POPULATION ECOLOGY

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Age-related reproductive effort in reindeer (*Rangifer tarandus*): evidence of senescence

Abstract Age-specific rates of survival and reproduction in iteroparous organisms remain a key issue in population ecology. How patterns of survival vary with age in large herbivores is well known; much less is known regarding age-specific patterns of reproduction. The senescence hypothesis predicts a progressive loss of function accompanied by decreased performance with age. The terminal investment hypothesis predicts that the proportion of resources a mother invests (i.e. effort relative to costs) is expected to increase toward the end of her life-span, when the number of offspring she can expect to rear in the future is low. Assuming that the costs remain stable, the terminal investment hypothesis predicts increased reproductive effort with age. We used data on body weight of 1,956 semi-domestic reindeer (*Rangifer tarandus*) calves from females with known age and weight to test these two (not mutually exclusive) hypotheses. Body weight of calves clearly decreased after 7 years of age was reached (also after controlling for female body weight), which was in support of the senescence hypothesis. We can conclude that either the terminal investment hypothesis is wrong, and/or the reproductive costs increase with age in female reindeer.

Keywords Aging · Body weight · Cervids · Female reproductive effort · Life history

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Introduction

Age-specific rates of survival and reproduction in iteroparous organisms remain a key issue in population ecology. Such information is necessary in order to use age-structured population models (Tuljapurkar and Caswell 1997; Coulson et al. 2001). Recent comparative studies and reviews provide great insight into how patterns of survival vary with age in large herbivores (Gaillard et al. 1998a, 2000b; Loison et al. 1999). However, much less is known regarding age-specific patterns of reproduction, particularly for older females [but see e.g. Bérubé et al. (1999); Ericsson et al. (2001)]. Two different hypotheses provide somewhat contrasting predictions regarding reproductive effort of old females. The senescence hypothesis predicts a progressive loss of function accompanied by decreased performance with age (Kirkwood and Austad 2000; Mysterud et al. 2001). In contrast, the terminal investment hypothesis predicts that the proportion of resources a mother invests is expected to increase toward the end of her life-span, when the number of offspring she can expect to rear in the future is low (Gadgil and Bossert 1970; Trivers 1972; Pianka and Parker 1975; Clutton-Brock 1984). Since the terminal investment hypothesis predicts parental effort relative to costs of reproduction to the female (Trivers 1972; Evans 1990), these hypothesis are not mutually exclusive.

Using data on body weight of 1,956 semi-domestic reindeer (*Rangifer tarandus*) calves from females of known age and weight, we tested whether reproductive effort (body weight of calf) increases or decreases with advancing age of the mother. The terminal investment hypothesis relates to parental effort relative to the costs (Evans 1990), while the senescence hypothesis does not. We therefore tested these relationships both before and after controlling for female body weight, as body weight may at least partly correlate with costs (Clutton-Brock 1984). Further, there is suggested to be a strong link between female body weight and longevity (Gaillard et al. 2000a). We therefore also tested whether any rate of re-

Table 1 Sample sizes and weights (kg) of females and calves for semi-domestic reindeer of different ages (estimates for calf weight are least squares means from the model including mother's age, mother's weight, calf's sex, calf's sex×mother's age and mother's age×mother's weight)

Age of female (years)	2	3	4	5	6	7	8	9	10	11	12
Number of females	176	190	186	191	159	129	177	205	167	50	26
Mean weight of females	63.455	65.842	70.855	71.340	71.390	69.868	71.313	69.229	71.467	71.140	67.077
SE (female weight)	0.444	0.428	0.432	0.427	0.468	0.519	0.441	0.412	0.456	0.834	1.156
Adjusted mean weight of calf	23.677	24.678	25.534	25.670	25.816	26.278	26.246	25.824	24.927	25.429	24.320
SE (calf weight)	0.284	0.221	0.192	0.194	0.216	0.224	0.199	0.177	0.208	0.376	0.560

productive senescence (i.e. a decline in calf weight with age) was dependent on female body weight.

Materials and methods

We used data from a study on semi-domestic reindeer conducted in Riast/Hylling grazing district, south-central Norway (Lenvik et al. 1988). Body mass of 1,969 females of known age was recorded in March 1984. Based on 1,656 known mother-calf relationships, the sex and the body weight of calves were determined during the third week of July (mother's age-specific sample sizes in Table 1). All animals from this herd are tagged as calves, and hence age of females is known exactly. The mother-calf relationship was established at about 2 months of age based on which female the calf was following. Data from this study is described in detail elsewhere (Lenvik et al. 1988). The previous analyses of this dataset, though testing for age and weight-related effects on calf weights, did not test for any possible effect of senescence, and was only used to provide a basis for future artificial selection in semi-domestic reindeer (Lenvik et al. 1988).

Statistical analyses

We used linear models to establish the relationship between weight of offspring and age and weight of mother. We ran two models, both with and without controlling for mother's weight. As the relationship between calf weight and mother's age is predicted to be nonlinear (e.g. Mysterud et al. 2001), we also considered a second-order polynomial of age (the top of the curve was used to define prime age). Sex of offspring and the interaction between sex of offspring and age of mother was also included in the model.

As it is difficult to consider interactions between body weight of females and a quadratic term for age, and since no senescence is expected prior to 8 years of age (Gaillard et al. 2000a; Mysterud et al. 2001; see also Results), we ran a separate model including females aged 8 years or older [see Mysterud et al. (2001) for a similar approach].

As the relationship between weight and reproduction may differ among primiparous and multiparous (Langvatn et al. 1996), we also tested for an interaction between body weight and age. In order to reliably interpret interactions of two continuous variables (age and weight of female), we standardized body weight of females (mean=0; SD=1) and restricted the analysis to a multiplicative term between body weight and age (Portier et al. 1998; Mysterud et al. 2000, 2001). Analyses were carried out in SAS (SAS 1998) and S-Plus (Venables and Ripley 1994).
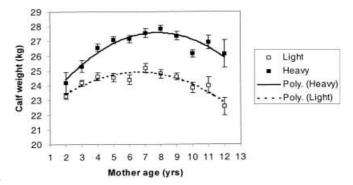

Fig. 1 The relationship between reindeer calf weight (±1 SE) and mother's age for heavy (i.e. weight above average) and light (i.e. weight below average) females. Calf weights are least squares means adjusted for calf's sex. "Poly" is brief for polynomial curve fitting

Results

Body weight of reindeer calves, and hence one aspect of female reproductive effort with respect to offspring, peaked for mothers at 7 years of age, both when not including ($R^2=0.122$; $n=1956$; Table 2) and when including female body weight in the model ($R^2=0.360$; Table 2). Weight of offspring declined when considering only females aged 8 years or older in the model (Table 2). The senescence hypothesis was therefore supported. Calf body weight was positively correlated with females' body weight (Table 2). However, the relationship between weight of mother and reproductive output varied with age of the mother (i.e. a significant interaction between mother's weight and age; Table 2). Heavy, young females produced lighter calves than heavy, old females, while both young and old light individuals produced offspring of about similar weight (Fig. 1). For old females, the decline in calf mass with female age was similar for light and heavy females, i.e. there was no interaction between age and body weight of female for old females (Table 2). Male calves were heavier than female calves.

Table 2 Results from analyses of how reproductive effort (calf weight) in reindeer females varies as a function of age, with and without controlling for body weight in the model, and when considering only old females. Only significant factors were included in models when estimating parameters (with least squares)

Variable	df	F	P	Least square estimate	SE
All females (n=1,656)					
Intercept				22.600	0.421
Calf's sex	1,1654	15.07	<0.001	–1.772	0.139
Mother's age	1,1653	172.04	<0.001	1.856	0.127
(Mother's age)^2	1,1652	174.90	<0.001	–0.130	0.010
Calf's sex×mother's age	1,1651	2.16	0.1414		
All females (n=1,656)					
Intercept				13.956	1.634
Calf's sex	1,1654	17.31	<0.001	–1.719	0.125
Mother's weight	1,1653	35.83	<0.001	0.152	0.025
Mother's age	1,1652	83.35	<0.001	1.218	0.127
(Mother's age)^2	1,1651	84.03	<0.001	–0.088	0.010
Mother's age×weight	1,1650	5.12	0.024	0.152	0.025
Calf's sex×mother's age	1,1649	2.63	0.105		
Females≥8 years (n=625)					
Intercept				33.424	1.002
Calf's sex	1,623	83.300	<0.001	–1.883	0.219
Mother's weight	1,622	179.800	<0.001	1.448	0.110
Mother's age	1,621	25.650	<0.001	–0.513	0.101
(Mother's age)^2	1,620	0.250	0.612		
Mother's age×weight	1,619	0.160	0.700		
Calf's sex×mother's age	1,618	0.630	0.427		

There was no evidence that reproductive effort towards males relative to female offspring varied with female age (i.e. no interaction between sex of offspring and mother's age; Table 2).

Discussion

Although the life-history of large herbivores is commonly split into young, prime-aged and senescent stages when discussing survival patterns (Caughley 1966; Gaillard et al. 1998a, 2000b), data on age-specific reproductive rates are scarce. This is probably because reproductive senescence seems to occur at a later stage than survival senescence (Bérubé et al. 1999), and it is therefore even more difficult to obtain such data. Earlier studies nevertheless indicated a decline in the proportion of females reproducing after prime-age was reached, but this was based on data where age determination was partly unreliable [for horses *Equus caballus* (Garrott et al. 1991)] or based on either tabular data or many ages pooled in classes [for red deer *Cervus elaphus* (Langvatn et al. 1996); bighorn sheep *Ovis canadensis* (Festa-Bianchet 1988)]. Only recently has convincing evidence of a declining proportion of females lambing [in bighorn sheep (Bérubé et al. 1999)], a reduced litter size [in moose *Alces alces* (Ericsson and Wallin 2001)] and decreased productivity [in roe deer *Capreolus capreolus* (Gaillard et al. 1998b; Hewison and Gaillard 2001)] with increasing age of female been reported. Our study provides corroborative evidence for this pattern, as we found that body weight of calves clearly declines with age after females reach 7 years of age.

While we now can state fairly confidently that the senescence hypothesis applies not only to survival but also to reproduction in ungulates, much less is known regarding (terminal) investment patterns. Parental investment is, by definition "any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the costs of the parent's ability to invest in other offspring" (Trivers 1972; Evans 1990). In contrast, parental input or effort is the care or resources actually provided for the offspring irrespective of its cost (Evans 1990), and hence, in our study we have data on parental effort. It is commonly assumed that reproductive costs may be a function of body size in ungulates (Clutton-Brock 1984). However, even after controlling for female body mass, weight of offspring declined with age for females 7 years or older. As the reindeer herd is semi-domestic and our data are transversal, we cannot rule out that selection may affect the pattern observed; we might expect the herdsmen to remove less productive individuals. However, this would make our estimates more conservative, and should therefore not affect our conclusion. We can therefore conclude that either the terminal investment hypothesis is wrong, or the reproductive costs increase with age. Unfortunately, data on mass loss in females [and hence a reliable measure of reproductive costs in capital breeders (Festa-Bianchet et al. 1998)] was not available.

On the island of Rum, Scotland, red deer calf condition relative to mother's condition in early winter in-

creased with age (Clutton-Brock 1984). Our data was from mid July, and it may be that old females provide more care post-natally (Green 1990). Evidence has been presented showing that older mothers showed higher tolerance towards and spent longer time nursing offspring [in bison *Bison bison* (Green 1990)], and that they were better at targeting the effort to the most critical period for the offspring [in horses *E. caballus* (Cameron et al. 2000)]. Still, we regard it unlikely that the lighter calves of older females found in July are heavier when they reach winter, as most of their growth occurs in early summer. For red deer from Rum, no data on body weight or size was presented, only calf condition relative to female condition (Clutton-Brock 1984). Body size may be equally or more important than condition for winter survival, since the energetic costs of travelling in snow are closely related to chest height (Parker et al. 1984). Evidence in favour of the terminal investment hypothesis in ungulates is therefore not convincing. Until solid data on mass loss of females prior to and after breeding is available, it is premature to conclude whether or not the terminal investment hypothesis applies to ungulates.

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