

Body mass and individual fitness in female ungulates: bigger is not always better

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In female vertebrates, differences in fitness often correspond to differences in phenotypic quality, suggesting that larger females have greater fitness. Variation in individual fitness can result from variation in life span and/or variation in yearly reproductive success, but no study has yet assessed the relationships between the components of fitness and phenotypic quality while controlling for life span. We tried to fill this gap using data from long-term monitoring (23 years) of marked roe deer and bighorn sheep, two ungulates with very different life histories. In both species, we found a strong positive relationship between an adult female's mass and her probability of reaching old age: over the long term, bigger is indeed better for ungulate females. On the other hand, we found no evidence in either species that heavier females had higher fitness when differences in life span were accounted for: over the short term, bigger is not necessarily better. Our results indicate that, while broad differences in phenotypic quality affect individual fitness, when differences in life span are accounted for phenotypic quality has no residual effect on fitness. Therefore, within a given range of phenotypic quality, bigger is not always better, for reasons which may differ between species.

Keywords: *Capreolus capreolus*; lifetime reproductive success; life span; *Ovis canadensis*; phenotypic quality

1. INTRODUCTION

Long-term studies of marked individuals have revealed that substantial individual variation in fitness, often estimated by lifetime reproductive success (LRS), occurs for both sexes in natural populations under a variety of breeding systems or ecological contexts (Clutton-Brock 1988; Newton 1989). Variation in fitness can originate from variation in the number of breeding attempts (which mostly depends upon life span), number of offspring per breeding attempt and offspring survival. Previous studies of vertebrates have reported that most variation in individual fitness is accounted for by the variation in offspring survival (Clutton-Brock 1988) and in life span (Newton 1989) rather than by variation in fecundity.

The individual characteristics which can lead to variation in fitness include sex (Clutton-Brock 1988), cohort (Rose *et al.* 1998) and body size (Leboeuf & Reiter 1988). In some birds, the largest individuals have the greatest fitness, but other studies have found no association between fitness and body size (Newton 1989). Large mammal females are generally considered to be capital breeders (Stearns 1992) and, therefore, should show a strong relationship between individual body mass and reproductive success. In some ungulates, larger females give birth to larger offspring than smaller females (Kojola 1993; Birgersson & Ekvall 1997) and large offspring tend to be more likely to survive than small ones (e.g. Guinness *et al.* 1978). Large females may therefore wean more offspring than small females for a given number of breeding attempts. However, because of the

logistic difficulties of measuring adult body mass in large mammals, the relationship between mass and individual fitness remains unclear.

Here we examine the effect of mass on female fitness for two ungulates, roe deer (*Capreolus capreolus*) and bighorn sheep (*Ovis canadensis*), which differ markedly in their life histories. The survival of adult female ungulates is generally high with little year-to-year variation (Gaillard *et al.* 1998b), but little is known about the relationship between survival and body mass (Bérubé *et al.* 1999). After assessing whether adult body mass affects life expectancy in both species, we tested whether larger females have higher fitness than smaller females after accounting for the differences in female longevity.

2. MATERIAL AND METHODS

(a) Study areas, species and populations

We studied two populations with markedly different dynamics: bighorn sheep on Ram Mountain in Canada and roe deer at the Trois Fontaines reserve in France. Bighorn sheep are medium-sized caprins which prefer open areas. Adult males are around 1.6 times heavier than adult females (Festa-Bianchet *et al.* 1996). Ewes give birth to a single lamb in May–June and can be considered capital breeders because their body mass affects their reproductive costs and their reproductive effort one year affects their body mass the following year (Festa-Bianchet *et al.* 1998). Roe deer are small, forest-dwelling ungulates. They are almost monomorphic, with males heavier than females by less than 10% (Andersen *et al.* 1998). Roe deer females usually give birth to twin fawns in May–June and appear to rely almost exclusively on food resources available within their home range to satisfy the energetic costs of lactation. Relative to bighorn

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sheep, roe deer females can thus be considered income breeders (Andersen *et al.* 1998, p. 288).

The bighorn population varied considerably in density during the study and density dependence was evident for age at first breeding (Jorgenson *et al.* 1993), lamb survival (Portier *et al.* 1998) and yearling survival (Jorgenson *et al.* 1997). In contrast, the roe deer population at Trois Fontaines was kept stable by yearly removals (Gaillard *et al.* 1993) and showed no evidence of density dependence (Gaillard *et al.* 1998c). Further details about the study sites and populations are published elsewhere (Gaillard *et al.* 1993; Festa-Bianchet *et al.* 1995).

Here we used data collected from 1975 to 1998, when over 98% of bighorn ewes and *ca.* 70% of roe deer does were individually marked with visual collars. All females included in our analyses were of known age because they were first captured when aged less than one (roe deer) or two (bighorn sheep) years. Bighorn sheep were caught in a corral trap between May and October. Over 95% of the females were caught each year and the yearly resighting probability was over 0.99 (Jorgenson *et al.* 1997). Roe deer were caught using net drives in January–February. The yearly capture probability for females was about 0.50 (Gaillard *et al.* 1993). Intensive observations took place every year in both study sites during summer and autumn in order to assess the reproductive success of marked females.

(b) *Measuring life span and body size*

Roe deer females give birth for the first time at two years of age (Gaillard *et al.* 1998c). At Trois Fontaines, the proportion of lactating two year olds was equal to that of older females (Gaillard *et al.* 1998a). By two years of age, roe deer females have reached *ca.* 95% of their maximum body mass (J.-M. Gaillard, M. Festa-Bianchet, D. Delorme and J. Jorgenson, unpublished data). Thus, we defined the adult life span in roe deer as the longevity of females that lived more than two years. For bighorn sheep, age at first lambing was density dependent and at peak density most ewes delayed primiparity until four years of age (Gallant 1999). By four years of age, ewes have reached almost 95% of their maximum body mass (Festa-Bianchet *et al.* 1996). We thus defined the adult life span in bighorn as the longevity of ewes that lived more than four years.

We excluded females which died from human-related causes (including road kills, removals for scientific purposes and capture mortalities). Because of the very high resighting rate (0.99) of bighorn ewes, the last sighting was used to assess their longevity. For roe deer does, combining winter captures and intensive observations from March to December provided a resighting rate of 0.84 (J.-M. Gaillard, unpublished data). Thus, the last recapture or resighting of an individual was used to assess its longevity. To obtain unbiased measures of longevity, one should only use cohorts for which all females had died by the time of the last sampling (e.g. Clutton-Brock *et al.* 1988). Because roe deer and bighorn females can live for more than 16 years (Loison *et al.* 1999), few cohorts could have been included in our analyses. Therefore, we measured adult life span as the probability of females which lived over two (roe deer) or four (bighorn) years surviving to a threshold age. The onset of survival senescence is after seven years of age in both species (Loison *et al.* 1999) and we used that as the threshold age. We thus examined a much larger sample of bighorn ewes than that analysed by Bérubé *et al.* (1999).

We used the mass of adult females as a measure of phenotypic quality. We did not have a mass-independent measure of body condition. For this comparison, the average adult mass was

preferable to their average condition because between-individual variation in condition is expected to be weak in an income breeder such as roe deer (Andersen *et al.* 1998) and for a capital breeder such as bighorn sheep body condition varies from year to year (Festa-Bianchet 1998) and is affected by their reproductive effort (Festa-Bianchet *et al.* 1998). The body mass of bighorn ewes follows a pronounced seasonal cycle (Festa-Bianchet *et al.* 1996) and varies between years depending on their reproductive status (Festa-Bianchet *et al.* 1998). For each ewe older than four years, we used their mass adjusted to 15 September (see Festa-Bianchet *et al.* (1996) for details on mass adjustment) and averaged for all years used to assess reproductive success (see § 2(c)). For adult roe deer females, individual mass is stable both within and between years (Hewison *et al.* 1996). For each female older than two years, we used the mean body mass measured during captures in January–February.

(c) *Assessment of reproductive success and individual fitness*

We measured reproductive success by the number of weaned offspring. Offspring survival to weaning should be strongly affected by a mother's characteristics, while non-maternal factors should become more important after the period of maternal care. In bighorn sheep, experimental early weaning had no effect on lamb survival (Festa-Bianchet *et al.* 1994) and lamb survival from weaning to one year was affected by the population density but not by maternal mass or previous reproductive effort (Festa-Bianchet *et al.* 1998). Most roe deer fawn mortalities occurred before weaning (Gaillard *et al.* 1997) and the winter survival of fawns was high (Gaillard *et al.* 1993).

The yearly reproductive status of marked females was assessed from repeated observations of female–offspring associations during summer and autumn. Females whose offspring survived to July (roe deer) or October (bighorn) were classified as reproducing successfully.

In both species, their yearly reproductive success was age independent for adult females aged less than 14 years (Gaillard *et al.* 1998a; Bérubé *et al.* 1999). For this paper, we assumed that no female older than 14 years weaned any offspring. However, for bighorn sheep population density had a strong effect on reproductive success (Festa-Bianchet *et al.* 1998). We thus divided bighorn ewes into three classes of population density: females for which reproductive success was (i) only monitored at low density, (ii) monitored at both low and high density (referred to as intermediate density) and (iii) only monitored at high density. The density at Ram Mountain increased during our study and, as in our previous work (Festa-Bianchet *et al.* 1998), we used 1988 as the cut-off year between low- and high-density periods.

We estimated female individual fitnesses by using the dominant eigenvalue (λ) of Leslie matrices, as proposed by McGraw & Caswell (1996) and recently applied to human populations by Käär & Jokela (1998). Using individual λ -values rather than long-term reproductive success to estimate fitness accounts for the between-female differences in their timing of reproduction. Using fitness measures based on reproductive success instead of λ led to similar results (J.-M. Gaillard and M. Festa-Bianchet, unpublished data). For each female of known longevity, we built an individual Leslie matrix (table 1) in which the age-specific fertilities (f_x) of the female were measured as half the reproductive success observed in the field (assuming an equal sex ratio of the offspring). Individual λ -values were calculated by using S-plus software (Venables & Ripley 1994). For most animals,

Table 1. An example of an individual Leslie matrix

(A female roe deer (FR) from Trois Fontaines, France, was born in May 1981 and died in February 1987. She gave birth to eight fawns, six of which survived to weaning, leading to an individual fitness λ of 1.325.)

age class					
1	2	3	4	5	6
0	0	1	1	1	0
1	0	0	0	0	0
0	1	0	0	0	0
0	0	1	0	0	0
0	0	0	1	0	0
0	0	0	0	1	0

reproductive success was not known for every year of reproductive life. When less than 50% of the data on reproductive success was lacking, we estimated the missing values. In roe deer, the between-female variation in reproductive success was pronounced (Gaillard *et al.* 1998a). To estimate missing data for a given female, we therefore used the average reproductive success in years when that female was monitored. In bighorn, the yearly variation in lamb survival was more marked than the between-female variation because of strong density-dependent recruitment (Festa-Bianchet *et al.* 1998). We thus used the average reproductive success calculated from females monitored during a given year to estimate the missing yearly reproductive success of females. Females of unknown reproductive success during more than 50% of the years of their reproductive life span were excluded from the analyses.

(d) Data analyses

We used logistic regression to test for a relationship between the probability of surviving beyond seven years for females that reached two (roe deer) or four (bighorn) years. We could not use standard multiple regression to test the effect of mass on fitness after accounting for longevity due to the statistical dependency between λ and longevity at the individual level. Therefore, we used the residuals from the regression of body mass on longevity as a measure of mass for a given longevity. We denote this measure as corrected body mass. All tests were performed using GLIM (Francis *et al.* 1993).

3. RESULTS

(a) Body mass and adult life span

For 119 bighorn females whose mean adult mass ranged from 56.8 to 84 kg, the probability of surviving beyond seven years of age (P_7) increased with mass (M) ($\text{logit}(P_7) = -6.75 + 0.118M$, $\chi^2 = 5.51$, d.f. = 1 and $p = 0.019$; figure 1a). Likewise, for 112 roe deer does ranging from 19.75 to 29 kg, the probability of surviving past seven years (P_7) increased with mass ($\text{logit}(P_7) = -5.40 + 0.234M$, $\chi^2 = 5.55$, d.f. = 1 and $p = 0.018$; figure 1b). These models suggest that, in roe deer, a 10% increase in metabolic mass (to account for species differences in body mass) (Peters 1983) in the middle of the adult female body mass range would increase the probability of surviving beyond seven years of age by about 29%: a roe deer doe whose mass increased from 24 to 27 kg would

enjoy an increase in P_7 from 0.55 to 0.71. In bighorn sheep, a 10% increase in metabolic mass would increase their survival probability by 15%: a bighorn ewe whose mass increased from 69 to 78 kg would enjoy an increase in P_7 from 0.80 to 0.92.

(b) Body mass and fitness

The fitness of bighorn ewes averaged 1.063 ± 0.153 for 59 females monitored throughout their life span, whose mean body mass averaged 69.63 ± 5.07 kg. As expected, mass increased with longevity ($p = 0.015$). The relationship between fitness and ewe mass corrected for longevity did not vary according to the population density ($F = 0.653$, d.f. = 2,53 and $p = 0.525$). Fitness was affected by density ($F = 9.587$, d.f. = 2,55 and $p = 0.0003$; figure 2a) with an average of 1.118 ± 0.101 at low density, 1.155 ± 0.048 at intermediate density and only 0.986 ± 0.172 at high density. There was no relationship between the corrected body mass and fitness of ewes ($F = 0.209$, d.f. = 1,55 and $p = 0.649$; figure 2a). For these ewes, reproductive success was known in 83.4% of years. Restricting the sample to 44 females for which reproductive success was known in at least 75% of years (mean of 91.3%) did not alter the results. The individual fitness averaged 1.055 ± 0.170 . No relationship was found between fitness and ewe mass ($F = 0.092$, d.f. = 1,40 and $p = 0.763$; figure 2a) while density markedly affected fitness ($F = 7.340$, d.f. = 2,40 and $p = 0.002$; figure 2a).

The 53 roe deer does monitored over their life span had an average λ of 1.279 ± 0.380 and their body mass averaged 24.15 ± 1.89 kg. As expected, mass increased with longevity ($p = 0.016$). There was no relationship between fitness and corrected body mass ($r = 0.218$ and $p = 0.116$; figure 2b). Three females with an λ of 0 were outliers (see figure 2b). Removing these individuals led to an even lower correlation between fitness and corrected body mass ($r = 0.158$ and $p = 0.273$). For these does, reproductive success was reported in 79.0% of the years. Restricting the sample to 30 females for which reproductive success was known in at least 75% of years (mean of 92.6%) did not alter the results. The average fitness was 1.322 ± 0.239 . No relationship was found between fitness and corrected body mass ($r = 0.097$ and $p = 0.630$; figure 2b).

4. DISCUSSION

A striking feature of our results was the interspecific consistency of the relationships between survival and body mass despite major differences in taxonomy and ecological characteristics. In both species, the probability of an adult female reaching old age increased markedly with adult mass, suggesting that over the long term 'bigger is better' for ungulate females. On the other hand, in both species, fitness was not affected by mass when the differences in longevity were accounted for. Over the short term, therefore, bigger is not necessarily better.

Bérubé *et al.* (1999) found that longevity was positively correlated with mass at six years of age for bighorn ewes at Ram Mountain. Our results firmly establish that adult body mass is a predictor of life expectancy for female ungulates. Larger females may be advantaged over smaller ones because of their lower relative metabolic

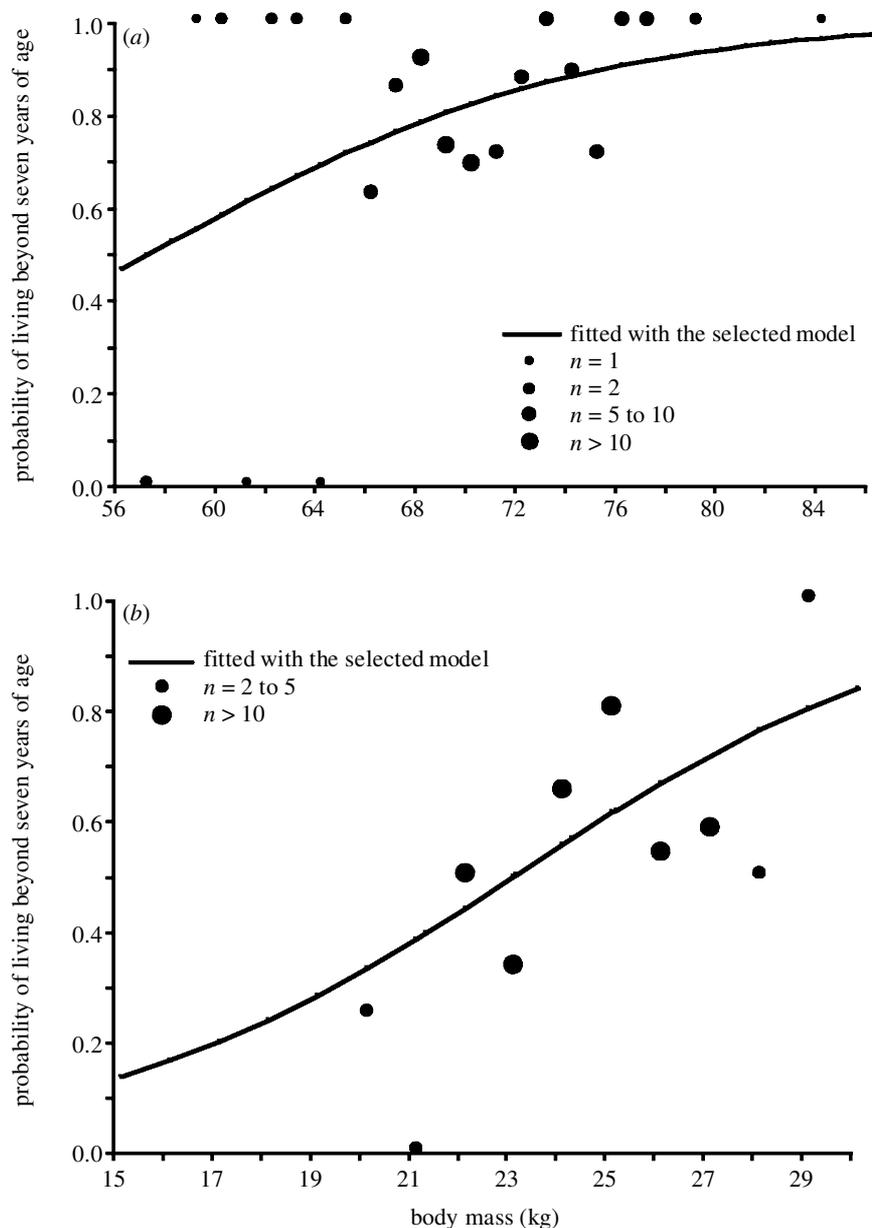


Figure 1. Relationship between the probability of surviving beyond seven years of age and adult body mass for females of (a) bighorn sheep at Ram Mountain and (b) roe deer at Trois Fontaines. The logistic regression calculated from individual data is shown (statistically significant in both cases). Points (of different size according to the sample size) indicate the average survival probabilities for each class of 1-kg mass.

rate, which may increase survival under harsh climatic conditions or during short-term food scarcity. Because of the relationship between adult life span and body mass, large females live through more breeding attempts than smaller ones. The relative effect of this relationship upon female lifetime reproduction will depend on population dynamics. When offspring survival is high and varies little over the years, variance in fitness will depend mostly on the number of breeding attempts and large females should have greater fitness than small ones. Some birds (Newton 1989), bats (Ransome 1995) and feral horses (Berger 1986) clearly belong to this category. However, when offspring survival is low or variable from year to year, the number of breeding attempts accounts for a lower proportion of the variation in fitness, which should instead depend mostly upon offspring survival. Such is the

case, for example, in red deer (*Cervus elaphus*) (Clutton-Brock *et al.* 1988) or pronghorn (*Antilocapra americana*) (Byers 1997). With variable offspring survival, the extent to which large females enjoy greater fitness than small females will depend partly on the relationship between yearly reproductive success and phenotypic quality.

The absence of a positive relationship between fitness and the body mass of adult females after correcting for longevity is surprising. Previous studies of some birds (Newton 1989) and red deer (Clutton-Brock *et al.* 1988) have reported that larger females raise more offspring than smaller females, but those studies did not account for individual longevity. Within a population, individuals can be ranked according to phenotypic quality, from covariation of small size, short life and low yearly reproductive success (poor-quality individuals) to covariation with

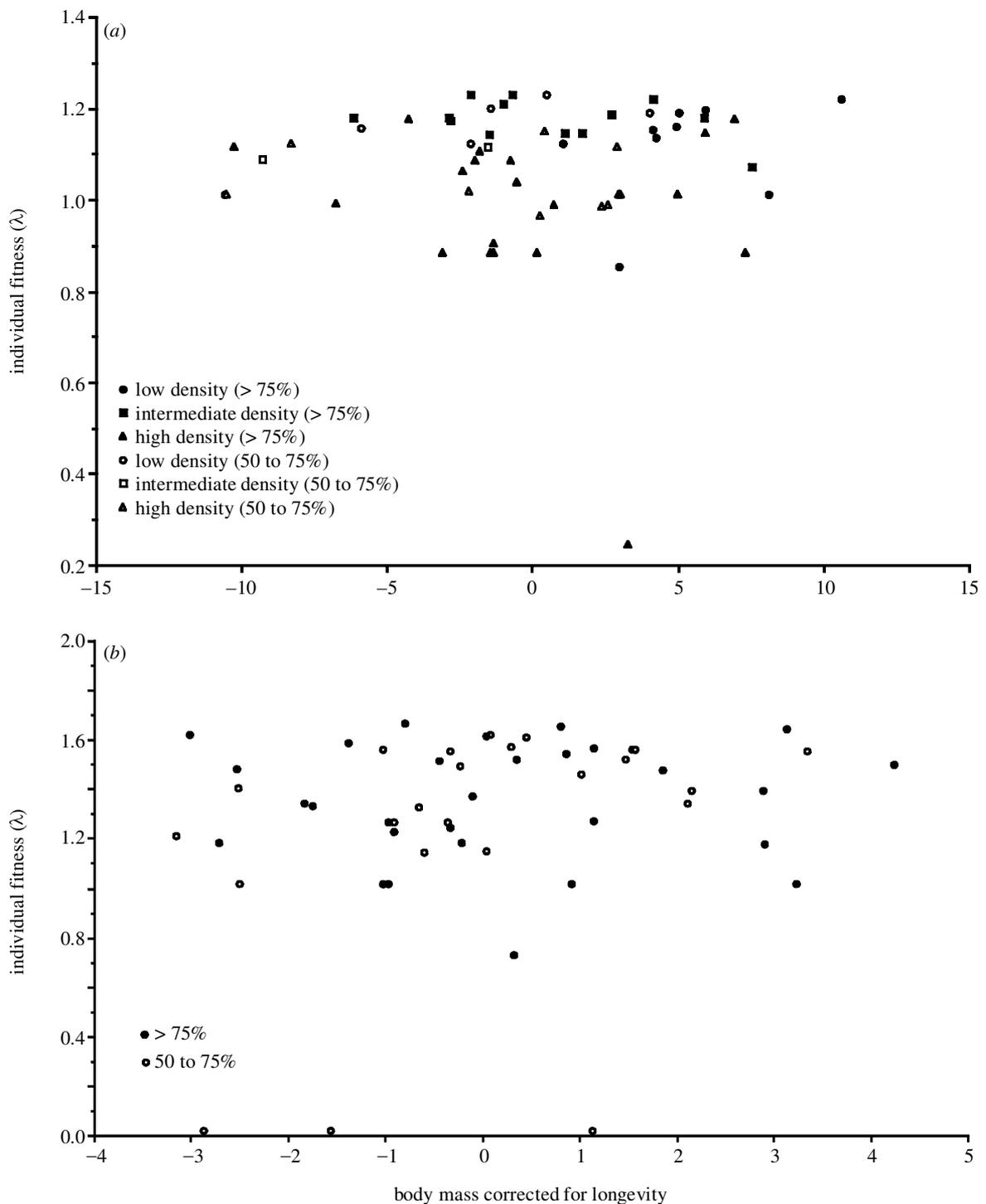


Figure 2. Relationship between individual fitness (λ) and adult mass corrected for longevity (the residuals from the regression of body mass on longevity) of (a) bighorn ewes monitored over their lifetime at three density levels and for which reproductive success was known between 50 and 75% of years ($n=59$) or in more than 75% of years ($n=44$), and (b) roe deer does monitored over their lifetime for which reproductive success was known between 50 and 75% of years ($n=53$) or in more than 75% of years ($n=30$).

opposite trait values (high-quality individuals) (Dobson *et al.* 1999). Thus, high-quality females could be more successful in raising offspring in a given year and live longer than poor-quality females. We found that females with fitness higher than the median were on average *ca.* 2 kg or 8% (roe deer) and 3 kg or 4% (bighorn sheep) heavier than females with lower than median fitness. Individual differences in fitness may partly be due to long-term cohort effects on body mass, which have been

previously reported in roe deer (Gaillard *et al.* 1997) and other ungulates (Albon *et al.* 1987; Post *et al.* 1997). However, when the differences in adult life span were accounted for, the differences in body mass between females were no longer related to the large variation in individual fitness observed in both species (coefficients of variation of 14.4% in bighorn and of 29.7% in roe deer). Two hypotheses may account for these results. First, the effect of female phenotypic quality on fitness may depend

on the causes of offspring mortality. When most sources of mortality are care independent, such as predation or disease (Lycett *et al.* 1998), individual reproductive success may be independent of maternal phenotypic quality. Offspring mortality in both populations appears to be mostly care dependent (Gaillard *et al.* 1997; Portier *et al.* 1998); therefore, reproductive success should be related to maternal attributes. Alternatively, phenotypic quality may not have the same effects on fitness and yearly reproductive success. The variance in individual fitness may be caused by negative (compensation) or positive (depensation) autocorrelation between the yearly reproductive success as well as by heterogeneity between individuals (Sydeman & Nur 1994). In roe deer, depensation and heterogeneity between females in reproductive success were evident through family effects (Gaillard *et al.* 1998a). Therefore, the absence of a relationship between individual fitness and the mass of females after correcting for longevity in this species cannot be explained by interdependency between successive reproductive attempts. Female attributes other than mass, such as home range quality (Strandgaard 1972), may explain the between-female variation in fitness for a given longevity. For bighorn ewes, the yearly reproductive success was condition dependent (Festa-Bianchet 1998). Successful reproduction one year led to lower condition and lower reproductive success the following year (Festa-Bianchet *et al.* 1998). Possibly, compensation between successive reproductive attempts may prevent larger females from performing better than smaller ones over a fixed set of breeding attempts, particularly when the differences in life span are accounted for. In addition, heavy ewes do not appear to provide more maternal care to their lambs than light ewes (Festa-Bianchet & Jorgenson 1998). Because fitness is strongly affected by longevity in female ungulates (Clutton-Brock 1988; Bérubé *et al.* 1999) and heavier females have a long life expectancy, there may be little selection for increased maternal investment in any one year to avoid any survival costs.

The existence of a positive association between adult life span and body mass for both bighorn sheep and roe deer suggests that the high-quality–low-quality continuum of phenotypes is a general pattern among long-lived animals. However, when differences in life span are accounted for, the influence of mass on individual fitness appears to be weak. We propose that, within a limited range of phenotypic quality, bigger is not always better, for reasons which may differ between species. In ungulates, the fitness benefits of large body size may mostly be expressed over the long term.

Anne Loison, Dominique Pontier and two anonymous referees provided constructive comments on earlier drafts of this paper. The roe deer research was financed by the Office National de la Chasse and the Centre National de la Recherche Scientifique. The bighorn sheep research was financed by the Natural Sciences and Engineering Research Council of Canada, the Foundation for North America Wild Sheep, the Alberta Sports, Recreation, Parks and Wildlife Fund and the Université de Sherbrooke. We thank the many people who assisted us in the field. Bill Wishart and Bernard Boisaubert made substantial contributions to all phases of the Ram Mountain and Trois Fontaines projects, respectively.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.