

Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality

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Body mass is a key determinant of fitness components in many organisms, and adult mass varies considerably among individuals within populations. These variations have several causes, involve temporal and spatial factors, and are not yet well understood. We use long-term data from 20 roe deer cohorts (1977–96) in a 2600 ha study area (Chizé, western France) with two habitats contrasting in quality (rich oak forest in the North versus poor beech forest in the South) to analyse the effects of both cohort and habitat quality on adult mass (i.e. median body mass between 4 and 10 years of age) of roe deer (*Capreolus capreolus*). Cohort strongly influenced the adult body mass of roe deer in both sexes: males born in 1994 were 5.2 kg heavier when aged between 4 and 10 years old than males born in 1986, while females born in 1995 were 4.7 kg heavier between 4 and 10 years old than females born in 1982. For a given cohort, adult males were, on average, 0.9 kg heavier in the rich oak forest than in the poor beech forest. A similar trend occurred for adult females (0.5 kg heavier in the oak forest). The effects of cohort and habitat were additive and accounted for ca. 40% of the variation observed in the adult mass of roe deer at Chizé (males: 41.2%; females: 40.2%). Population density during the spring of the birth accounted for about 35% of cohort variation, whereas rainfall in May–June had no effect. Such delayed effects of density at birth on adult body mass probably affect population dynamics, and might constitute a mechanism by which delayed density-dependence occurs in ungulate populations.

Keywords: *Capreolus capreolus*; ungulates; cohort variation; habitat quality; delayed density-dependence; long-term monitoring

1. INTRODUCTION

Body mass plays a fundamental role in shaping variation in life-history traits both at the interspecific (Peters 1983; Calder 1984) and the intraspecific (Sadleir 1969; Clutton-Brock 1991) levels. In ungulates, the individual body mass is a determinant of juvenile survival (Gaillard *et al.* (1997) in roe deer *Capreolus capreolus*; White *et al.* (1987) in mule deer *Odocoileus hemionus*), adult survival (Bérubé *et al.* (1999) in bighorn sheep *Ovis canadensis*), litter size (Hewison (1996) in roe deer) and age at first breeding (Albon *et al.* (1983) in red deer; Gaillard *et al.* (1992) in roe deer). The assessment of the causes of variation in individual body mass is therefore necessary to understand the population dynamics of many ungulates.

Previous studies have mainly focused on the juvenile stage. In temperate ungulates population density and

climatic conditions during the spring of birth and during the first winter have been reported to influence both birth mass and mass at the onset of winter (Sæther 1985; Clutton-Brock & Albon 1989). Much less is known about the factors that shape variation in adult body mass, although adult mass has direct consequences for fitness. For instance, in both bighorn sheep and roe deer, female longevity is positively correlated with mass during the prime-age stage (Gaillard *et al.* 2000). Adult body mass also seems to be a good predictor of reproductive success in red deer for both sexes (Clutton-Brock *et al.* 1988). However, both the difficulty of assessing the age of adult ungulates reliably (Hamlin *et al.* 2000) and the logistical difficulty of manipulating large animals mean that data on the causes of variation in adult body mass of ungulates are scarce. Using an unusually long-term dataset based on regular captures of known-aged individuals, we tested whether variations in sex-specific adult body mass of roe deer can be accounted for by temporal and spatial structuring factors.

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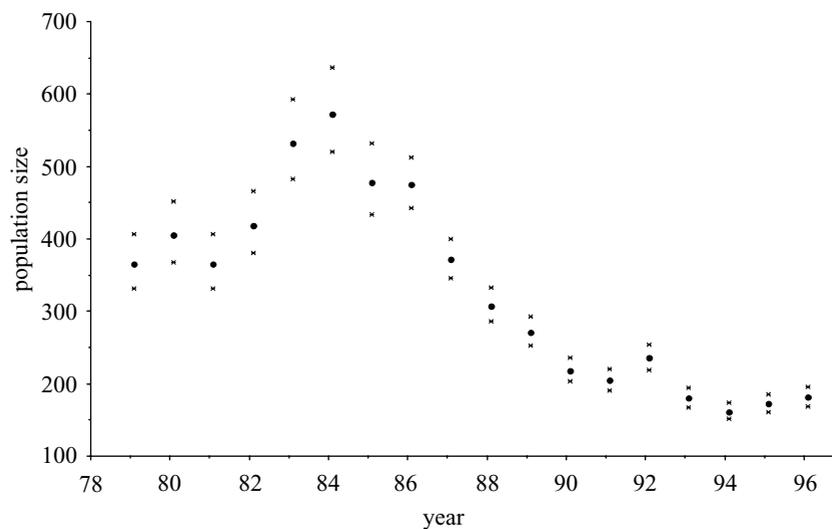


Figure 1. Population size of roe deer at Chizé throughout the study period (1979–1996). Estimates (with 95% confidence limits) were obtained from capture–mark–recapture modelling (see Gaillard *et al.* 1993 for details) and correspond to the number of roe deer older than 1 year in March.

Environmental factors, such as density and weather, can have powerful effects on adult body mass in a given year for ungulates that stock body reserves (Festa-Bianchet *et al.* (1996, 1998) in bighorn sheep). However, these factors are not expected to affect the adult mass of income breeders such as roe deer (Jönsson 1997) since in this species adult body mass varies very little over time (Andersen *et al.* 2000). There is increasing evidence for postponed effects of conditions during the spring of birth in temperate vertebrates (see Lindström 1999 for a review) and ungulates in particular (cohort effects *sensu* Albon *et al.* (1987)). In capital breeders, long-lasting effects on the fitness of cohort variation in birth weight (in males) or of density and spring temperature at birth (in females) have been reported for red deer (Kruuk *et al.* 1999) but early body mass had little effect on the adult mass of either sex in bighorn sheep (Festa-Bianchet *et al.* 2000). No study, to our knowledge, has examined whether environmental conditions at birth have long-lasting effects in income breeders such as roe deer: our first prediction is that cohort effects will occur.

Recent work on red deer (Coulson *et al.* 1997; Conradt *et al.* 1999; Milner-Gulland *et al.* 2000) has demonstrated that spatial heterogeneities in habitat quality can induce spatial variability in individual condition, suggesting that spatial variation could be as important as temporal variation in shaping individual variability, though few studies have considered spatial and temporal factors simultaneously. In roe deer, the body mass of fawns is habitat dependent irrespective of density, fawns being heaviest in the richest habitat (i.e. the habitat with abundant high-quality food; Pettorelli *et al.* (2001)). Our second prediction, therefore, is that habitat quality influences the adult body mass of roe deer.

2. MATERIAL AND METHODS

(a) Study area

The study was carried out in the Chizé reserve, 2614 ha of enclosed forest in western France (46°05' N, 0°25' W). The climate is oceanic with mild winters and hot, dry summers. The

dominant trees are deciduous. According to a geological map (Lambertin 1992), the distribution of the main plant species and the nitrogen content of the plants (Pettorelli *et al.* 2001), we distinguished two habitats contrasting in quality within the reserve. The northern area is covered by 1397 ha of oak forest, while 1143 ha of beech forest cover the southern part of the reserve. The principal food plants for roe deer in spring and summer (oak (*Quercus* spp.), hornbeam (*Carpinus betulus*), maple (*Acer campestre*), hawthorn (*Crataegus monogyna*) and dogwood (*Cornus* spp.); Duncan *et al.* (1998)) occur more frequently in the north than in the south. Moreover, within species, plants in the north have a higher nitrogen content than in the south. The oak forest was therefore a richer habitat for roe deer than the beech forest.

(b) Roe deer populations

The roe deer population at Chizé has been intensively monitored for more than 20 years (1978–2000). During this time-period the population was managed, but it went through a cycle of abundance, from 150 to 600 individuals and, through management, the numbers were regulated by a combination of natural, density-dependent and artificial factors (Gaillard *et al.* 1993). Each year, between 8 and 12 days of captures are organized between October and March (mainly January and February). We used data from 110 adult males and 129 adult females, which were caught and weighed using an electronic balance at least once (average of 2.38 and 2.67 times for males and females, respectively) as adults (i.e. aged 4–10 years, see § 2c) between 1978 and 2000. All individuals were marked as fawns, so we used only known-aged individuals. For each individual captured, the cohort (i.e. year of birth), the mass, the sex and the zone of capture (north versus south) were noted.

(c) Methods

From a longitudinal analysis of sex-specific growth curves based on first-order differences (M. Festa-Bianchet, M. Gaillard, D. Delorme and J. T. Jorgenson, unpublished data), body mass does not change between the ages of 4 and 10 years in both males and females. We therefore defined adult body mass as the median measure for individuals captured on one or more occasions between 4 and 10 years of age.

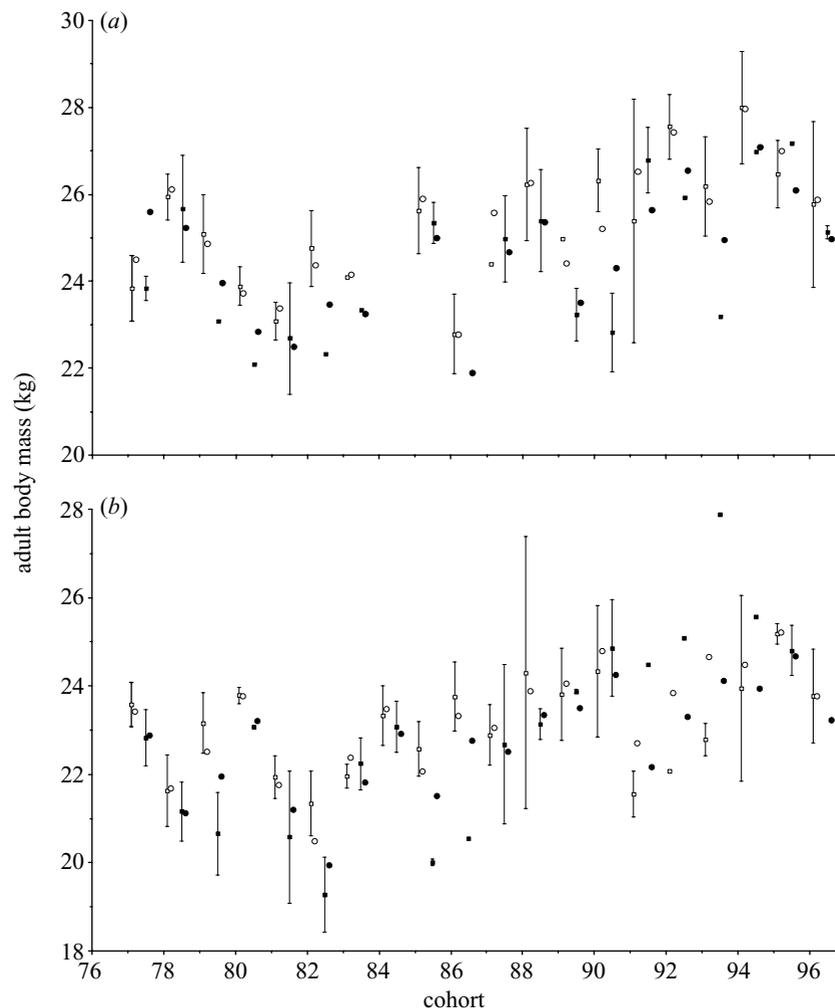


Figure 2. Mean body mass of (a) adult male and (b) female roe deer (4–10 years of age) in each cohort in the Chizé reserve (France): expected values (circles) from the selected model include additive effects of cohort and habitat (north: open symbols; south: filled symbols) and observed values (± 1 s.e., squares).

To attribute a habitat type to each roe deer captured, we checked where its captures took place. Adult roe deer living in forests in continental Europe are highly sedentary (Strandgaard 1972; Hewison *et al.* 1998), so we can reliably assume that the individuals were captured in the habitat type where they lived. Seven individuals (five females and two males) were caught equally often in both habitat types, so they were discarded. To test for cohort variation, we obtained the adult mass for roe deer belonging to 20 female and 19 male cohorts (1977–1996; data for 1984 were missing for males).

(d) Statistical procedures

Because roe deer show slight, but significant, sexual dimorphism in size, and between-sex differences in life-history traits (Andersen *et al.* 1998), we conducted separate tests for males and females. The effects of cohort (20 or 19 modalities depending on sex) and habitat type (two modalities) on adult mass were analysed by a two-way ANOVA using GLIM software (Francis *et al.* 1993). We then sought to account for cohort variation using the most probable sources of environmental variation, population density and rainfall in May–June, which account for most of the temporal variation in fawn body mass (Gaillard *et al.* 1996) and early survival (Gaillard *et al.* 1997). Accurate estimates of population density based on the capture–mark–recapture monitoring (Gaillard *et al.* 1993) were available

between 1979 and 1996 (figure 1). Total rainfall in May–June was obtained from Météo France for the same years. We thus restricted the analysis of causes of cohort variation to 17 male and 18 female cohorts. To test for the possible effects of density and spring rainfall on yearly variation of adult body mass, we used the observed sex- and habitat-specific median mass of adult roe deer in two ANCOVA procedures (one per sex with density and spring rainfall as covariates, median mass as a variable and habitat as a factor). We tested for a possible effect of an interaction between density and spring rainfall by fitting the effect of the product density \times spring rainfall (see Portier *et al.* (1998) for an application of such a procedure). In order to assess the proportion of variation in adult mass that was accounted for by the effects of cohort and habitat type and the proportion of cohort variation that was accounted for by density and/or rainfall in May–June, we measured the r^2 value of least-square regressions of sex-specific adult mass, predicted by the models we selected, on observed sex-specific adult mass (Sokal & Rohlf 1995).

3. RESULTS

For both males and females, there were no significant interactions between the effects of habitat type and cohort on adult body mass (both $p > 0.18$). In support of our first prediction, cohort significantly influenced adult body

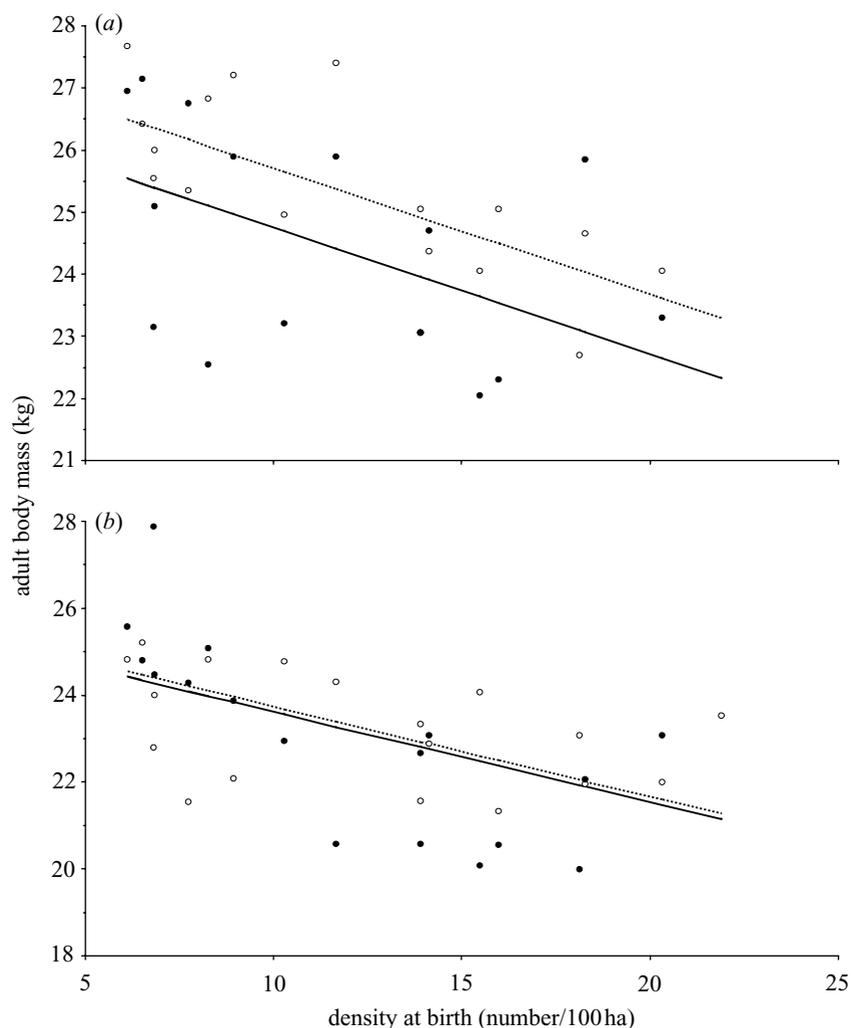


Figure 3. Cohort-specific body mass of (a) adult male and (b) female roe deer (4–10 years of age) according to population density at birth in the Chizé reserve (France): expected from the selected model including additive effects of density at birth and habitat (north: dotted line; south: continuous line) and observed (north: open circles; south: filled circles).

mass in both males ($F = 3.06$, d.f. = 18, 90, $p = 0.0002$) and females ($F = 3.49$, d.f. = 19, 108, $p < 0.0001$). Males born in 1994 (27.9 kg) were 5.2 kg heavier when adult than males born in 1986 (22.7 kg, figure 2a) while females born in 1995 (25.2 kg) were 4.7 kg heavier as adult than females born in 1982 (20.4 kg, figure 2b). Such a marked cohort variation still occurred consistently when we restricted the data to those animals that were caught at a specific age during adulthood (table 1). Likewise, in support of our second prediction, males were significantly heavier in the rich oak forest than in the poor beech forest ($F = 4.99$, d.f. = 1, 90, $p = 0.028$). For a given cohort, the mass difference in adult males was, on average, 0.9 kg. A similar trend occurred for females ($F = 2.63$, d.f. = 1, 109, $p = 0.11$) that weighed 0.5 kg more in the oak forest. The selected model thus involved additive effects of habitat type and cohort (figure 2). Regressing the adult body mass expected from the additive effects of cohort and habitat type on observed body mass led to quite high r^2 values (0.402 and 0.412 for females and males, respectively). The additive effects of cohort and habitat type therefore accounted for ca. 40% of the variation observed in individual body mass.

When assessing the respective roles of population density and rainfall in May–June in accounting for observed cohort variation (while accounting for habitat effect), we found very similar results for both sexes. In both cases there was no interaction between rainfall and density ($F = 1.42$, d.f. = 1, 28, $p = 0.24$ and $F = 1.43$, d.f. = 1, 30, $p = 0.24$ for males and females, respectively). Rainfall in May–June of the year of birth had no effect on body mass ($F = 0.0085$, d.f. = 1, 29, $p = 0.93$ and $F = 0.27$, d.f. = 1, 31, $p = 0.61$ for males and females, respectively). Population density at birth, however, strongly influenced cohort-specific adult mass in both sexes ($F = 11.34$, d.f. = 1, 29, $p < 0.0001$ and $F = 11.14$, d.f. = 1, 31, $p < 0.0001$ for males (figure 3a) and females (figure 3b), respectively). When we restricted the data to those animals that were caught at a specific age during adulthood, the strong negative effect of population density at birth on adult mass occurred consistently in both sexes (table 1). The magnitude of this delayed density-dependence was remarkably similar in both sexes (slopes of -0.208 ± 0.051 in males versus -0.203 ± 0.0529 in females, Wald test, $\epsilon = 0.066$, $p = 0.47$). Thus, within quite a large range of densities (i.e. between 6 and 22 individuals per square

Table 1. Influence of the density in the year of birth on age-specific body mass of adult male (a) and female (b) roe deer in the Chizé reserve (France). For both sexes, the table shows for each age during adulthood (age) the mean body mass of the heaviest cohort (heaviest mass), the density at birth of the heaviest cohort (density for heaviest), the mean body mass of the lightest cohort (lightest mass), the density at birth of the lightest cohort (density for lightest), the number of cohorts sampled (N), and the slope of the regression of cohort-specific body mass on density at birth (slope \pm 1 s.e.).

(a) males						
age	heaviest mass	density for heaviest	lightest mass	density for lightest	N	slope (\pm 1 s.e.)
4	27.4	8.8	21.7	18.0	17	-0.263 (0.062)
5	28.8	8.8	22.3	13.8	15	-0.149 (0.105)
6	29.8	7.6	22.4	14.0	15	-0.263 (0.108)
7	27.2	6.0	23.0	15.3	13	-0.175 (0.086)
8	30.7	6.7	23.3	10.2	12	-0.327 (0.125)
9	27.8	7.6	22.5	13.8	11	-0.107 (0.170)
10	27.8	8.1	23.8	13.8	9	-0.239 (0.149)
(b) females						
4	24.8	6.4	19.5	13.8	18	-0.079 (0.070)
5	25.3	6.4	20.3	15.8	18	-0.089 (0.067)
6	27.0	6.0	20.6	13.8	15	-0.114 (0.084)
7	25.4	6.7	21.5	20.2	15	-0.142 (0.058)
8	25.3	8.8	20.0	15.8	14	-0.096 (0.101)
9	24.9	8.1	21.2	13.8	12	-0.041 (0.080)
10	25.7	8.1	20.6	20.2	12	-0.253 (0.087)

kilometre), adult body mass of both sexes decreased by about 1 kg for each increase of five roe deer per square kilometre in density. Regressing the cohort- and habitat-specific adult body mass expected from population density during the spring of birth on the observed body mass led to r^2 values of 0.346 and 0.378 for females and males, respectively. This indicates that population density accounted for *ca.* 35% of the variation observed in the body mass of roe deer of different cohorts.

4. DISCUSSION

The adult body mass in roe deer of both sexes in the Chizé population was strongly influenced by additive effects of the year of birth and of the habitat type. Together, cohort and spatial variations accounted for *ca.* 40% of the individual variation in adult mass. The strong cohort variation was partly accounted for by variations in the population density during the spring of birth, showing a strong delayed density-dependence in this roe deer population, which influenced both sexes to the same extent.

As expected from the between-habitat differences in quality, adult males were heavier in the rich oak forest than in the poor beech forest, as were the females. Such a positive covariation between mass and habitat quality has also been found for fawn body mass (Pettorelli *et al.* 2001). Under an ideal free distribution, we would expect equal individual quality among habitat types, the negative effects of higher density balancing the positive effects of quality in the best habitats (Fretwell & Lucas (1970); see Conrard *et al.* (1999) and Wahlström & Kjellander (1995) for case studies on ungulates). Despite a period of high density in the Chizé population between 1982 and 1986 (Gaillard *et al.* 1993) that led to sharp density-dependent responses in age at first breeding (Gaillard *et al.* 1992),

juvenile survival (Gaillard *et al.* 1997) and fawn body mass (Gaillard *et al.* 1996), between-habitat differences in density, if they occur, did not balance between-habitat differences in quality that consistently influenced mass in all sex and age classes of roe deer (Pettorelli *et al.* 2001). Such pervasive effects of habitat quality may result from the very sedentary habits of adult roe deer at Chizé (N. Pettorelli, J.-M. Gaillard, G. Van Laere, D. Delorme, P. Duncan and D. Maillard, unpublished data), which limit exchanges between habitats.

The other factor that structured variations in adult mass of roe deer was the cohort. In both sexes, a 5 kg difference occurred in adult body mass according to the year of birth (\pm 20% of mean body mass). Among the environmental conditions during the spring of birth that could cause these variations, population density had a strong influence. Similar findings were reported in a Swedish roe deer population that varied markedly in size: roe deer born at low density were almost 2 kg heavier when more than 3 years of age than those born at high density (Kjellander 2000). Cohort variation in adult mass of roe deer can therefore be interpreted as illustrating a process of delayed density-dependence since population density during the spring of birth had long-lasting effects on body mass in these populations. Such cohort effects on body mass have previously been described in sheep (Gunn 1977) and red deer (Post *et al.* 1997). However, climatic variation during the spring, rather than density at birth, accounted for long-lasting cohort effects in these studies. In these previous studies (Gunn 1977 and Post *et al.* 1997), climatic conditions during spring accounted for long-lasting cohort effects. In our study, on the other hand, we did not find any evidence of an effect of climatic conditions during spring (rainfall), but found that only density accounted for long-lasting cohort effects. This was positively related to

early fawn survival (Gaillard *et al.* 1997) and winter mass of fawns (Gaillard *et al.* 1996). Thus, roe deer at Chizé that were born during years of high density not only grew more slowly than fawns born at low density (Gaillard *et al.* 1996), but were also unable to compensate for low initial growth (this study). Under such conditions, early growth of fawns may be a good predictor of individual performance later in life, as reported in male white-tailed deer (Schultz & Johnson 1995), red deer (Kruuk *et al.* 1999) and male bighorn sheep (Festa-Bianchet *et al.* 2000). Our first prediction is therefore supported by this analysis: there are long-lasting cohort effects on adult body mass in both sexes of this income breeder. These represent 20% of body mass that is probably stronger than cohort effects in capital breeders: female bighorn sheep born during a low-density period (cohorts 1975–1987) were thus only 0.7 kg heavier as adults (i.e. 6–12 years of age) than those born during the high-density period (M. Festa-Bianchet and J.-M. Gaillard, unpublished data). In the larger, capital breeding bighorn sheep, the importance of environmental conditions at birth may be reduced because these animals grow for more than one year (Festa-Bianchet *et al.* 2000).

Does the heavy mass of large roe deer translate into a fitness advantage? The proportion of females breeding and offspring survival both appear to be independent of body mass: virtually all adult females reproduced annually at Chizé (98% of females older than 20 months; Gaillard *et al.* (1992)) and Gaillard *et al.* (2000) reported that female reproductive success did not depend on female mass for a given longevity in a high-performance population at Trois Fontaines. However, adult mass of females may influence reproductive success in more resource-limited populations of roe deer. Similarly, nothing is currently known about the possible influence of body mass on reproductive success in male roe deer. Conversely, the heaviest females live longest and thus have more breeding opportunities (Gaillard *et al.* 2000) and the heaviest females have the largest litter sizes (Hewison 1996; Andersen *et al.* 2000; Hewison & Gaillard 2001; P. Kjellander, G. Cederlund and O. Liberg, unpublished data). There may therefore be substantial fitness advantage of large body mass, especially in adult females. The strong cohort effect on the adult body mass of roe deer is likely to influence their population dynamics. During the last decade, time-series analyses have demonstrated the pervasive occurrence of delayed density-dependence in ungulate populations (Solberg *et al.* (1999) in moose; Aanes *et al.* (2000) in reindeer; Forchhammer *et al.* (1998) in red deer; Fryxell *et al.* (1991) in white-tailed deer). Although most of these studies involved harvested populations in which delayed effects may come from humans, the strength of cohort variation in adult body mass reported in our study suggests that high density at the time of birth might be a mechanism whereby delayed density-dependence occurs. We therefore suggest that time-lags generated by the delayed effects of density at birth on adult mass should occur in roe deer population dynamics. Further research is needed to understand and to model such complex dynamics.

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REFERENCES

- Aanes, R., Saether, B.-E. & Oritsland, N. A. 2000 Fluctuations of an introduced population of Svalbard reindeer: the effects of density-dependence and climatic variation. *Ecography* **23**, 437–443.
- Albon, S. D., Mitchell, B. & Staines, B. W. 1983 Fertility and body mass in female red deer: a density-dependent relationship. *J. Anim. Ecol.* **52**, 969–980.
- Albon, S. D., Clutton-Brock, T. H. & Guinness, F. E. 1987 Early development and population dynamics in red deer. II. Density-independent effects of cohort variation. *J. Anim. Ecol.* **56**, 69–81.
- Andersen, R., Duncan, P. & Linnell, J. D. C. 1998 *The European roe deer: the biology of success*. Oslo: Scandinavian University Press.
- Andersen, R., Gaillard, J. M., Linnell, J. D. C. & Duncan, P. 2000 What shapes maternal care in an income breeder? A study of contrasting populations of European roe deer. *J. Anim. Ecol.* **69**, 672–682.
- Bérubé, C., Festa-Bianchet, M. & Jorgenson, J. T. 1999 Individual differences and reproductive senescence in bighorn ewes. *Ecology* **80**, 2555–2565.
- Calder, W. A. 1984 *Size, function and life history*. Harvard University Press.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Clutton-Brock, T. H. & Albon, S. D. 1989 *Red deer in the Highlands*. Oxford: Blackwell Scientific.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1988 Reproductive success in male and female red deer. In *Reproductive success. Studies of individual variation in contrasting breeding systems* (ed. T. H. Clutton-Brock), pp. 325–343. University of Chicago Press.
- Conradt, L., Clutton-Brock, T. H. & Guinness, F. E. 1999 The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia* **120**, 218–224.
- Coulson, T., Albon, S. D., Guinness, F. E., Pemberton, J. & Clutton-Brock, T. H. 1997 Population substructure, local density, and calf winter survival in red deer. *Ecology* **78**, 852–863.
- Duncan, P., Tixier, H., Hofman, R. R. & Lechner-Doll, M. 1998 Feeding strategies and the physiology of digestion in roe deer. In *The European roe deer: the biology of success* (ed. R. Andersen, P. Duncan & J. D. C. Linnell), pp. 91–116. Oslo: Scandinavian University Press.
- Festa-Bianchet, M., Jorgenson, J. T., King, W. J., Smith, K. G. & Wishart, W. D. 1996 The development of sexual dimorphism: seasonal and lifetime mass changes of bighorn sheep. *Can. J. Zool.* **74**, 330–342.
- Festa-Bianchet, M., Gaillard, J. M. & Jorgenson, J. T. 1998 Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* **152**, 367–379.
- Festa-Bianchet, M., Jorgenson, J. T. & Réale, D. 2000 Early development, adult mass, and reproductive success in bighorn sheep. *Behav. Ecol.* **11**, 633–639.
- Forchhammer, M. C., Stenseth, N. C., Post, E. & Langvatn, R. 1998 Population dynamics of Norwegian red deer: density dependence and climatic variation. *Proc. R. Soc. Lond. B* **265**, 341–350. (DOI 10.1098/rspb.1998.1301.)
- Francis, B., Green, M. & Payne, C. 1993 *The GLIM system, release 4 manual*. Oxford: Clarendon Press.
- Fretwell, S. D. & Lucas, H. L. 1970 On territorial behaviour

- and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**, 16–36.
- Fryxell, J. M., Hussell, D. J. T., Lambert, A. B. & Smith, P. C. 1991 Time lags and population fluctuations in white-tailed deer. *J. Wildl. Mngmt* **55**, 377–385.
- Gaillard, J.-M., Sempéré, A. J., Van Laere, G., Boutin, J. M. & Boisaubert, B. 1992 Effects of age and body mass on the proportion of females breeding in a population of roe deer. *Can. J. Zool.* **70**, 1541–1545.
- Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B. & Pradel, R. 1993 Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* **62**, 778–791.
- Gaillard, J.-M., Delorme, D., Boutin, J.-M., Laere, G. V. & Boisaubert, B. 1996 Body mass of roe deer fawns during winter in 2 contrasting populations. *J. Wildl. Mngmt* **60**, 29–36.
- Gaillard, J.-M., Delorme, D., Van Laere, G., Duncan, P. & Lebreton, J. D. 1997 Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**, 502–513.
- Gaillard, J.-M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. 2000 Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Lond. B* **267**, 471–477. (DOI 10.1098/rspb.2000.1024.)
- Gunn, R. G. 1977 The effects of two nutritional environments from 6 weeks pre-partum to 12 months of age on lifetime performance and reproductive potential of Scottish blackface ewes in two adult environments. *Anim. Prod.* **25**, 155–164.
- Hamlin, K. L., Pac, D. F., Sime, C. A., DeSimone, R. M. & Dusek, G. L. 2000 Evaluating the accuracy of ages obtained by two methods for Montana ungulates. *J. Wildl. Mngmt* **64**, 441–449.
- Hewison, A. J. M. 1996 Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriol.* **41**, 187–198.
- Hewison, A. J. M. & Gaillard, J.-M. 2001 Phenotypic quality and senescence affect different components of reproductive output in roe deer. *J. Anim. Ecol.* **70**, 600–608.
- Hewison, A. J. M., Vincent, J. P. & Reby, D. 1998 Social organisation of European roe deer. In *The European roe deer: the biology of success* (ed. R. Andersen, P. Duncan & J. D. C. Linnell), pp. 189–220. Oslo: Scandinavian University Press.
- Jönsson, K. I. 1997 Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66.
- Kjellander, P. 2000 Density dependence in roe deer population dynamics. Unpublished PhD thesis, Swedish University of Agricultural Sciences, Uppsala.
- Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E. & Guinness, F. E. 1999 Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proc. R. Soc. Lond. B* **266**, 1655–1661. (DOI 10.1098/rspb.1999.0828.)
- Lambertin, V. 1992 *Carte géologique de la forêt domaniale de Chizé*. Paris: Office National des Forêts.
- Lindström, J. 1999 Early development and fitness in birds and mammals. *Trends Ecol. Evol.* **14**, 343–348.
- Milner-Gulland, E. J., Coulson, T. N. & Clutton-Brock, T. H. 2000 On harvesting a structured ungulate population. *Oikos* **88**, 592–602.
- Peters, R. H. 1983 *The ecological implications of body size*. Cambridge University Press.
- Pettorelli, N., Gaillard, J.-M., Duncan, P., Ouellet, J. P. & Van Laere, G. 2001 Population density and small scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* **128**, 400–405.
- Portier, C., Festa-Bianchet, M., Gaillard, J.-M. & Yoccoz, N. G. 1998 Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool.* **245**, 271–278.
- Post, E., Stenseth, N. C., Langvatn, R. & Fromentin, J.-M. 1997 Global climate change and phenotypic variation among red deer cohorts. *Proc. R. Soc. Lond. B* **264**, 1317–1324. (DOI 10.1098/rspb.1997.0182.)
- Sadler, R. M. F. S. 1969 *The ecology of reproduction in wild and domestic animals*. London: Methuen.
- Sæther, B.-E. 1985 Annual variation in carcass weight of Norwegian moose in relation to climate along a latitudinal gradient. *J. Wildl. Mngmt* **49**, 977–983.
- Schultz, S. R. & Johnson, M. K. 1995 Effects of birth date and body mass at birth on adult body mass of male white-tailed deer. *J. Mamm.* **76**, 575–579.
- Sokal, R. R. & Rohlf, F. J. 1995 *Biometry*, 3rd edn. New York: W. H. Freeman and Company.
- Solberg, E., Saether, B.-E., Strand, O. & Loison, A. 1999 Dynamics of a harvested moose population in a variable environment. *J. Anim. Ecol.* **68**, 186–204.
- Strandgaard, H. 1972 The roe deer (*Capreolus capreolus*) population at Kalö and the factors regulating its size. *Danish Rev. Game Biol.* **7**, 1–205.
- Wahlström, K. & Kjellander, P. 1995 Ideal free distribution and natal dispersal in female roe deer. *Oecologia* **103**, 302–308.
- White, G. C., Garrott, R. A., Bartmann, R. M., Carpenter, L. H. & Alldredge, A. W. 1987 Survival of mule deer in northwest Colorado. *J. Wildl. Mngmt* **51**, 852–859.

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