How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study

Carole Toïgo, Jean-Michel Gaillard, Guy Van Laere, Mark Hewison and Nicolas Morellet

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We tested the influence of population density and of drought intensity (measured as the Gaussen Index in spring and summer of the year of birth) on winter body mass, hind foot length, and body condition of roe deer fawns. Body mass decreased with increasing density and increased with increasing Gaussen Index in summer, in a similar way for both males and females. Hind foot length of males showed the same response. On the other hand, hind foot length of females decreased with increasing density only after dry summers, hence when environmental conditions were very harsh. Body condition was affected neither by density nor by drought intensity. Our results indicate that body mass and size are much better indicators of phenotypic quality than body condition in roe deer. The sex-specific responses of body size to environmental conditions could correspond to a differential allocation in favour of daughters by heavier than average roe deer mothers.

C. Toïgo (c.toigo@oncfs.gouv.fr) and G. Van Laere, Office National de la Chasse et de la Faune Sauvage, 5 Allée de Bethléem, Z.I. Mayencin, F-38610 GIERES, France. – J.-M. Gaillard, UMR CNRS 5558 Biométrie et Biologie Evolutive, Univ. Claude Bernard Lyon 1, 43, boulevard du 11 novembre 1918, F-69622 Villeurbanne Cedex, France. – A. J. M. Hewison and N. Morellet, Comportement et Ecologie de la Faune Sauvage, INRA, BP 52627, F-31326 Castanet-Tolosan Cedex, France.

In ungulates, phenotypic quality shapes most life-history traits, and thereby strongly influences individual fitness. As a general rule, large and heavy males have preferential access to females through better fighting abilities (Clutton-Brock et al. 1982 on red deer *Cervus elaphus*, Byers 1997 on pronghorn *Antilocapra americana*, McElligott et al. 2001 on fallow deer *Dama dama*), or through mate choice by females (Bro-Jorgensen 2002). Likewise, large and heavy females have higher lifetime reproductive success because they live longer (Gaillard et al. 2000 on roe deer *Capreolus capreolus* and bighorn sheep *Ovis canadensis*) reproduce earlier (Saether and Haagerund 1985 on moose *Alces alces*, Green and Rothstein 1991 on bison *Bison bison*, Williamson 1991 on red lechwe *Kobus leche leche*, Gaillard et al. 1992 on roe deer,

Langvatn et al. 1996 on red deer), have a higher probability to wean a young (Clutton-Brock et al. 1988 on red deer, Côté and Festa-Bianchet 2001 on mountain goat *Oreamnos americanus*), and have larger litter size (Hewison and Gaillard 2001 on roe deer) than small and light females. Furthermore, the influence of phenotypic quality on life history traits and thereby on population dynamics is not limited to adult individuals. Indeed, in ungulate species of temperate areas large and heavy juveniles of both sexes enjoy higher survival over their first winter than light and small juveniles (Clutton-Brock et al. 1992 on Soay sheep *Ovis aries*, Gaillard et al. 1993a on roe deer, Loison et al. 1999 on red deer, Côté and Festa-Bianchet 2001 on mountain goat) so that the number of individuals recruited to the population

in a given year is directly related to the mean phenotypic quality of that cohort. Moreover, juvenile phenotypic quality is often a good predictor of adult phenotypic quality, especially under harsh environmental conditions (Albon et al. 1992 on red deer, Clutton-Brock et al. 1992 on Soay sheep, Pettorelli et al. 2002 on roe deer) or when strong sexual selection does not allow males to compensate for a shortfall in growth in early life (Pélabon 1997 on fallow deer, Toïgo et al. 1999 on alpine ibex *Capra ibex ibex*). Therefore, identifying the factors that shape juvenile phenotypic quality is essential for a better understanding of how variation in life history traits determine population dynamics.

One major determinant of juvenile phenotypic quality is the quantity and quality of food resources available to the mother during the last third of gestation and during lactation (Oftedal 1984). In temperate environments, forage availability depends both on climatic conditions of spring and summer which determine primary production (Lesage et al. 2000), and on density-dependent competition for food (Patterson and Power 2002). Several studies have reported an effect of environmental conditions on juvenile phenotypic quality. For instance, the body mass of mountain goat kids increased with the quality of the vegetation during lactation (Côté and Festa-Bianchet 2001), climatic conditions during the winter in utero affected the birth mass of Soay sheep (Forchhammer et al. 2001) and the autumn body mass of reindeer *Rangifer tarandus* calves (Weladji and Holand 2003), and food availability during summer influenced the autumn body mass of moose calves (Ericsson et al. 2002). Likewise, population density shapes juvenile phenotypic quality in many ungulate species. Juvenile body mass decreases with increasing density in roe deer (Gaillard et al. 1996), red deer (Mysterud et al. 2001), male moose (Ferguson et al. 2000), bighorn sheep (Leblanc et al. 2001), and Soay sheep (Clutton-Brock et al. 1992). The influence of climatic factors on juvenile body size may be both density- and sex-dependent. That is, climatic influences are often more marked at high density (Weladji and Holand 2003) and among males for highly dimorphic and polygynous species in which growth rates strongly differ between the sexes (Post et al. 1999 on red deer, Toïgo et al. 1999 on ibex, Ferguson et al. 2000 on moose, Côté and Festa-Bianchet 2001 on mountain goat, Leblanc et al. 2001 on bighorn sheep).

In most previous studies, phenotypic quality has been measured as body mass. However, body mass is a composite of two components, body size and body condition (usually expressed as a residual of body mass on body size, see Schulte-Hostedde et al. 2005 for a recent validation of this measure). In fact heavier individuals are usually larger than lighter ones (size component), while among similar-sized individuals heavier ones are usually in better body condition than lighter ones (condition component, e.g. Dobson 1992).

According to Klein (1964, pp. 232), "the skeleton has been shown to have a higher priority for growth than muscle or fat tissue and is therefore less affected by nutritional deficiencies in the diet than total body mass". Body mass of juveniles is therefore expected to be more variable over years and to respond more quickly to environmental variations than their body size. When environmental conditions are such that body mass is affected but body size is not, then body condition is also expected to vary in the same way as body mass. Along a continuum from good to bad environmental conditions, body mass is thus expected to decrease first, whereas body size should be quite stable, so that body condition should thus decrease. Under very harsh environmental conditions, both body mass and body size should decrease, so that no trend should thus be observed for body condition. To our knowledge, such predictions for differential responses of mass, size and condition of individuals to varying environmental harshness have never been tested in ungulates. Hence, we looked for the influence of climatic variation and changes in population density on body mass, body size and body condition of roe deer fawns during a long-term population monitoring. More specifically, we tested the following three hypotheses: 1) body mass should decrease as soon as environmental conditions deteriorate, i. e. when density increases or when climatic conditions become harsh; 2) in contrast, body size should decrease only under the very worst environmental conditions, and thus climatic conditions and density should interact to shape body size and body condition; 3) as roe deer are only slightly dimorphic ungulates, male and female juveniles are expected to respond in a similar way to environmental variation (climatic conditions or population density).

Methods

Study site

The study was conducted in the 2614 ha Reserve of Chizé, managed by the Office National des Forêts and the Office National de la Chasse et de la Faune Sauvage. The Chizé Reserve is situated near the Atlantic Ocean in south-western France (46°05′N, 0°25′W) and is characterised by an oceanic climate with mediterranean influences, with mild winters (mean daily temperature in January is 5.5°C) and hot and dry summers (mean daily temperature in July is 20.4°C and total rainfall in July–August is 98 mm). The soils of the Chizé forest are shallow and calcareous. Three broad vegetation associations of varying quality for roe deer are found at Chizé (Pettorelli et al. 2003). The richest habitat for roe deer is an oak *Quercus* spp. forest with mainly hornbeam *Carpinus betulus* coppice (covering 1046 ha). About one third of the area (815 ha) is poor roe deer habitat

consisting of beech *Fagus sylvatica* forest on limestone with virtually no coppice. The understory is dominated by woodfalse-brome *Brachypodium* spp., butcher's broom *Ruscus aculeatus*, ivy *Hedera helix*, wild madder *Rubia peregrina*, and wood melick *Melica uniflora*. Neither woodfalse-brome nor butcher's broom are favoured forage of roe deer. Ivy, which is highly selected by roe deer in winter, decreased following a peak in roe deer abundance in 1983–1984. The remainder of the Chizé forest (758 ha), an oak forest in which the coppice is mainly Montpellier maple *Acer monspessulanum*, is of intermediate quality. The productivity of the entire forest is quite low due principally to the summer droughts (long-term average of 3.77 m^3 of wood produced/ha/yr, data from Inventaire National Forestier).

Roe deer data

The population has been intensively monitored by capture-mark-recapture (CMR) methods since 1978. Every winter in January–February, roe deer are captured with vertical nets (see Gaillard et al. 2003 for further details). Some of the captured animals are exported for introduction or reinforcement of other populations. The other animals are marked with numbered collars to allow identification from a distance, and released. There is no hunting. Body mass and hind foot length of all captured animals have been measured each year since 1987. We therefore analyse here data collected over 18 consecutive years. Roe deer were weighed to the nearest 500 g. The outstretched hind foot was measured from the heel (top of the calcaneum) to the tip of the hoof to the nearest mm. The hind foot has one of the highest growth priorities during skeletal development of juvenile ungulates (Klein 1964).

A high proportion of the population (>70%) was marked during each year of the study to ensure that reliable estimates of population size were available for each year (estimation from generalisation of the Cormack-Jolly-Seber model, Gaillard et al. 2003). The Chizé roe deer population fluctuated markedly during the study period (1987–2003). The population size decreased from ca 400 roe deer >1 yr of age in March 1987 to 160 in March 1994, was then maintained at ca 200 roe deer >1 yr of age until 2000, and increased to ca 400 individuals >1 yr of age in March 2003. The population decreased between 1987 and 1994 due both to high annual removals and density-dependent responses of demographic parameters (delayed age at primiparity, Gaillard et al. 1992 and low recruitment rate, Gaillard et al. 1997). The recent population increase occurred because few roe deer were removed annually.

Climate

We obtained meteorological data from a Météo France station situated in the reserve. We calculated the Gaussen Index in spring (April–May) and summer (June–August), as the amount of precipitation minus twice the mean temperature (Gaussen Index, Dajoz 1973). The Gaussen Index (GI) is a measure of the water available for vegetation (Dajoz 1973), and has been previously related to ungulate performance (Gaillard et al. 1997, Garel et al. 2004). GI in spring determines vegetation growth, and thus is a proxy of the quantity of food available to roe deer during the spring and the beginning of the summer (i.e. end of gestation and lactation). GI in summer influences the duration of green forage as well as its quality (Becker et al. 1994), and therefore provides a proxy of food availability during the lactation period up to and around weaning.

Analyses

We studied body mass, body size (indexed by hind foot length), and body condition of 8–9 month-old fawns measured during the January–February capture sessions in relation to deer density calculated in the winter preceding birth and to both spring and summer GI in the year of birth.

As fawn body mass has been shown to increase from January to February in this population by ca 0.3 kg (Gaillard et al. 1996), we standardized body mass and body size to February values. We log-transformed body mass and hind foot length to normalise the data. We then calculated the mean of both variables for each cohort and each sex. Body condition was calculated as the residuals of the regression of log-transformed body mass on log-transformed hind foot length of each individual (see e.g. Schulte-Hostedde et al. 2005), fitted separately for males and females. An average body condition was then calculated for each cohort and each sex.

We first calculated the correlation coefficients between density and GI in both spring and summer, to assess their independence. We then tested whether sex, density, and GI had an effect on mean cohort body mass, hind foot length, and body condition using linear models. All cohort-specific estimates of mass, size, and condition were weighted by the inverse of their variance, following recommendations of Burnham et al. (1987). We tested the main effects of sex, density, GI in spring and summer, as well as their 2-way, 3-way, and 4-way interactions. As recommended by Burnham and Anderson (1998), our model selection was based on the Akaike Information Criterion corrected for small sample size (AICc). In general we selected the model with the lowest AIC. As is often the case in ANOVAs or regression, our AICc values were negative (Burnham and Anderson

1998). The lowest AICc had therefore the highest absolute value. When the ΔAICc (i.e. the difference of AICc between models) was <2, we used the criterion of parsimony, selecting the simplest of the two models.

We performed Wald tests to assess whether the effect of every factor or covariate included in the selected model was statistically significant. All the statistical analyses were performed using R software (Anon. 2004).

Results

Over the study period, density, GI in spring (GISp), and GI in summer (GISm) were not correlated (correlation coefficients between GISm and GISp = −0.19, t = −0.790, DF = 16, p = 0.441; GISm and density = −0.14, t = −0.561, DF = 16, p = 0.583; GISp and density = 0.06, t = 0.245, DF = 16, p = 0.809), allowing us to consider them as independent variables in the same model.

Body mass

The best model to explain variation in body mass included the additive effects of sex, density, and GI in summer (Table 1). Male fawns were on average 0.8 kg (± 0.367, Wald test, $\chi^2 = 4.752$, p = 0.040) heavier than female fawns. Mean cohort body mass increased with increasing GI in summer with a slope of 0.0014 (± 0.0006) (Wald test, $\chi^2 = 5.44$, p = 0.027, Fig. 1a), and decreased with increasing density with a slope of −0.0182 (± 0.0046) (Wald test, $\chi^2 = 15.65$, p = 0.0004, Fig. 1b) in a similar way for males and females. This model accounted for 47% of body mass variation among cohorts. GI in spring had no effect on mean cohort body mass of either sex.

Body size

Three models including the effects of sex, density, and GI in summer received equivalent support with ΔAICc near 0: the additive model, the model including the interaction between density and GI in summer (Table 2), and the model including the interaction between sex and GI in summer. To disentangle between those 3 models, we decided to conduct separate analyses for males and females.

Density and GI in summer had additive effects on male hind foot length, whereas GI in spring had no effect (Table 3a). Mean cohort body size of male fawns decreased with density with a slope of −0.0050 (± 0.001) (Wald test, $\chi^2 = 14.79$, p = 0.001, Fig. 2a), and increased with GI in summer with a slope of 0.0005 (± 0.0002) (Wald test, $\chi^2 = 6.25$, p = 0.013, Fig. 2b). The additive effects of density and GI accounted for 63% of the inter-annual variability of mean cohort hind foot length for male fawns.

Density and GI in summer had an interactive effect on female fawn hind foot length, whereas GI in spring had no influence (Table 3b). To further investigate this interaction, we separated cohorts born in dry summer years (negative GI) from cohorts born in wet summer years (positive GI), and tested for the effect of density in both cases. We found a negative correlation between mean cohort hind foot length of female fawns and density only for cohorts born in dry summer years (slope = −0.0072, SE = 0.0015, Wald test, $\chi^2 = 23.04$, p = 0.003, Fig. 3), whereas density had no significant effect on body size of female fawns born in wet summer years (slope = −0.0013, SE = 0.0008, Wald test, $\chi^2 = 2.641$, p = 0.170, Fig. 3).

The hind foot of male fawns was significantly longer than that of female fawns (331.8 mm, SE = 13.2 vs 325.9 mm, SE = 13.2, F = 50.536, DF = 1, 998, p < 0.0001).

Table 1. Model selection of the analysis of variation in mean cohort body mass of roe deer fawns. M0: null model, Np: number of parameters, ΔAICc: difference of AICc between a given model and the model with the lowest AICc, s: sex, n: density, GISp: Gaussen Index in spring of the year of birth, GISm: Gaussen Index in summer of the year of birth, ":" denotes interactive effects between factors, and "+" denotes additive effects. The selected model appears in bold. Only models with a ΔAICc <8 are presented.

Model	Np	AICc	ΔAICc
M0+n+s+GISm	**4**	**−34.221**	**0**
M0+n+s+GISm+GISp	5	−32.733	1.488
M0+n+s+GISm+n:GISm	5	−32.490	1.731
M0+n+s+GISm+n:s	5	−32.442	1.779
M0+n+s+GISm+s:GISm	5	−32.297	1.924
M0+n+s	3	−31.192	3.029
M0+n+s+GISm+GISp+n:GISp	6	−30.326	3.895
M0+n+s+GISm+GISp+s:GISp	6	−30.237	3.984
M0+n+s+GISm+GISp+GISp:GISm	5	−30.157	4.064
M0+n+s+GISm+GISp+n:GISm+n:GISp+GISm:GISp+n:GISm:GISp	9	−29.503	4.718
M0+n	2	−28.684	5.537
M0+n+s+GISm+n:s+n:GISm+s:GISm+n:s:GISm	8	−26.231	7.99

Table 2. Model selection of the analysis of variation in mean cohort hind foot length of roe deer fawns. M0: null model, Np: number of parameters, ΔAICc: difference of AICc between a given model and the model with the lowest AICc, s: sex, n: density, GISp: Gaussen Index in spring of the year of birth, GISm: Gaussen Index in summer of the year of birth, ":" denotes interactive effects between factors, and "+" denotes additive effects. The selected models appear in bold. Only models with a ΔAICc <8 are presented.

Model	Np	AICc	ΔAICc
M0+n+s+GISm	**4**	**−59.696**	**0**
M0+n+s+GISm+n:GISm	**5**	**−59.643**	**0.053**
M0+n+s+GISm+s:GISm	**5**	**−58.923**	**0.773**
M0+n+s+GISm+n:s+n:GISm+s:GISm+n:s:GISm	8	−58.414	1.282
M0+n+s+GISm+n:s	5	−57.739	1.957
M0+n+s+GISm+GISp+GISp:GISm	5	−57.180	2.516
M0+n+s+GISm+GISp	5	−57.031	2.665
M0+n+s+GISm+GISp+n:GISp	6	−55.236	4.46
M0+n+s+GISm+GISp+s:GISp	6	−54.173	5.523
M0+n+s+GISm+GISp+n:GISm+n:GISp+GISm:GISp+n:GISm:GISp	9	−53.812	5.884
M0+n+s	3	−53.421	6.275

Body condition

The null model (i.e. constant body condition), and the model including an effect of density on body condition were equally supported (ΔAICc =0.318, Table 4). However, changes in density only accounted for 5% of observed variation in body condition, and the slope of the density-dependent relationship was not significantly different from 0 (slope = −0.0038, SE =0.0028, Wald test, $\chi^2 =1.84$, p =0.180). We therefore retained the model of constant body condition (Table 4). Notably, body condition did not differ between male and female fawns, and was not affected by GI in spring or summer, nor by density (Table 4).
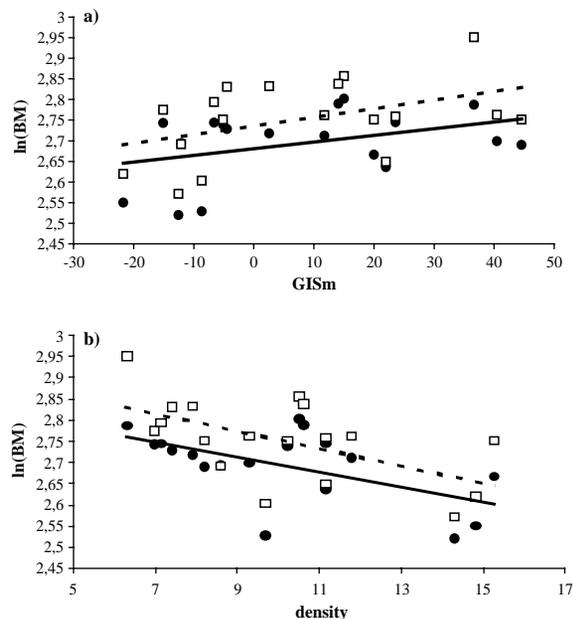

Fig. 1. Relationship between log-transformed body mass (ln(BM)) and a) the Gaussen Index in summer (GISm) b) the population density expressed as the number of roe deer 100 ha^{-1} in the Chizé population for males (open squares and dotted line) and females (filled circles and unbroken line).

Discussion

The phenotypic quality of roe deer fawns was influenced by density and climatic conditions during the summer following birth through effects on both body size and body mass. Body condition of fawns, however, did not respond to variation in environmental conditions. In support of our first prediction, body mass decreased linearly with both increasing density and decreasing Gaussen Index in summer. On the other hand, our second and third predictions were only partially supported. While body mass of both sexes was similarly influenced by additive effects of density and Gaussen Index during summer, the response of body size to environmental factors was sex-specific: female fawn size in winter only decreased with increasing population density after dry summers whereas additive effects of both density and Gaussen Index in summer influenced male size. Our results therefore do not support strictly similar responses of roe deer phenotypic quality to environmental variations between the sexes. Likewise, our results do not support the hypothesis that mass is more sensitive than size to environmental conditions, especially for males.

Roe deer females are income breeders (Andersen et al. 2000) that do not accumulate body reserves, and thereby show little seasonal variation of body mass (Hewison et al. 1996). Roe deer females are thus expected to respond immediately to changes in food resource availability during the spring-summer when reproductive energetic costs peak (Mauget et al. 1999). Roe deer females should thus meet the high energy requirements of the last third of gestation and of lactation (Oftedal 1984) by using food resources available at this time. The Gaussen Index (Dajoz 1973) during spring and summer is an index of the water available for plants during the vegetative development, and therefore positively influences vegetation production (Becker et al. 1994) and thereby the quantity and quality of the food available to mothers during the end of gestation (spring) and during lactation

Table 3. Model selection of the analysis of variation in mean cohort hind foot length of a) male and b) female roe deer fawns. M0: null model, Np: number of parameters, ΔAICc: difference of AICc between a given model and the model with the lowest AICc, s: sex, n: density, GISp: Gaussen Index in spring of the year of birth, GISm: Gaussen Index in summer of the year of birth, ":" denotes interactive effects between factors, and "+" denotes additive effects. The selected model appears in bold. Only models with a ΔAICc <8 are presented.

Model	Np	AICc	ΔAICc
a)			
M0+n+GISm	**3**	**−25.510**	**0**
M0+n+GISm+GISp	4	−22.295	3.215
M0+n+GISm+n:GISm	4	−22.149	3.361
M0+n	2	−20.856	4.654
M0+n+GISm+GISp+n:GISp	5	−18.966	6.544
M0+n+GISm+GISp+GISm:GISp	5	−18.576	6.934
b)			
M0+n+GISm+n:GISm	**4**	**−39.451**	**0**
M0+n	2	−32.238	7.213
M0+n+GISm+GISp+n:GISp	5	−31.792	7.659
M0+n+GISm+GISp+GISm:GISp	5	−31.756	7.695

(summer). The positive effect of a high Gaussen Index during summer on fawn mass and size the following winter that we report here could therefore be expected. On the other hand, the absence of any influence of spring Gaussen Index on fawn mass and size the following winter suggests that the availability of food resources during late gestation-early lactation is less important for winter mass of fawns. However, spring conditions markedly influence fawn birth mass and size (see Gaillard et al. 1993b for evidence on roe deer). Our
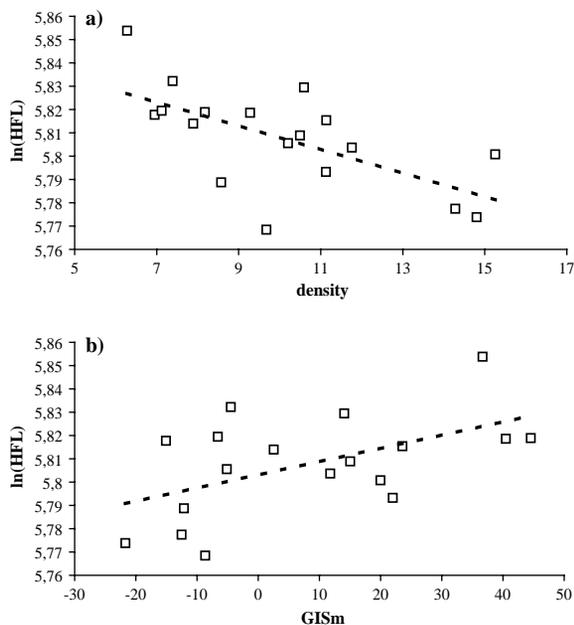

Fig. 2. Relationship between log-transformed hind foot length (ln(HFL)) of male fawns and a) the population density, expressed as the number of roe deer 100 ha^{-1} b) the Gaussen Index in summer (GISm) in the Chizé population.

results thus suggest that fawns with light birth weight are able to compensate for a bad start in life, as previously reported in two other roe deer populations (Gaillard et al. 1993c, Pelliccioni et al. 2004) and other ungulates (see Pélabon 1997 on fallow deer). While roe deer fawns seem to be able to compensate during their first summer for a bad start in life, a low mass in winter cannot be compensated for, generating cohort effects on adult body mass (Pettorelli et al. 2002 on roe deer, Solberg et al. 2004 on moose, Mysterud et al. 2001 on red deer). On the other hand, the relatively low variation of the Gaussen Index in spring (CV =0.20 vs 0.51 in summer) may lead to only little variation of food availability during spring in our study. Thus, a low yearly variation in resources during spring could simply explain why the Gaussen Index in spring had no effect on fawn cohort mass and size.

As expected, the phenotypic quality of a given cohort was density-dependent. While fawn body mass decreased linearly with increasing density in a similar fashion for both sexes, the density-dependent response of body size differed between sexes. Male fawn body size decreased linearly with density irrespective of climatic conditions, whereas female body size in winter was negatively affected by density only after dry summers. Contrasting effects of environmental conditions on males and females have been previously highlighted in highly dimorphic and polygynous ungulates in which different tactics of energy allocation to growth and reproduction are observed among sexes (see Clutton-Brock 1991 for a review). For instance, Post et al. (1999) reported that earlier plant phenology, and thereby higher availability of food resources during lactation, increased female but not male body mass of red deer calves. In mountain goats, female survival to one year of age decreased when food availability in the spring of birth was limited, whereas the survival of males was not affected (Côté and Festa-Bianchet 2001). We did not expect such sex-specific responses to environmental conditions in roe deer which are only slightly dimorphic in size (male fawns were only 4% heavier than female fawns at Chizé, this study). In contrast to highly dimorphic and poly-gynous ungulates, previous studies have suggested that higher maternal allocation towards daughters by heavier than average mothers has evolved in roe deer (Hewison et al. 2005) because high quality daughters may out-reproduce high quality sons. Under such conditions, the best mothers may increase their inclusive fitness by maximizing as far as possible the care they provide to their daughters. This differential allocation in favour of daughters by heavier than average mothers could account for the sex-specific responses of body size to environmental conditions that we observed in this study. It has previously been reported in the Chizé population that when density increases and/or climatic conditions deteriorate, fawn survival decreases (Gaillard et al. 1997)
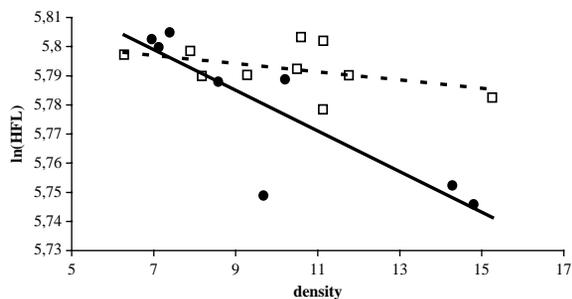
Fig. 3. Relationship between log-transformed hind foot length of female fawns and population density expressed as the number of roe deer 100 ha^{-1} in relation to the Gaussen Index in summer (filled circles = dry years, open circles = wet years) in the population of Chizé.

and hence heavier than average mothers become increasingly more successful relative to lighter than average mothers in raising fawns (Gaillard et al. 1998). As a result, under moderately harsh environmental conditions the proportion of fawns surviving to winter produced by heavier than average mothers increases. In this situation the average quality of the female fawn cohort is maintained, as we observed for example at high density but wet summers. However, under very harsh conditions, such as during dry summers at high deer density, even the best mothers may not be able to provide extra-maternal care to daughters (see Byers and Moodie 1990 for a similar argument on pronghorn). Hence, in this case, as we observed, female fawn body size decreases.

The lack of a response of body condition of roe deer fawns to a wide range of changes in environmental conditions likely is due to synchronous responses of body size and body mass, especially for males: under harsh conditions, fawns are both lighter and smaller. It seems that, while there is an ongoing debate about the pertinence of the allometric measure of body condition

Table 4. Model selection of the analysis of variation in mean cohort body condition of roe deer fawns. M0: null model, Np: number of parameters, ΔAICc: difference of AICc between a given model and the model with the lowest AICc, s: sex, n: density, GISp: Gaussen Index in spring of the year of birth, GISm: Gaussen Index in summer of the year of birth, ":" denotes interactive effects between factors, and "+" denotes additive effects. The selected models appear in bold. Only models with a ΔAICc <8 are presented.

Model	Np	AICc	ΔAICc
M0 = null model	**1**	**−41.856**	**0**
M0 + n	**2**	**−41.538**	**0.318**
M0 + n + s + GISm	4	−40.728	1.128
M0 + n + s + GISm + GISp	5	−40.213	1.643
M0 + n + s	3	−39.756	2.1
M0 + n + s + GISm + GISp + GISp:-GISm	5	−38.470	3.386
M0 + n + s + GISm + GISp + n:GISp	6	−37.786	4.07
M0 + n + s + GISm + n:GISm	5	−37.694	4.162
M0 + n + s + GISm + n:s	5	−36.937	4.919
M0 + n + s + GISm + GISp + s:GISp	6	−36.360	5.496
M0 + n + s + GISm + s:GISm	5	−36.060	5.796

(Green 2001, Schulte-Hostedde et al. 2005), our study shows that body mass and size are much better indicators of phenotypic quality in roe deer fawns.

References

Albon, S. D., Clutton-Brock, T. H. and Langvaten, R. 1992. Cohort variation in reproduction and survival: implications for population demography. – In: Brown, R. D. (ed.), The biology of deer. Springer, pp. 15–21.

Andersen, R. et al. 2000. Factors affecting maternal care in an income breeder, the European roe deer. – J. Anim. Ecol. 69: 672–682.

Anon. 2004. R: a language and environment for statistical computing. – R foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org <http://r.project.org/ >.

Becker, M., Nieminen, T. M. and Geremia, F. 1994. Short-term variation and long-term changes in oak productivity in northeastern France. The role of climate and atmospheric CO_2. – Ann. Sci. For. 51: 447–492.

Bro-Jorgensen, J. 2002. Overt female mate competition and preference for central males in a lekking antelope. – Proc. Nat. Acad. Sci. USA 99: 9290–9293.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. – Springer.

Burnham, K. P. et al. 1987. Design and analysis methods for fish survival experiments based on release-recapture. – Am. Fish. Soc. Monogr. 5.

Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. – Univ. of Chicago Press.

Byers, J. A. and Moodie, J. D. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. – Behav. Ecol. Sociobiol. 26: 157–164.

Clutton-Brock, T. H. 1991. The evolution of parental care. – Princeton Univ. Press.

Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. 1982. Red deer: behavior and ecology of two sexes. – Univ. of Chicago Press.

Clutton-Brock, T. H., Albon, S. D. and Guinness, F. E. 1988. Reproductive success in male and female red deer. – In: Clutton-Brock, T. H. (ed.), Reproductive success. Univ. of Chicago Press, pp. 325–343.

Clutton-Brock, T. H. et al. 1992. Early development and population fluctuations in Soay sheep. – J. Anim. Ecol. 61: 381–396.

Côté, S. D. and Festa-Bianchet, M. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. – Oecologia 127: 230–238.

Dajoz, R. 1973. Précis d'écologie. – Gauthier Villars.

Dobson, F. S. 1992. Body mass, structural size, and life history patterns of the Columbian ground squirrel. – Am. Nat. 140: 109–125.

Ericsson, G., Ball, J. P. and Danell, K. 2002. Body mass of moose calves along an altitudinal gradient. – J. Wildl. Manage. 66: 91–97.

Ferguson, S. H., Bisset, A. R. and Messier, F. 2000. The influences of density on growth and reproduction in moose *Alces alces*. – Wildl. Biol. 6: 31–39.

Forchhammer, M. C. et al. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. – J. Anim. Ecol. 70: 721–729.

Gaillard, J.-M. et al. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). – Can. J. Zool. 70: 1541–1545.

Gaillard, J.-M. et al. 1993a. Roe deer survival patterns: a comparative analysis of contrasting populations. – J. Anim. Ecol. 62: 778–791.

Gaillard, J.-M., Delorme, D. and Jullien, J.-M. 1993b. Effects of cohort, sex and birth date on body development of roe deer (*Capreolus capreolus*) fawns. – Oecologia 94: 57–61.

Gaillard, J.-M., Delorme, D. and Jullien, J.-M. 1993c. Croissance précoce et poids à l'entrée de l'hiver chez le faon de chevreuil (*Capreolus capreolus*). – Mammalia 57: 359–366.

Gaillard, J.-M. et al. 1996. Body mass of roe deer fawns during winter in 2 contrasting populations. – J. Wildl. Manage. 60: 29–36.

Gaillard, J.-M. et al. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. – Oecologia 112: 502–513.

Gaillard, J.-M. et al. 1998. Family effect on growth and survival of juvenile roe deer. – Ecology 79: 2878–2889.

Gaillard, J.-M. et al. 2000. Body mass and individual fitness in female ungulates: bigger is not always better. – Proc. R. Soc. B 267: 471–477.

Gaillard, J.-M. et al. 2003. Effects of hurricane Lothar on the population dynamics of European roe deer. – J. Wildl. Manage. 67: 767–773.

Garel, M. et al. 2004. The effects of a severe drought on mouflon lamb survival. – Proc. R. Soc. B (Suppl.) 271: S471–S473.

Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? – Ecology 82: 1473–1483.

Green, W. C. H. and Rothstein, A. 1991. Trade-offs between growth and reproduction in female bison. – Oecologia 86: 521–527.

Hewison, A. J. M. and 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. et al. 1996. Annual variation in body composition of roe deer (*Capreolus capreolus*) in moderate environmental conditions. – Can. J. Zool. 74: 245–253.

Hewison, M. A. J. et al. 2005. Big mothers invest more in daughters – reversed sex allocation in a weakly polygynous mammal. – Ecol. Lett. 8: 430–437.

Klein, D. R. 1964. Range-related differences in growth of deer reflected in skeletal ratios. – J. Mammal. 45: 226–235.

Langvatn, R. et al. 1996. Climate, plant phenology and variation in age at first reproduction in a temperate herbivore. – J. Anim. Ecol. 65: 653–670.

Leblanc, M., Festa-Bianchet, M. and Jorgenson, J. T. 2001. Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. – Can. J. Zool. 79: 1661–1670.

Lesage, L. et al. 2000. Quality of plant species utilized by northern white-tailed deer in summer along a climatic gradient. – Ecoscience 7: 439–451.

Loison, A., Langvatn, R. and Solberg, E. 1999. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. – Ecography 22: 20–30.

Mauget, C., Mauget, R. and Sempéré, A. J. S. 1999. Energy expenditure in European roe deer fawns during the suckling period and its relationship with maternal reproductive cost. – Can. J. Zool. 77: 389–396.

McElligott, A. G. et al. 2001. Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? – Behav. Ecol. Sociobiol. 49: 266–272.

Mysterud, A. et al. 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. – Proc. R. Soc. B 268: 911–919.

Oftedal, O. T. 1984. Body size and reproductive strategy as correlates of milk energy output in lactating mammals. – Acta Zool. Fenn. 171: 183–186.

Patterson, B. R. and Power, V. A. 2002. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. – Oecologia 130: 62–71.

Pélabon, C. 1997. Is weight at birth a good predictor of weight in winter for fallow deer? – J. Mammal. 78: 48–54.

Pelliccioni, E. R., Scremin, M. and Toso, S. 2004. Early body development of roe deer *Capreolus capreolus* in a sub-Mediterranean ecosystem. – Wildl. Biol. 10: 107–113.

Pettorelli, N. et al. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. – Proc. R. Soc. B 269: 747–753.

Pettorelli, N. et al. 2003. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. – Oecologia 137: 363–369.

Post, E. et al. 1999. Environmental variation shapes sexual dimorphism in red deer. – Proc. Nat. Acad. Sci. USA 96: 4467–4471.

Saether, B.-E. and Haagenrud, H. 1985. Life history of the moose *Alces alces*: relationship between growth and reproduction. – Holarct. Ecol. 8: 100–106.

Schulte-Hostedde, A. I. et al. 2005. Restitution of mass-size residuals: validating body condition indices. – Ecology 86: 155–163.

Solberg, E. J. et al. 2004. Lasting effects of conditions at birth on moose body mass. – Ecography 27: 677–687.

Toïgo, C., Gaillard, J.-M. and Michallet, J. 1999. Cohort affects growth of males but not females in Alpine ibex (*Capra ibex ibex*). – J. Mammal. 80: 1021–1027.

Weladji, R. B. and Holand, O. 2003. Global climate change and reindeer: effects of winter wheather on the autumn weight and growth of calves. – Oecologia 136: 317–323.

Williamson, D. T. 1991. Condition, growth and reproduction in female red lechwe (*Kobus leche leche* Gray 1850). – Afr. J. Ecol. 29: 105–117.

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