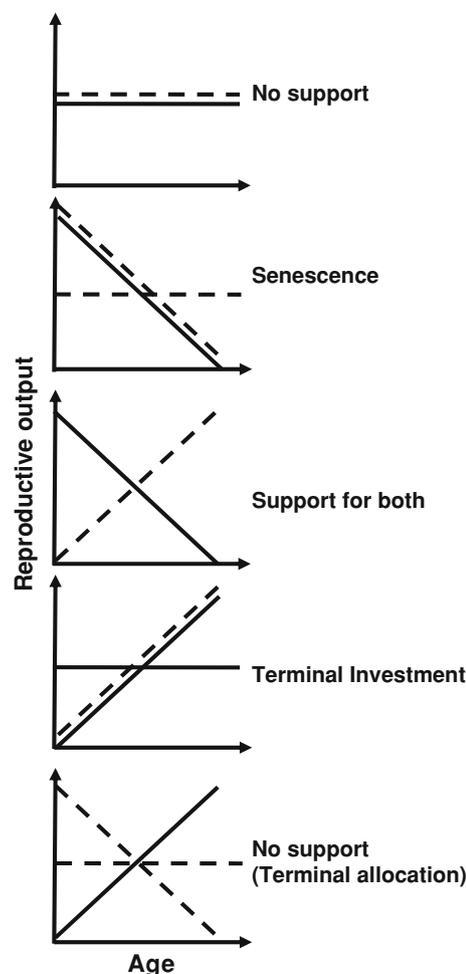


Fig. 1 Schematic illustration of the five major patterns for age-dependent reproductive output measured either by reproductive allocation (continuous black lines) or reproductive investment (discontinuous black lines). How these patterns support the senescence and terminal investment hypotheses is indicated. Lines refer to different components of reproductive output. To increase visual clarity overlapping lines are offset

analyses of senescence (Cam et al. 2002; Nussey et al. 2008). After investigating how body mass of female reindeer varies with age, we will assess to what extent senescence or terminal allocation shape age-specific variation in reproductive output of reindeer.

Materials and methods

Study area and reindeer data

The data are from the Kaamanen Experimental Reindeer Station in Inari, Finland (61°10'N), where reindeer are free-ranging in large-scale seasonal grazing enclosures (altogether 43.8 km²) most of the year, excluding the calving (Eloranta and Nieminen 1986) period when they are kept in a more confined calving paddock (about 50 ha). The animals receive supplemental feeding only during winter (Holand et al. 2003). The herd was established in the late 1960s with about 20 males and 60 females, and our dataset covers the period from 1969 to 2002. Since then, there has been a systematic monitoring of the animals for several aspects of their biology (e.g., physiology, behavior). The data-collection procedure is presented in detail elsewhere (Eloranta and Nieminen 1986). Reindeer is a strongly polygynous species, with a high sexual dimorphism in size (Geist 1999). Reindeer females give birth to a single offspring within a short calving period usually in May or June depending on latitude (Skogland 1989).

Newborn calves were caught by hand after the mother has licked them dry, weighed with a lever scale to the nearest 0.1 kg, ear marked with numbered ear tags and sexed. The birth dates of the newborns as well as the reproductive status of all females (i.e., whether a female produced a calf or not) were also recorded. The age and the weight of the mothers were already known as they were weighed either at birth or when joining the population. The calving area was examined daily and carcasses found were collected and examined. In this way, mortality among calves during the calving period was recorded as well as the causes of mortality (see Eloranta and Nieminen 1986). All animals were weighed before being released into their summer enclosures in June. Additionally, individuals were weighed in spring prior to calving and in autumn during slaughtering (mostly calves), and their fecundity recorded. This allowed us to have information about growth (or decay) for most animals, as well as their calving success and survival (neonatal, pre-weaning and adult).

Some definitions

In this work, “reproductive output” corresponds to the overall outcome of a reproductive attempt by a reindeer

female (i.e., the number and size of offspring produced at the end of the maternal care period). It includes several life history traits such as calving success, birth mass, early growth, weaning success and weaning mass, and can be partitioned into different components (e.g., pre- vs. post-parturition). “Maternal energy expenditures” were measured only for females that gave birth by: (1) the absolute change in female mass between June and September, (2) the change in female mass between June and September relative to the autumn mass of calves in autumn, or (3) the absolute change in autumn mass between 2 consecutive years.

Statistical analyses

We used linear and generalized linear mixed model (using the R software; R Development Core Team 2008) to assess the effect of female age on body mass, components of reproductive output and maternal energy expenditures. Because of repeated measurements on individual females, we included female identity as a random factor in all models to take into account non-independence among observations from the same individual (e.g., Pinheiro and Bates 2000). We used the R library lme4 and function lmer to fit mixed models (Bates 2005). Variance components are given as the two estimated variances (between individual females, σ_{ID}^2 and within individual females, σ_{res}^2). To assess how much the fixed covariates explain of the total variation, we also give the variance components with no covariate included (i.e., with the random components only). We used threshold (=piecewise linear) models to analyze the occurrence of life stages within which life history traits would have identical relationships with age. These models provided adequate description of the non-linear relationships between the response variables and age, and led to easier presentation of the timing of life stages than e.g., additive models. We used Akaike’s information criterion (AIC) adjusted for small sample sizes (AIC_c) to find the best models, restricting ourselves to a series of models with two or three thresholds for age, and assessing linearity of relationships for each segment fitting second-order polynomials in addition to linear models. AIC_c values were calculated assuming that one variance component counted as one parameter, which is adequate when assessing models describing variation at the population level (i.e., average; Vaida and Blanchard 2005). With unbalanced designs, there are unresolved issues regarding the most robust calculations of *P*-values and confidence intervals associated with estimates of fixed effects (D. Bates, unpublished data). We used Markov chain Monte Carlo (MCMC; function mcmcscamp) methods to calculate 95% confidence intervals and SE provided by lmer for comparisons. We did not consider the number of thresholds when assessing the number of parameters used in AIC_c calculations, considering that

values for thresholds were chosen a priori on the basis of known age stages in ungulates (e.g., Gaillard et al. 2000b). Linear models (i.e., assuming normal distribution and constant variance of residuals and random effects) were used for body mass as response variable. As diagnostics, we plotted residuals as well as predicted random effects to check that there were no outliers and that residuals had approximately constant variance.

We included Year as a factor in all the models to control for yearly variation of the components of reproductive output. Year could be considered either as a random or a fixed factor: we decided to include it as a fixed factor because the distribution of year effects was not approximately normal and the AIC generally clearly favored models with year as a fixed factor. Note, however, that similar main results were obtained when running models with Year as a random term. Calf sex (to control for sexual size dimorphism in reindeer; Weladji et al. 2003) and calving date measured by the Julian date of birth (to account for growth) were also included in models when required. Calf survival was also entered as a factor in models where maternal change in body mass was the response to assess cost of reproduction and how it influences age-specific patterns in maternal expenditure. To account explicitly for selective appearance (sensu van de Pol and Verhulst 2006), we used age at first successful reproduction (Age_fsr), defined here as the earliest age at which females produced a calf and the calf survived until weaning (Weladji et al. 2008). As some females were slaughtered before they had reproduced successfully, we used the age at which these were removed from the herd. This underestimates the true age of first reproduction, but removing these females from the analyses did not affect the results. In this managed population in which most females were slaughtered, selective disappearance was not an issue.

Results

Age-related changes in female mass

One female was very light at 2 years of age (41 kg vs. 60 kg for the second lightest one). We thus chose to remove this female from the analyses, although including or not including this female did not change the model selection. As expected, female mass in autumn changed a lot with age when we accounted for among-year differences and individual heterogeneity. Threshold models were better than simple polynomial models with no threshold (Table 1). The best model was a two-stage model with a threshold at 3.5 years of age involving a strong linear growth before 3.5 years of age [slope of 3.98 kg/year (SE = 0.32; MCMC 95% confidence interval (CI) 3.09–4.76)] and then a

Table 1 Model selection [using Akaike's information criterion (AIC) adjusted for small sample sizes (AIC_c)] from a set of threshold (with one or two thresholds) and polynomial (*Poly*; including constant, linear, and >1 order poly) models fitted to assess variation in female body mass in relation to their age

One threshold	3.5	4.5	5.5
1 + 2	5,301.37	5,293.13	5,313.31
p1 + 2	5,399.13	5,292.22	5,291.11
1 + p2	5,287.40 ^a	5,293.40	5,315.35
p1 + p2	5,289.14	5,289.09	5,289.19
Two thresholds	3.5 and 10.5	3.5 and 11.5	4.5 and 11.5
1 + 2 + 3	5,298.90	5,300.76	5,294.45
p1 + 2 + 3	5,297.53	5,298.99	5,293.14
1 + p2 + 3	5,289.26	5,288.27	5,295.33
1 + 2 + p3	5,298.12	5,299.41	5,294.52
Poly only			
Constant	5,555.53		
Age	5,458.91		
Poly2	5,322.71		
Poly3	5,293.79		
Poly4	5,291.42		

The first rows show the threshold age(s). Sample size was 900 observations on 258 females. Female identity and year were also included in the model. Individual terms for threshold models can be linear (simple numbers) or quadratic (*p*). For example, *p1* means that the relationship before the threshold or the first stage is quadratic; *p3* means that the third stage is quadratic; *1 + p2* means that the model has one threshold, the first stage is linear and the second stage is quadratic

^a The selected model

quadratic growth [slope of 0.94 (0.19; 0.54–1.50) and quadratic term of -0.089 (0.023; -0.15 to -0.034)]. From this model, body mass increased until about 5.5 years and remained high and stable until about 11.5 years of age, and then decreased (Fig. 2). We thus considered prime-age females as those aged between 5.5 and 11.5 years of age in this population. Age_fsr did not affect female body mass [0.476 kg/year (0.381)]. Variance components from the best model showed a larger contribution of individual heterogeneity than residual within-individual variation ($\sigma_{ID}^2 = 33.3$, $\sigma_{Res}^2 = 10.5$), whereas the variance components from the null model showed that the covariates of the best model explained much of the within-individual variation ($\sigma_{ID}^2 = 36.8$, $\sigma_{Res}^2 = 30.8$). When we dropped female identity from the model, the mass change with increasing age remained unchanged [slope of 4.03 (0.59)] before 3.5 years of age and a quadratic growth [slope of 1.10 (0.33) and quadratic term of -0.095 (0.040)] from 3.5 years of age onwards. Such age-specific patterns of female body mass support the hypothesis of senescence.

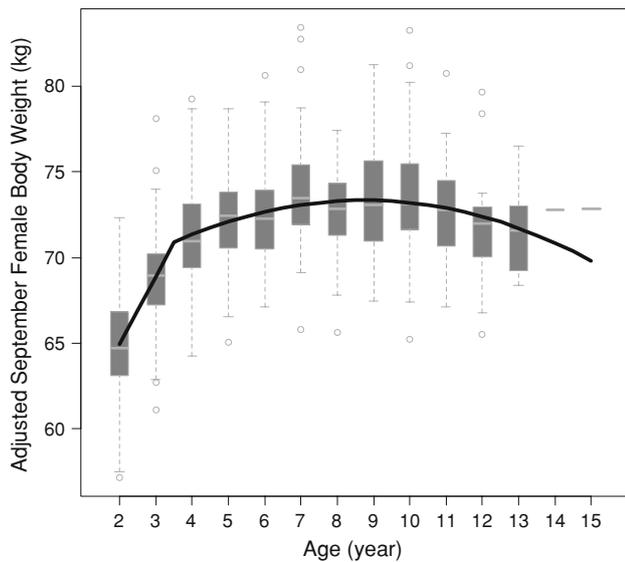


Fig. 2 Box plot of the body mass of female (\pm SE) in autumn (adjusted for random individual effect and fixed effect of year) plotted against female age. Boxes show the 25–75% quartiles. The black line corresponds to the best-fitted model

Age-related reproductive output: pre-parturition period

When other sources of variation were accounted for, the birth mass of calves was significantly influenced by female age (Table 2). Two threshold models provided similar fits to the data: a two-stage model involving a linear increase in birth mass with increasing age up to 5.5 years of age [slope of 0.19 kg/year (0.039; 0.12–0.27)], and then a decrease [slope of -0.042 (0.019; -0.078 to -0.003); Fig. 3], and a three-stage model involving the same linear increase in birth mass up to 5.5 years [slope of 0.19 (0.039; 0.10–0.30)], a slight decrease between 5.5 and 11.5 years of age [slope of -0.046 (0.021; -0.12 to 0.00)], and then a steeper decrease for females older than 11.5 years [slope of 0.61 (0.44; -0.47 to 2.84) and quadratic term of -0.42 (0.21; -1.70 to 0.64)]. Both models therefore indicated that calf birth mass decreases with age over the last breeding attempts. Other sources of variation in calf mass included individual heterogeneity, birth date [with a decrease in mass with increasing date, slope of -0.012 kg/day (0.0047)], year [difference between the extreme years 2002 (heaviest) and 1991 (lightest) is 0.82 kg (0.16)], sex [male calves being 0.34 kg (0.060) heavier at birth than female calves], and mother body mass [with an increasing birth mass with increasing female mass, slope of 0.034 calf kg/mother kg (0.0059)]. Age_fsr negatively affected calf mass [-0.120 kg/year (0.049)], but otherwise did not change parameter estimates of fixed effects and variance components (e.g., the between-individual SD changed from 0.44 to 0.43). Variance components from the best model showed a larger contribution of residual within-individual

Table 2 Model selection (using AIC_c) from a set of threshold (with one or two thresholds) and poly (including constant, linear, and >1 order poly) models fitted to assess variation in calf body mass at birth in relation to the age of their mother

One threshold	3.5	4.5	5.5
1 + 2	1,703.56	1,695.45	1,692.13 ^a
p1 + 2	1,701.24	1,695.87	1,694.22
1 + p2	1,695.28	1,694.04	1,693.76
p1 + p2	1,696.51	1,695.77	1,695.88
Two thresholds	4.5 and 11.5	5.5 and 10.5	5.5 and 11.5
1 + 2 + 3	1,696.12	1,693.69	1,693.62
p1 + 2 + 3	1,696.87	1,695.82	1,695.76
1 + p2 + 3	1,696.43	1,695.78	1,695.75
1 + 2 + p3	1,695.00	1,692.13	1,691.58
Poly only			
Constant	1,712.56		
Age	1,715.91		
Poly2	1,693.64		
Poly3	1,695.04		
Poly4	1,696.83		

The first rows show the threshold age(s). Sample size was 696 observations on 225 females. Calf sex, birth date, mother mass in June, age at first successful reproduction, and year were also included in the model. For example, *p1* means that the relationship before the threshold or the first stage is quadratic; *p3* means that the third stage is quadratic; *1 + p2* means that the model has one threshold, the first stage is linear and the second stage is quadratic

^a The selected model

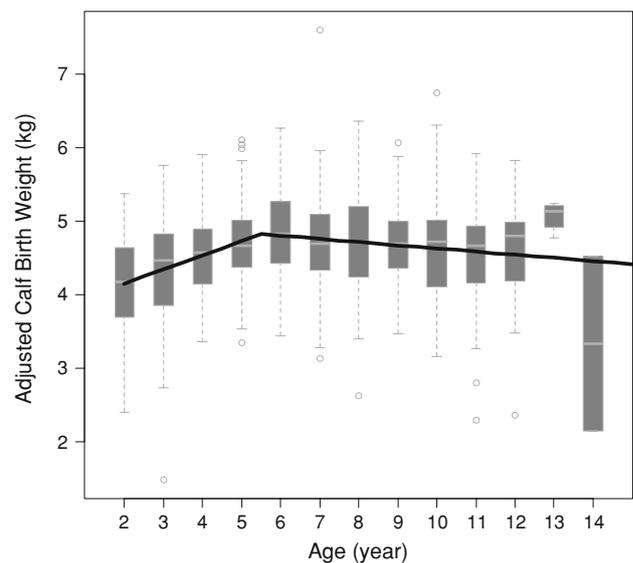


Fig. 3 Box plot of the reproductive allocation measured by adjusted calf birth mass by female age (years). Boxes show the 25–75% quartiles. The black line corresponds to the best-fitted model

Table 3 Model selection (using AIC_c) from a set of threshold (with one or two thresholds) and poly (including constant, linear, and >1 order poly) models fitted to assess variation in autumn calf body mass in relation to the age of their mother

One threshold	3.5	4.5	5.5	6.5
1 + 2	2,489.45	2,489.61	2,489.58	2,489.21
p1 + 2	2,491.59	2,491.42	2,491.16	2,490.15
1 + p2	2,489.72	2,489.51	2,489.51	2,489.78
p1 + p2	2,491.30	2,491.72	2,491.68	2,491.56
Two thresholds	3.5 and 10.5	3.5 and 11.5	4.5 and 11.5	5.5 and 11.5
1 + 2 + 3	2,489.27	2,489.22	2,489.39	2,489.49
p1 + 2 + 3	2,491.33	2,491.29	2,491.41	2,491.39
1 + p2 + 3	2,491.12	2,490.97	2,490.91	2,490.93
Poly only				
constant	2,487.06 ^a			
Age	2,487.43			
Poly2	2,488.86			
Poly3	2,490.21			
Poly4	2,491.25			

The first rows show the threshold age(s). Sample size was 424 observations on 160 females. Calf sex, birth date, mother mass in June, age at first successful reproduction, and year were also included in the model. For example, *p1* means that the relationship before the threshold or the first stage is quadratic; *p3* means that the third stage is quadratic; *1 + p2* means that the model has one threshold, the first stage is linear and the second stage is quadratic

^a The selected model

variation than between-individual variation ($\sigma_{ID}^2 = 0.192$, $\sigma_{Res}^2 = 0.509$), whereas the variance components from the null model showed that the covariates of the best model explained some part of the within-individual variation ($\sigma_{ID}^2 = 0.224$, $\sigma_{Res}^2 = 0.745$). When we dropped the mother mass from the model, the age-specific pattern remained unchanged. Thus, the calf birth mass decreased with increasing age over the last breeding attempts both in absolute and relative scales, supporting the senescence hypothesis. It is noteworthy that when we dropped female identity from the model, the decrease in birth mass with increasing age after 5.5 years of age was no longer significant [slope of -0.032 kg/year (0.20)], indicating that individual heterogeneity in quality prevented the detection of senescence.

Age-related reproductive output: post-parturition/pre-weaning period

We did not detect marked effect of female age on autumn calf mass, and the best model did not include any effect of age (Table 3). However, the observed relationship between

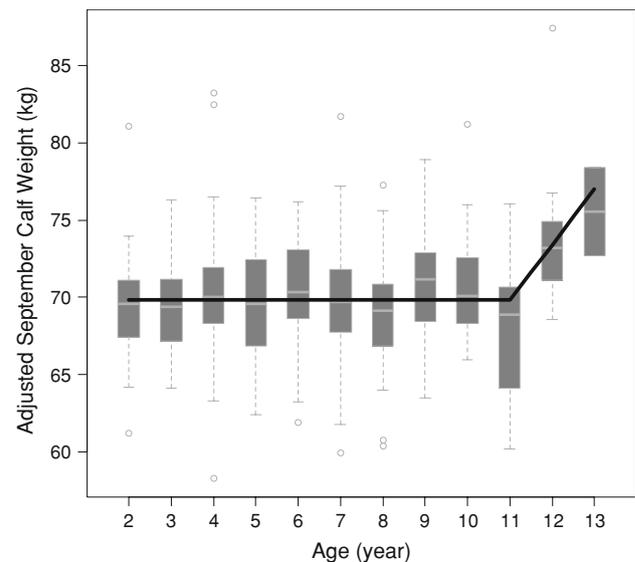


Fig. 4 Box plot of the reproductive allocation measured by adjusted autumn mass of calves by female age (years). Boxes show the 25–75% quartiles. The black line corresponds to the best-fitted model

autumn calf weight and the age of the mother (Fig. 4) led us to investigate higher threshold values. Then the model with one threshold at 11 years of age followed by a linear increase provided a better fit ($AIC_c = 2,485.02$) than the model with no effect of age ($AIC_c = 2,487.06$). A model with a polynomial effect after age 11 provided an even better fit ($AIC_c = 2,481.23$) but this was due to one female aged 16 years. Removing this female led to the best model being the model with a linear increase after age 11 years (constant model, $AIC_c = 2,482.22$; linear with threshold, $AIC_c = 2,476.29$; linear with polynomial after 11 years, $AIC_c = 2,476.38$; Fig. 4). In autumn, calf mass decreased with increasing birth date [slope of -0.29 kg/day (0.031)], varied among years, and male calves were 3.32 kg (0.44) heavier than female calves, and weight increased with increasing mother mass [slope of 0.23 calf kg/mother kg (0.037)]. Age_{fsr} negatively affected calf mass [-0.79 kg/year (0.35)], but otherwise did not change parameter estimates of fixed effects and variance components. Variance components from the best model showed a much smaller contribution of individual heterogeneity than residual within individual variation ($\sigma_{ID}^2 = 3.53$, $\sigma_{Res}^2 = 16.8$), whereas the variance components from the null model showed that the covariates of the best model explained both substantial parts of the between- and within-individual variation ($\sigma_{ID}^2 = 8.03$, $\sigma_{Res}^2 = 37.1$). When we dropped female identity from the model, the pattern remained unchanged with no marked effect of age and only a tendency of increasing autumn mass with mother age [slope of 0.15 kg/year (0.097; -0.038 to 0.34)]. On the other hand, when we dropped female body mass from the best model, a marked effect of age resulted: autumn mass of calves

Table 4 Model selection (using AIC_c) from a set of threshold (with one or two thresholds) and poly (including constant, linear, and >1 order poly) models fitted to assess how change in female body mass (June–September; a measure of maternal expenditure) varies with their age

One threshold	3.5	4.5	5.5
1 + 2	2,165.68	2,165.95	2,164.38
p1 + 2	2,165.75	2,167.42	2,166.34
1 + p2	2,165.46	2,166.30	2,166.14
p1 + p2	2,162.49 ^a	2,165.89	2,167.63
Two thresholds	3.5 and 10.5	3.5 and 11.5	4.5 and 11.5
1 + 2 + 3	2,167.85	2,167.25	2,167.74
p1 + 2 + 3	2,167.83	2,167.06	2,169.05
1 + p2 + 3	2,165.86	2,167.74	2,168.56
1 + 2 + p3	2,167.54	2,164.92	2,165.09
Poly only			
Constant	2,209.70		
Age	2,169.18		
Poly2	2,163.69		
Poly3	2,164.91		
Poly4	2,167.10		

The first rows show the threshold age(s). Sample size was 381 observations on 157 females. Calf sex, female mass in June, age at first successful reproduction, female identity, calf mass in autumn, calf survival and year were also included in the model. For example, *p1* means that the relationship before the threshold or the first stage is quadratic; *p3* means that the third stage is quadratic; *1 + p2* means that the model has one threshold, the first stage is linear and the second stage is quadratic

^a The selected model

increased [slope of 0.50 kg/year (0.09; 0.33 to 0.67)] likely in response to an increase in female mass with age. These results do not support either the senescence or the terminal allocation hypotheses. Alternatively, these results could also suggest compensation between the negative effects of senescence and positive effects of terminal allocation.

Age-related energy expenditures: senescence or terminal allocation

When accounting for both female identity and body mass in June, variation in female mass between June and September was best fitted by a one-threshold model and by the second-order polynomial model (Table 4). As expected, mass gain strongly decreased with age up to 3.5 years when females reach the end of their growth period. From 3.5 to about 7–8 years of age, female mass gain decreased with increasing age, and then increased with age in old age [slope of -1.43 kg/year (0.37; -2.21 to -0.74) and quadratic term of 0.101 (0.043; 0.017–0.19); Fig. 5]. Mass

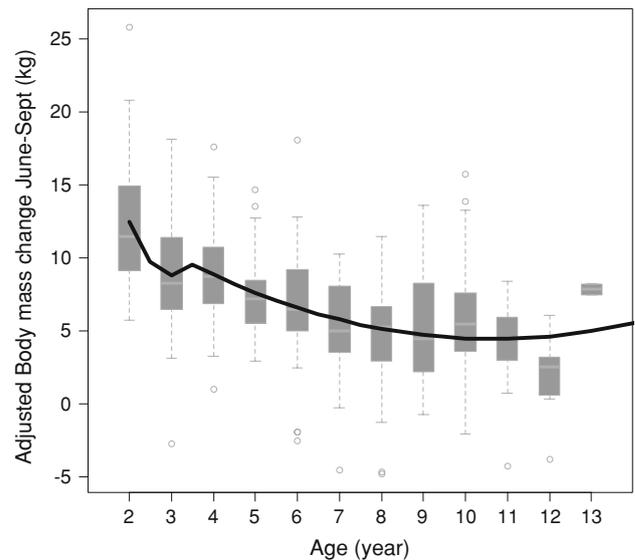


Fig. 5 Box plot of the change in female mass between June and September (i.e., from parturition to calf weaning). Boxes show the 25–75% quartiles. The black line corresponds to the best-fitted model

gain between June and September was not influenced by offspring sex [-0.31 kg (0.42) when producing a male calf compared to a female calf], varied among years, and did not change with mother mass [slope of 0.042 calf kg/mother kg (0.035)]. Age_fsr did not affect change in body mass [0.071 (0.287)]. Variance components from the best model showed a much smaller contribution of individual heterogeneity than residual within-individual variation ($\sigma^2_{ID} = 1.24, \sigma^2_{Res} = 14.9$), whereas the variance components from the null model showed that the covariates of the best model explained both the between- and within-individual variation ($\sigma^2_{ID} = 4.23, \sigma^2_{Res} = 28.5$). When dropping mother’s mass from the model the results remained similar, except that the decrease in mass gain with increasing age was linear instead of quadratic. Thus, on an absolute scale, the pattern of mass change between June and September supported the senescence hypothesis. For a given mass, old females were able to gain similar or even more mass than prime-aged ones, certainly because of the decrease in energy allocation of old females to offspring. This result thus contradicts the terminal allocation hypothesis. When we dropped female identity from the model, the pattern remained unchanged.

Calf mass in autumn had a marked positive effect on female change in mass between June and September [slope of 0.167 calf kg/mother kg (0.046; 0.079–0.265)]. When looking for differential effects of calf mass on mass gain according to mother age, we found no evidence for an effect of calf mass depending on female age [multiplicative term age × calf mass of 0.020 (0.013)]. When adding calf survival as a factor of variation in female mass gain, a marked negative effect occurred [difference of -3.43

Table 5 Model selection (using AIC_c) from a set of threshold (with one or two thresholds) and poly (including constant, linear, and >1 order poly) models fitted to assess how change in female body mass between 2 consecutive years (September–September; a measure of maternal expenditure) varies with their age

One threshold	3.5	4.5	5.5
1 + 2	2,438.06 ^a	2,438.52	2,442.47
p1 + 2	2,439.82	2,438.68	2,438.08
1 + p2	2,439.09	2,440.68	2,443.72
p1 + p2	2,439.88	2,440.59	2,440.24
Two thresholds	3.5 and 10.5	3.5 and 11.5	4.5 and 11.5
1 + 2 + 3	2,439.85	2,440.18	2,440.29
p1 + 2 + 3	2,441.59	2,441.98	2,440.66
1 + p2 + 3	2,440.07	2,440.06	2,442.30
1 + 2 + p3	2,442.00	2,442.35	2,442.38
Poly only			
Constant	2,520.40		
Age	2,466.50		
Poly2	2,447.22		
Poly3	2,439.13		
Poly4	2,440.27		

The first rows show the threshold age(s). Sample size was 435 observations on 163 females. Calf sex, female mass in June, age at first successful reproduction, female identity, calf mass in autumn, calf survival and year were also included in the model. For example, *p1* means that the relationship before the threshold or the first stage is quadratic; *p3* means that the third stage is quadratic; *1 + p2* means that the model has one threshold, the first stage is linear and the second stage is quadratic

^a The selected model

(0.733 kg)], indicating an energetic reproductive cost of raising a calf. Such a reproductive cost did not vary according to mother age [0.177 (0.255)]. The influence of raising a calf remained unchanged when we dropped the effect of female mass from the models.

Observed variation in difference in female body mass in autumn between 2 consecutive years (year before – current year) was best fitted by one-threshold models (Table 5). According to the most parsimonious model, mass gain between 2 consecutive years first decreased markedly with age up to 3.5 years [slope of -3.59 kg/year (0.555; -4.68 to -2.50)] when females reach the end of their growth period, and then decreased more slowly with age from 3.5 years of age onwards [slope of -0.271 (0.085; -0.439 to -0.104); Fig. 6]. Mass gain between 2 consecutive years was not influenced by offspring sex [-0.443 kg (0.382) when producing a male calf compared to a female calf] and varied among years. When including the strong negative effect of mother mass [slope of -0.265 (0.031)], the difference in body mass change with age for females older than 3.5 years

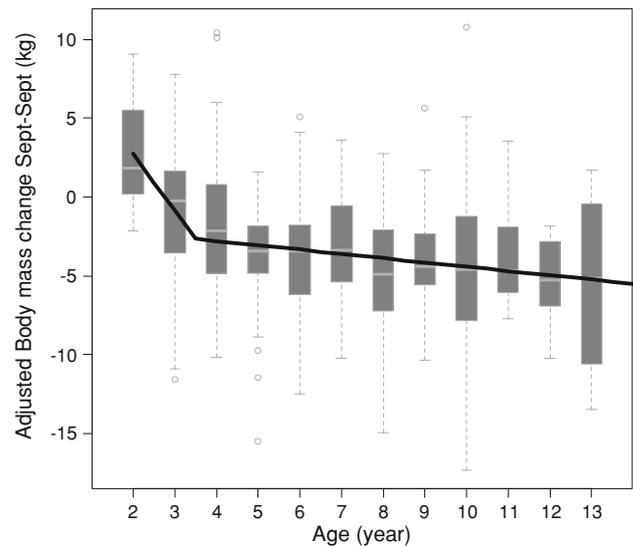


Fig. 6 Box plot of the change in female mass September–September (i.e., from calf weaning in a given year to calf weaning the following year). Boxes show the 25–75% quartiles. The black line corresponds to the best-fitted model

of age no longer occurred [slope of 0.020 (0.086)], so that senescence in body mass accounted for the observed pattern of body mass change between consecutive years. Age_{fsr} negatively affected change in body mass [-0.459 kg/year (0.224)], but otherwise did not change parameter estimates of fixed effects and variance components. The estimated variance for the between individual variance was 0 ($\sigma_{\text{Res}}^2 = 15.2$), whereas the variance components from the null model showed that the covariates of the best model explained both the between- and within-individual variation ($\sigma_{\text{ID}}^2 = 4.16$, $\sigma_{\text{Res}}^2 = 28.4$). When we dropped female identity from the model, the pattern remained unchanged. Calf mass in autumn did not influence female mass change between consecutive years [slope of 0.016 (0.045)]. When adding calf survival as a factor of variation in female mass gain, a marked negative effect occurred [difference of -1.818 (0.629; -3.07 to -0.57)], indicating an energetic reproductive cost of raising a calf. Such a reproductive cost increased with increasing mother age [difference of -3.77 (0.977) before 3.5 years of age and -0.554 (0.786) from 3.5 years of age onwards]. These results support both the hypotheses of senescence and terminal allocation.

Discussion

Age-specific maternal mass

By monitoring reindeer females from birth to death, we found that female body mass first increases strongly until the age of 3.5, and then increases slowly until 10–11 years

of age when the maximum body mass is reached, and then slightly decreases at older ages. Most ungulate females grow fast and reach maximum body mass early in life [e.g., 5 years in reindeer (Timisjärvi et al. 1982; Nieminen and Petersson 1990); 4 years in bighorn sheep *Ovis canadensis* (Festa-Bianchet et al. 1996); 5 years in moose *Alces alces* (Wallin et al. 1996); 2 years in roe deer *Capreolus capreolus* (Gaillard et al. 2000a); 6 years in mountain goat *Oreamnos americanus* (Festa-Bianchet and Côté 2008); 5 years in red deer (Mysterud et al. 2001)]. Likewise, the decrease in body mass among the oldest females reported here has been found in other ungulates such as bighorn or roe deer (Gaillard et al. 2003).

Age-related reproductive output and energy expenditure

Female reindeer showed age-related change in reproductive output, but with different patterns depending on which “component” of reproductive output was used. Calf mass at birth increased and then decreased with female age, thereby supporting the senescence hypothesis. In support of previous work on reindeer (Rönnegård et al. 2002; Weladji et al. 2002), calf mass at birth declined after about 5–6 years of age. A similar senescence pattern has been reported for other ungulates (see Mysterud et al. 2002; DelGiudice et al. 2007) as well as birds (e.g., Robertson and Rendell 2001). On the other hand, the autumn mass of calves did not change as females became older. The absence of age-specific change in calf mass in autumn can be interpreted either as not supporting either the senescence or the terminal allocation hypothesis, or supporting both in an exactly compensatory way. The allocation of milk to offspring is condition dependent (Clutton-Brock 1991; Landete-Castillejos et al. 2005) so we can expect old females to raise lighter fawns at the end of the weaning period than prime-aged females. However, for a given condition, females of different ages should adopt different tactics (Williams 1966). Prime-aged females with poor condition should trade energy allocation to offspring for their own survival, whereas old females should invest more in offspring. Such age-specific reproductive tactics (as reported by Holand et al. 2006 in this population) might account for the low variation of calf mass in autumn with mother’s age. Alternatively, a quite constant calf mass in autumn according to mother age could be attributed to the fact that calves born from old mothers might be able to compensate for a poor early growth during the summer under the mild environmental conditions reindeer of this population experience. In support of this, Gaillard et al. (1993) did not find any relationship between early development of fawns and body mass at the onset of winter in a highly productive population of roe deer [but see e.g.,

Solberg et al. (2008) for the absence of compensation in a highly productive population of moose].

Our results indicate that raising a calf is energetically more costly for old females than for prime-aged females because the mass gain decreased with increasing age among females that raised a calf. Ericsson et al. (2001) also found that older moose had to give birth to heavier offspring to achieve the same offspring summer survival as that for offspring of younger mothers. For reindeer in this study all females gained mass, but the somatic cost seemed relatively higher only for the oldest females, indicating that senescence (i.e., a decrease in the ability of gaining mass for a given reproductive output by old females) occurs. Obviously this could be attributed to senescence as we found that female body mass slightly decreased at older ages (Fig. 2), so that they have increasingly fewer resources to allocate to reproduction as they age due to individual loss of functional capacities in old age (Hamilton 1966; Kirkwood and Austad 2000; McCleery et al. 2008). Among prime-aged females (5.5–11.5 years old), females that weaned a calf were lighter in autumn by about 1.6 kg (SE = 0.66) than those that did not, which supports previous studies on reindeer (Kojola and Eloranta 1989; Gerhart et al. 1997; Rönnegård et al. 2002). Indeed, the measures of the female energy expenditure appeared to be age specific, and associated with a reproductive cost (of rearing) that also increased with increasing age. We therefore likely faced the case of terminal allocation, in which old females show evidence of senescence in some life history traits but succeed better to raise offspring than prime-age ones without any evidence of a fitness cost. Similar findings have been reported by Clutton-Brock (1984) on red deer for which calf condition increases with age relative to mother’s condition in early winter. However, Clutton-Brock (1984) found in addition that previous reproductive status negatively influenced calving success in red deer, as expected from the terminal investment hypothesis. In the present case of reindeer we did not report any evidence for reproductive costs in terms of future survival or reproduction (Weladji et al. 2008), so that the increasing effort to raise a calf shown by females when ageing we report here only supports the terminal allocation hypothesis.

Emerging patterns

Clearly reindeer show age-related differences in reproductive output, displaying mostly senescence and to a lesser extent terminal allocation processes depending on the reproductive components being studied. We found that the reproductive output generally increases with female age during the growth phase (age < 6 years), and varies more according to the reproductive component studied for old females, which had to compromise between increased needs for maintenance and allocation to offspring. Among

females that have stopped growing, calf mass at birth decreases with age, but not calf mass in autumn. Light calves born from old females were able to compensate for a bad start by autumn. However, from the available data it was not possible to tease apart the role of the mother (i.e., age-specific reproductive tactics, old females with better knowledge of the best foraging places) from the role of the calf (i.e., small calves spending more time foraging under favorable environmental conditions).

Among older females, increasing calf survival versus no-change in female mass could be seen either as a trade-off or just an effect of experience, as we have shown previously (see Weladji et al. 2006). Females were able to secure greater pre-weaning survival of their offspring at the cost of their own growth, suggesting a trade-off between allocation of resources to their growth and to the survival of their offspring. Indeed, calves born from old females had a higher survival rate than calves born from young females (see also Green and Rothstein 1991).

Hence, the age-specific pattern of reproductive output may be a complex interplay between an increase and a decrease in reproductive allocation at the individual level, because different life history components may respond to “ageing” in contrasting ways (Nussey et al. 2008; Descamps et al. 2008). We did not have enough fitness cost-related data to conclude on the terminal investment hypothesis, hence when we did find evidence of a direct cost of reproduction, we attributed the older age pattern to a “terminal allocation tactic”. In line with a recent suggestion that ageing patterns should be examined in multiple traits (Nussey et al. 2008), our research clearly shows that senescence, a decline in performance in old age, is the prevalent pattern in reindeer. Consistently, removing female identity from our models yielded a different pattern, suggesting also that individual heterogeneity in quality could prevent one from detecting senescence (see Weladji et al. 2008; Descamps et al. 2008).

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