

Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females

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Abstract. There is increasing evidence that environmental conditions experienced early in life can markedly affect an organism's life history, but the pathways by which early environment influences adult phenotype are poorly known. We used long-term data from two roe deer (*Capreolus capreolus*) populations (Chizé and Trois-Fontaines, France) to investigate the direct and indirect (operating through fawn body mass) effects of environmental conditions during early life on adult body mass. We found that environmental conditions (population size and spring temperatures) around birth influenced body mass of adult females through both direct and indirect effects in both populations. The occurrence of direct effects means that, for a given fawn body mass, adult female mass decreases with adverse conditions in early life. In contrast, we found no evidence for direct effects of early-life conditions on adult body mass of males, suggesting the existence of sex-specific long-term responses of body mass to stressful early conditions. Our results provide evidence that early environmental conditions influence the adult phenotype through persistent effects over the body development in wild mammal populations.

Key words: *Capreolus capreolus*; cohort effects; developmental plasticity; early life; environmental conditions; fetal programming; long-lasting effect; path analysis.

INTRODUCTION

Body mass has been intensively studied in a wide range of vertebrates because it shapes the demographic performance of individuals (birds, Haramis et al. 1986; mammals, Gaillard et al. 2000; reptiles, Marquis et al. 2008). In mammals, body mass at weaning is positively associated with subsequent juvenile survival in the Columbian ground squirrel *Spermophilus columbianus* (Skibiél et al. 2009) and adult body mass is an important component of individual quality among large herbivores (Hamel et al. 2009). This correlation between body mass and survival or reproduction has led to the successful use and incorporation of body mass in demographic studies (Sauer and Slade 1987, Gamelon et al. 2012). For example, temporal changes in the body mass distribution of a population influence its dynamics and growth rate, explaining the phenotypic variation and the selection process occurring on that trait with climate change in several wild populations (Pelletier et al. 2007, Ozgul et al. 2010).

While phenotypic attributes such as age and sex account for most observed variation in adult body mass

(Stearns 1992), environmental conditions, especially during early life, are now seen as also playing a major role (Larsson and Forslund 1991, Pettorelli et al. 2002). Environmental conditions in early life generate short-term effects on life-history traits such as body mass and juvenile survival (Clutton-Brock et al. 1992) and also induce long-lasting effects on the same traits, i.e., between-individual differences are still detectable at the adult stage (Lummaa and Clutton-Brock 2002, Monaghan 2008). At the individual level, the long-lasting effects of early-life conditions correspond to the so-called “silver spoon effect” (Grafen 1988), by which individuals born under favorable conditions enjoy fitness benefits for their lifetime compared to individuals born under adverse conditions. At the population level, the “silver-spoon effect” translates into delayed cohort effects because individuals born the same year cope with similar environmental conditions during early life (Albon et al. 1987, Gaillard et al. 2003b). The magnitude of delayed cohort effects is tightly linked to the nutrition of individuals during their early life (Madsen and Shine 2000, Descamps et al. 2008). In roe deer (*Capreolus capreolus*) for instance, cohort effects are less pronounced in habitats providing the highest food quality (Pettorelli et al. 2006).

In wild populations, nutrition levels are usually inferred from proxies of food resources such as population density or climate conditions (Rickard et

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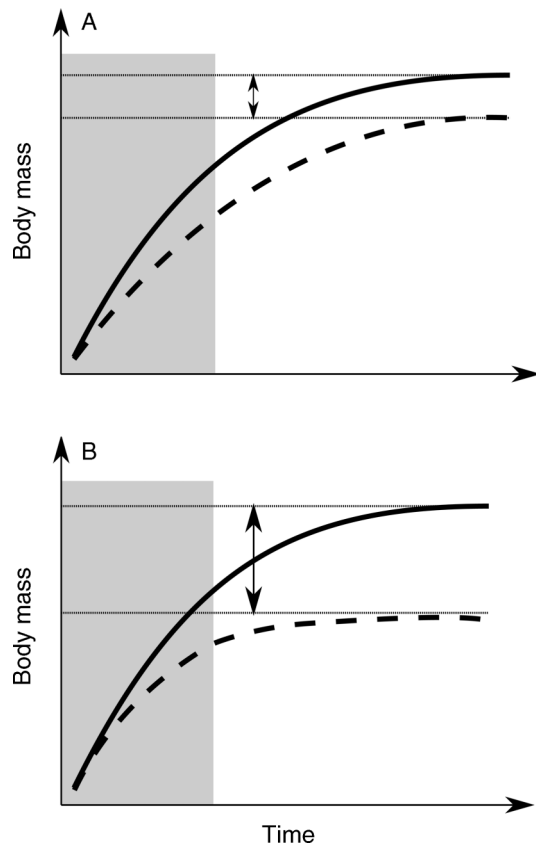


FIG. 1. Theoretical representation of two possible scenarios to explain long-lasting effects of early environmental conditions (shaded area) on adult body mass. Growth trajectories for individuals born under good (continuous lines) and poor (broken lines) conditions are displayed. Thin horizontal lines represent the asymptotic body mass. (A) Early environment influences early growth only. (B) Early environment influences adult body mass throughout the developmental process.

al. 2010). Accordingly, many studies have provided evidence of delayed cohort effects on adult body mass of large herbivores explained by weather or population density in the year of birth (Mysterud et al. 2002, Pettorelli et al. 2002, Solberg et al. 2004). At least two mechanisms may explain such observed relationships between environmental conditions during early life and adult body mass (Lummaa and Clutton-Brock 2002; Fig. 1). As a first and most commonly assumed mechanism (e.g., Pettorelli et al. 2002, Solberg et al. 2004) environmental conditions around the time of birth can influence early growth and thereby the juvenile body mass, which, in turn, determines adult body mass (mechanism 1, Fig. 1A). Second, environmental conditions in early life may influence adult body mass throughout the course of development (mechanism 2, Fig. 1B). In contrast to the first mechanism, late growth is also influenced by environmental conditions in early life. This second mechanism was first proposed from the early experimental works of McCance (1962) on captive

rats involving the manipulation of litter size. Rats from large litters received less milk than those from small litters during the 21-d suckling period. At this point, both groups were fed normally, but the smallest animals (from large litters) continued to diverge in body mass from the largest animals (see also Kapoor and Matthews 2005). Whether such an effect occurs in free-ranging populations of mammals is currently unknown. In comparison to the first mechanism, the difference of adult body mass between individuals born in poor and good environments is expected to be highest with the second mechanism (Fig. 1), therefore increasing individual heterogeneity in adult body mass. As such individual heterogeneity is the necessary starting point for natural selection to operate (Darwin 1859), disentangling these two mechanisms of long-lasting cohort effects is important.

Taking advantage of marked temporal variation in the environmental conditions recorded in two roe deer populations, we aimed to quantify how much of early-life conditions accounted for adult body mass via its effect on fawn body mass only vs. full growth period. Body growth of roe deer is monomolecular, a pattern in which growth rate decreases continuously from birth onwards (Portier et al. 2000). Individuals reach about 59–70% of their adult body mass within their first eight months of life (Andersen et al. 1998). Full body mass is reached at about 4 years of age and remains stable until 10 years of age in both males and females (Nussey et al. 2011). Because roe deer females are income breeders that rely almost exclusively on available food resources to meet the energetic costs of reproduction (Andersen et al. 2000), environmental conditions at birth should thus be a major determinant of fawn (5–8 months of age) and adult (between 4 and 10 years of age) body mass. If environmental conditions during early life affect adult body mass via early growth only, they should not influence adult body mass once the effects of fawn body mass are accounted for (mechanism 1, Fig. 1A). On the other hand, if environmental conditions during early life shape growth throughout the whole developmental process, it should still influence adult body mass once the effects of fawn body mass are accounted for (mechanism 2, Fig. 1B).

MATERIAL AND METHODS

Study areas and roe deer populations

The study was carried out in France in two fenced forests managed by the Office National des Forêts, the 2614-ha Réserve Biologique Intégrale of Chizé and the 1360-ha Territoire d'Étude et d'Expérimentation of Trois-Fontaines. These two study sites differ with respect to climatic conditions. Located in Western France (46°05' N, 0°25' W), Chizé has an oceanic climate under Mediterranean influence, with mild winters (daily temperature in January is $5.63^{\circ} \pm 0.36^{\circ}\text{C}$ [mean \pm SE]) and warm, often dry, summers (in July, daily temperature is $20.52^{\circ} \pm 0.28^{\circ}\text{C}$ and total

rainfall is 53.39 ± 4.03 mm [mean \pm SE]. On the other hand, Trois-Fontaines in Eastern France ($48^{\circ}43'$ N, $2^{\circ}61'$ W) has a continental climate with relatively colder winters (daily temperature in January is $3.07^{\circ} \pm 0.39^{\circ}\text{C}$) and warmer but generally wetter summers (in July, daily temperature is $19.57^{\circ} \pm 0.30^{\circ}\text{C}$ and total rainfall is 72.39 ± 6.76 mm).

At Chizé three habitats with contrasted quality (Pettorelli et al. 2001) have been identified in relation to the type of timber stand and coppice structure (from richest to poorest: oak (*Quercus* sp.) with hornbeam (*Carpinus betulus*), oak with Montpellier maple (*Acer monspessulanum*), and beech (*Fagus sylvatica*) with little coppice). Such a habitat structure was not found at Trois-Fontaines, where the forest appears more homogeneous. The primary productivity of the Chizé forest is quite low due to poor soils and frequent summer droughts, while Trois-Fontaines is a rich and productive forest due to high-quality soils and infrequent summer droughts. Long-term average wood production, which measures the potential biomass production, is $5.92 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at Trois-Fontaines vs. $3.77 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ at Chizé (Pettorelli et al. 2006). Accordingly, the demographic performance of roe deer was much higher at Trois-Fontaines than at Chizé (during the 1980s, $\lambda = 1.21$ at Trois-Fontaines vs. $\lambda = 1.04$ at Chizé; Nilsen et al. 2009), a difference mainly explained by the high pre- and post-weaning juvenile survival observed at Trois-Fontaines (Gaillard et al. 1993a, Gaillard 1997). Population size in both sites has been controlled by yearly removals in all years (but 2001–2003 at Trois-Fontaines and 2008–2011 at Chizé). Since 2000, roe deer at Chizé have been strongly limited by a combination of harsh climatic events and a relatively high density. No large predators or hunting of roe deer occurred in either site.

Roe deer data

Roe deer have been intensively monitored using capture–mark–recapture (CMR) methods since 1976 at Trois-Fontaines and 1978 at Chizé. Each year, between 8 and 12 capture sessions are carried out from October to March (mainly January and February). For each individual, sex, age, habitat type at Chizé, and body mass were recorded. We also assigned a Julian date (JD) to each capture event running from 1 October (JD 1) to 15 March (JD 166). Fawns (5–8 months of age) were identified by the presence of a tricuspid third premolar, which provides a reliable way to age deer <1 year old (Hewison et al. 2002). Roe deer belonged to 29 cohorts in both sites, born from 1979 to 2007 at Chizé and from 1977 to 2005 at Trois-Fontaines. We used data from known-aged animals only, weighed using an electronic balance, both as fawn and at least once as adult. Fawn body mass was adjusted for the date of capture to control for body growth that occurs over the capture season (Hewison et al. 2002). As expected, fawns grew by 0.016 ± 0.004 kg/day (mean \pm SE) and 0.020 ± 0.009

kg/day at Chizé and Trois-Fontaines, respectively. Adult body mass is the median of all measurements between 4 and 10 years of age (Pettorelli et al. 2002). Body mass of adult females was not influenced by pregnancy status because females were weighed right after the embryonic diapause (that ends in late December; Aitken 1974). Body mass is a composite measure of both body size and body condition (Dobson 1992). However, being income breeders (Andersen et al. 2000) roe deer do not accumulate body reserve for reproduction, so that individual variation in body mass is mostly associated with variation in size. Thus, growth in size and mass are tightly correlated in roe deer, as reported in both populations (Hewison et al. 2011) and respond similarly to changes in environmental conditions, while body condition does not (Toïgo et al. 2006).

Environmental variables

For each individual, we assessed how population size (POP, i.e., the number of roe deer older than 1 year in March) and weather conditions in the year of birth influenced body mass. Reliable and comparable estimates of POP were available using CMR methods in both populations (Gaillard et al. 2003a) because >70% of roe deer older than 1 year are individually marked. At Chizé, population density increased from 13 to 21 animals/km² between 1979 and 1984, then was reduced to around 6 animals/km² in 1994 and increased up to 19 animals/km² in 2006. Population density at Trois-Fontaines varied between 15 and 18 animals/km² from 1978 to 2001, after which the population was allowed to increase up to 25 animals/km² in 2005 due to a reduction of deer removals. We computed weather variables according to both the season and stage of development of roe deer in early life starting from January until August in year of birth. We obtained weather variables from Météo-France stations located <5 km from the study areas (Beauvoir-sur-Niort and Saint-Dizier for Chizé and Trois-Fontaines, respectively). There was virtually no difference in elevation between Météo-France stations and the study areas. We considered three different seasons, winter (January–March), spring (April–May), and summer (June–August). Because all individuals are in utero in winter but born in summer, we computed weather variables for each season. Weather conditions in winter were assessed using the mean temperature (T) and rainfall (R). In summer, we used the Bagnoul-Gausson drought index calculated as twice the mean temperature (in $^{\circ}\text{C}$) minus the mean precipitations (in mm) summed over June and August (Gaillard et al. 1997, Hamel et al. 2009). In spring, following Mysterud and Østbye (2006) and Panzacchi et al. (2009), we tested for the effects of average precipitation and temperature in April that corresponds to the last part of gestation for all females and May when some fawns are still in utero while others are born.

Statistical analyses

We used linear models (Rencher 2000) to analyze variation in fawn and adult body mass, and conducted separate analyses for each study area. As a first step, we tested for cohort variation in adult body mass for each sex using year of birth as a factor. At Chizé, we controlled for possible confounding effects of habitat quality (Pettorelli et al. 2002) by including habitat type as a third-level factor. Then, we investigated the effects of environmental conditions in year of birth on sex-specific body mass of adults. Our models included POP, weather variables, and sex to account for the weak sexual dimorphism in size of roe deer (Andersen et al. 1998). We explicitly tested the POP \times weather interactions (e.g., Portier et al. 1998).

Long-lasting effects of early conditions can be confounded with conditions experienced later in life (Descamps et al. 2008). This problem arises when environmental conditions in early life and in adulthood are correlated. While we did not detect any evidence of temporal autocorrelation for weather variables, we did for population size in both sites, with, respectively, a time lag of 3 and 1 years at Chizé and Trois-Fontaines (Appendix A). Similarly to Nussey et al. (2007), we controlled for the effect of population size experienced during the end of growth on adult body mass by including the average POP experienced between ages 1 and 4 (POP₁₋₄) in all models. We used a backward selection procedure, testing successively the first-order interactions and, if not significant, the main effects of covariates. Statistical significance was assessed by likelihood ratio test (LRT). We set the significance level α at 0.05. We checked for normality of residuals and homogeneity of variance graphically. The proportion of cohort variation in adult body mass explained by a given covariate was assessed by comparing models with the covariate (M_{cov}) to the cohort-dependent (M_{coh}) and constant (M_{cst}) models: $R^2 = (\text{deviance } M_{\text{cst}} - \text{deviance } M_{\text{cov}}) / (\text{deviance } M_{\text{cst}} - \text{deviance } M_{\text{coh}})$ (see Skalski et al. 1993).

To quantify the relative importance of the two mechanisms of long-lasting cohort effects, we analyzed direct and indirect (i.e., operating through fawn body mass) effects of environmental factors in year of birth on variation in adult body mass using path analyses (Shiple 2009). According to mechanism 1 (Fig. 1A), we should observe indirect effects only because environmental conditions in early life only influence early growth. Alternatively, according to mechanism 2 (Fig. 1B), both direct and indirect effects should be detected because environmental conditions in early life influence both early and late growth. Separate path analyses were conducted for males and females. Fawn and adult body mass and all environmental covariates retained from the previous analyses were entered into a path diagram. To calculate path coefficients, mass was log-transformed and all variables were standardized (mean = 0, SD = 1). Similarly to Mysterud et al. (2008), we tested the

significance of path coefficients by examining whether zero was included within the confidence interval at 95% of the estimated coefficients. We calculated partial R^2 to measure the effect size of direct and indirect effects. We used R software version 2.14 (R Development Core team 2011) to perform all analyses.

RESULTS

Cohort effects on adult body mass

At Chizé, habitat type did not influence adult body mass of males ($N = 146$, $F_{2,118} = 0.48$, $P = 0.62$) and females ($N = 173$, $F_{2,143} = 1.27$, $P = 0.29$). As expected, strong cohort variation occurred in adult body mass of both males (ranging from 21.0 kg in 2005 to 28.2 kg in 2000: $F_{25,118} = 4.09$, $P < 0.001$) and females (ranging from 19.1 kg in 2006 to 25.0 kg in 1992: $F_{27,143} = 3.67$, $P < 0.001$). T_{May} varied from a minimum of 11.14°C to a maximum of 18.33°C and POP ranged from 165 to 539 individuals older than 1 year (averaging 340 individuals across study years). When using environmental factors in early life to explain variation in adult body mass among cohorts, we found a statistically significant interactive effect between POP and T_{May} (Appendix B). The negative effect of density on adult body mass was greater when roe deer experienced a hot May in their year of birth (Appendix B). Adult body mass decreased with POP₁₋₄ (Appendix B). POP \times T_{May} interaction and POP₁₋₄ accounted for 88% of the observed cohort variation in adult body mass.

At Trois-Fontaines we detected cohort variation in adult body mass in females only ($N = 161$, $F_{28,132} = 2.21$, $P = 0.001$ for females and $N = 103$, $F_{26,76} = 0.78$, $P = 0.75$ for males), despite the fact that the range of adult body mass among cohorts was similar in both sexes (males born in 1979 were on average 5.6 kg heavier than males born in 2001 while females born in 1984 were 6.42 kg heavier than females born in 1995). Average temperatures during the spring of birth (T_{Apr} and T_{May}) had a negative effect on adult body mass (Appendix C) and accounted for 31% of the observed cohort variation in adult body mass.

Path analyses

For females at Chizé, the path diagram showed that the POP \times T_{May} interaction on adult body mass originated from both fawn body mass (indirect effects) and from direct effects (Fig. 2A). When both the direct and indirect effects of the POP \times T_{May} interaction were accounted for, body mass of adult females born in warm springs (i.e., warmer than the median temperature in May) decreased by about 1 kg for each increase of 100 roe deer at birth as compared with 0.54 kg when excluding the direct effects (Fig. 3A). Direct effects of POP \times T_{May} interaction accounted for about 5% of the observed variation in adult body mass of females (Fig. 2A). In contrast, we found no evidence for a direct effect of POP \times T_{May} interaction on body mass of adult males (Figs. 2B and 3B for a graphical representation). POP \times

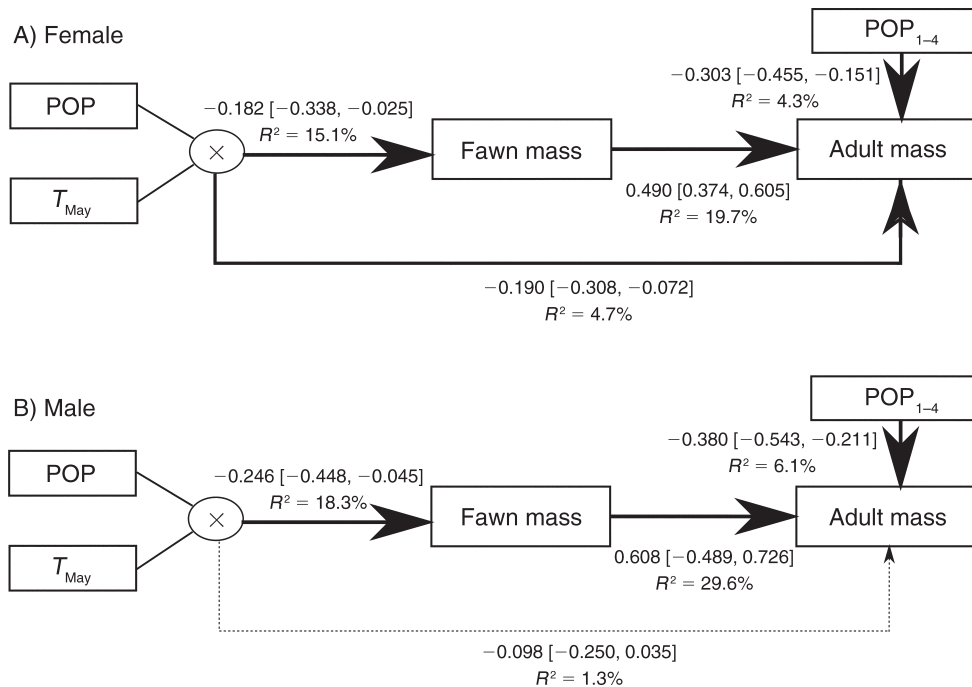


FIG. 2. Path diagrams showing how early environmental conditions directly and indirectly influence adult body mass (on a log scale) of (A) female and (B) male roe deer (*Capreolus capreolus*) at Chizé, France. Path coefficients are given with their associated 95% confidence limits in brackets. Solid lines indicate statistically supported effects (95% confidence limits exclude 0), and thin lines indicate nonstatistically supported effects (95% confidence limits include 0). Partial R^2 measures the marginal contribution of a pathway. POP stands for population size, T for average monthly temperatures, POP₁₋₄ for average population size experienced between ages 1 and 4, and “ \times ” for interactive effects.

T_{May} interaction influenced body mass of adult males via fawn body mass only (indirect effect).

For females at Trois-Fontaines, we detected indirect and negative effects of T_{Apr} and T_{May} on adult body mass (Fig. 4A). Only T_{Apr} showed an additional direct effect on adult body mass of females. However this direct effect only accounted for 1.4% of the observed variation in adult body mass of females. After accounting for the indirect and direct effects of T_{Apr} , body mass of adult females decreased by 0.55 kg for a 1°C increase in the average temperature of April as compared with 0.33 kg when excluding the direct effects (Fig. 3C). For males, there was evidence neither for direct or indirect effects of T_{Apr} and T_{May} on adult body mass, despite indirect effects in the expected direction (Figs. 4B and 3D).

DISCUSSION

Cohort variation in adult body mass of roe deer, which occurred at both sites, was associated with environmental conditions experienced in early life. At Chizé, adult body mass was negatively influenced by the POP \times T_{May} interaction (where “POP” stands for population size [the number of deer >1 year old in March] and “T” stands for the average temperature) while the average temperature in April had a negative influence at Trois-Fontaines. These results support the widespread occurrence of long-lasting effects of early

environmental conditions on life-history traits (reviewed in Lummaa and Clutton-Brock 2002, Gaillard et al. 2003b, and Monaghan 2008) and provide detailed pathways by which early environment generates such long-lasting cohort effects, using adult body mass as the response. In both sexes, environmental conditions early in life influenced adult body mass mainly through their effects on fawn body mass (indirect effects). Furthermore, the POP \times T_{May} interaction at Chizé and T_{Apr} at Trois-Fontaines also had negative direct effects on adult body mass of females. In contrast, we found no evidence for any direct effects of early-life conditions on adult body mass of males. These results mean that in males, early-life environmental conditions only affect early growth (as displayed in Fig. 1A), whereas in females, early-life conditions influence body growth throughout the whole developmental process (as displayed on Fig. 1B).

Cohort effects and spring environmental conditions

Variation in the quantity and quality of food resources around the time of birth is the major factor explaining the long-lasting effects of early environmental conditions on life-history traits (Madsen and Shine 2000, Descamps et al. 2008). In the two studied populations, high spring temperatures around birth had negative short-term and long-term effects on body mass. High temperatures in spring and early summer

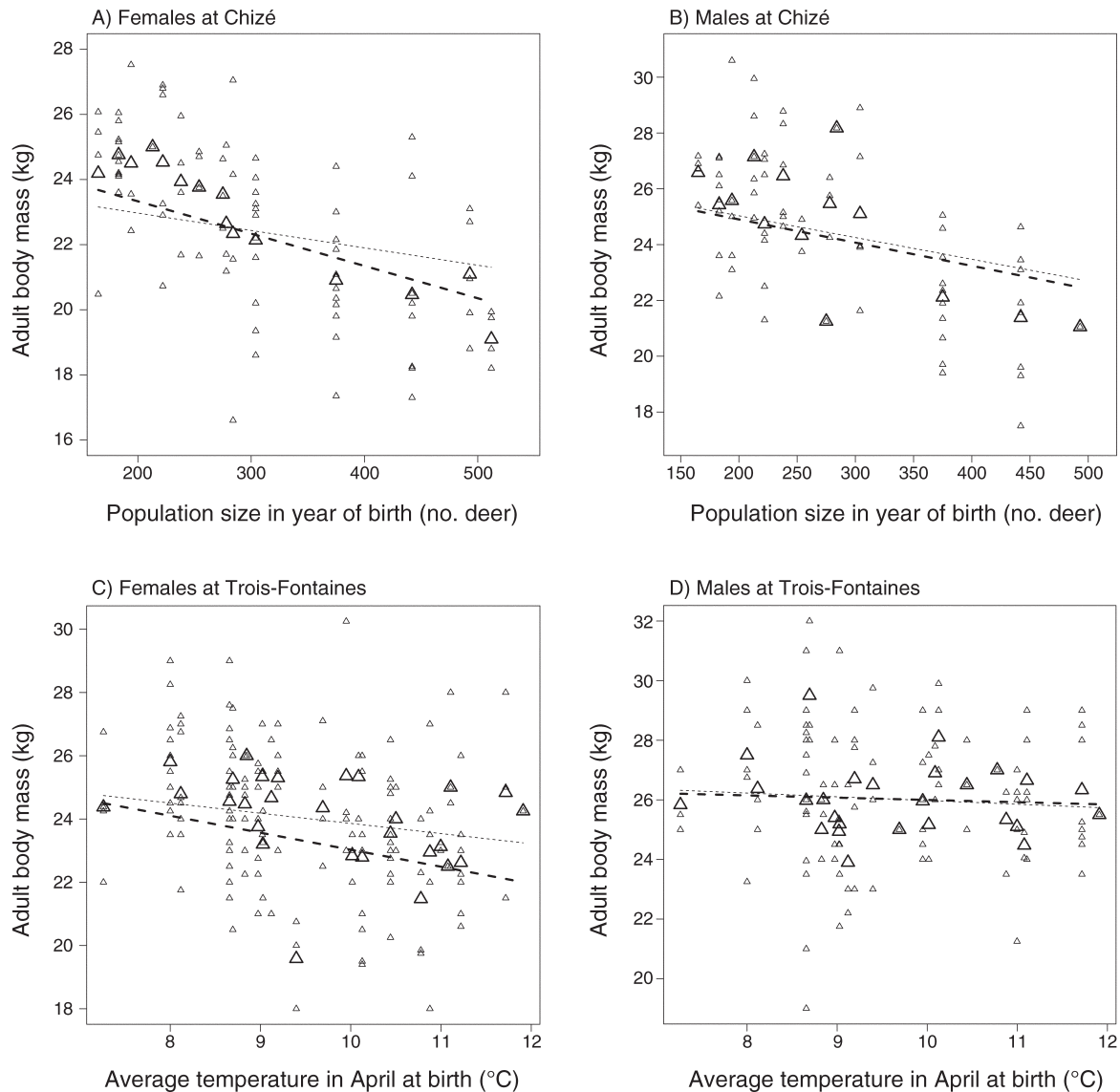


FIG. 3. Plot showing the direct and indirect effects of environment in early life (interacting effects of population size and temperatures in May at Chizé and effects of April temperatures at Trois-Fontaines) on adult body mass for both sexes. The thick dashed lines represent the predictions of the model with direct and indirect effects, whereas the thin dotted lines represent the predictions of the model with indirect effects only. The small gray triangles represent individual data, the large open triangles represent mean body mass for a given cohort. At Chizé, roe deer were divided into two groups: those that experienced (1) lower, and (2) equal or greater median temperatures in May at birth. We only represent here individuals that experienced equal or greater median temperatures in May at birth for convenience (but see Appendix D for complete graphical representations).

often correlate negatively with body mass of large herbivores in temperate areas (Albon et al. 1992 [red deer], Gaillard et al. 1996 [roe deer], Solberg et al. 2004 [moose]). The positive influence of a cool spring involves delayed lignification of the vegetation and, thereby, prolonged availability of high-quality forage (e.g., Solberg et al. 2004). Thus, being born during cool springs may be advantageous for the fawn through a relatively high growth rate. Being income breeders, roe deer females respond immediately to changes in food

resources during the last weeks of gestation and early lactation, when reproductive energy costs peak (Sadleir 1987), by adjusting the amount of energy allocated to their fawns. In addition, population density interacts with weather to shape adult body mass, as previously reported for other life-history traits of wild large herbivores (Bonenfant et al. 2009). At Chizé, for instance, the negative effect of density dependence on body mass was of greater magnitude when average temperatures in May were high.

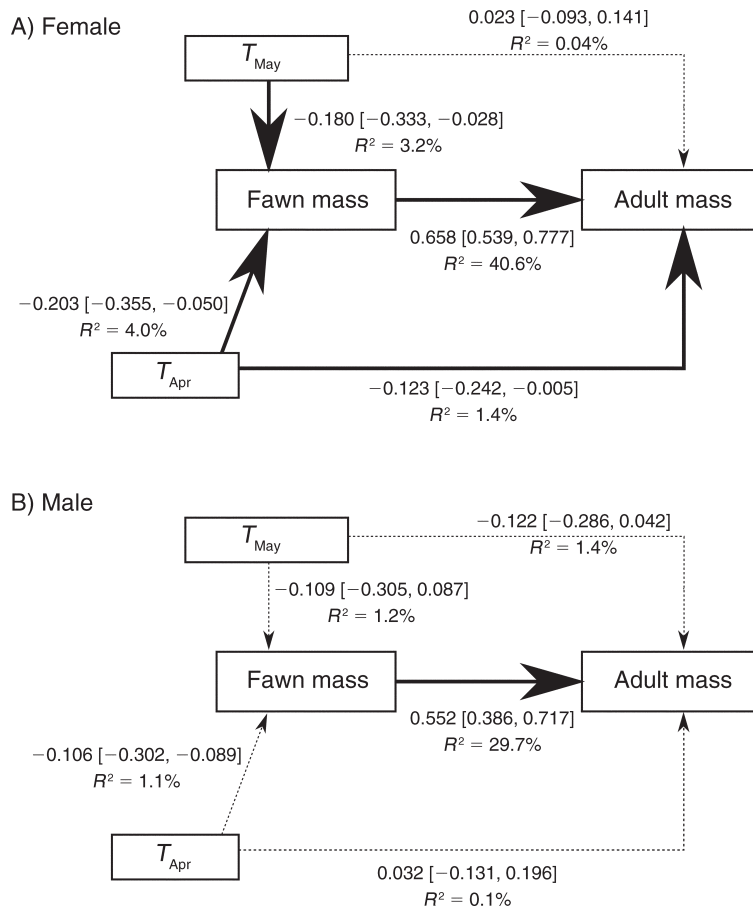


FIG. 4. Path diagrams showing how early environmental conditions directly and indirectly influence adult body mass (on a log scale) of (A) female and (B) male roe deer at Trois-Fontaines, France. Path coefficients are given with their associated 95% confidence limits in brackets. Solid lines indicate statistically supported effects (95% confidence limits exclude 0), and thin dotted lines indicate nonstatistically supported effects (95% confidence limits include 0). Partial R^2 measures the marginal contribution of a pathway.

Pathways generating long-lasting cohort effects on adult mass

In mammalian populations the effects of environmental conditions around the time of birth on adult body mass are commonly interpreted as evidence that early-life conditions influence early growth and thereby juvenile body mass, which in turn determines adult body mass (e.g., Pettorelli et al. 2002, Solberg et al. 2004). We found strong empirical support for such a mechanism. However, we also found a direct effect of early-life conditions on adult body mass of female roe deer, which was unrelated to their body mass as fawns, showing that early environmental conditions imprint their whole body growth trajectories. Environmental perturbations during early development, which lock individuals within a growth trajectory, directly determine the body mass of female roe deer later in life, independently of the postnatal environment they meet. That early nutrition can directly shape growth trajectories has been known for over 50 years from animal experiments (McCance 1962) but similar effects have

been previously reported in the wild for indeterminate growers only, such as water pythons (*Liasis fuscus*, Madsen and Shine 2000). Water pythons display a strong “silver-spoon effect,” whereby high prey abundance in the first year of life positively influences growth during their entire life. Our study indicates that adverse early-life conditions negatively influence both early and late growth in determinate growers such as female roe deer.

One reason for why body growth is continuously influenced by conditions in early life is that environmental stress during the crucial period of early life can permanently affect the body structure, physiology, and metabolism of individuals (Lucas 1991, Lummaa and Clutton-Brock 2002). For instance, the fetal stage is crucial for skeletal muscle development due to the lack of net increase in the number of muscle fibers after birth. A decrease in the number of muscle fibers due to food deprivation permanently reduces muscle mass and animal performance (Du et al. 2010). Animal breeders identified the fetal stages of development as the best time

window for nutritional management and manipulation, which can exert long-term effects on the growth performance of individuals (Du et al. 2010). As 75% of fetal growth occurs during the last two months of gestation in ruminants (Robinson et al. 1977), maternal stress during this period can have permanent and profound effects on offspring body structure. This mechanism can be involved in cohort effects, as we report here, but also in maternal effects (Rossiter 1991, Boonstra and Hochachka 1997) to explain between-individual differences within a given cohort through, for example, the heterogeneity in home-range quality among mothers (McLoughlin et al. 2007).

The two roe deer populations we studied live in contrasting environmental conditions. Trois-Fontaines has been a consistently highly productive forest, whereas Chizé has been markedly food-limited in several years. As a result, the average fawn mass in winter, which is a reliable measure of yearly environmental conditions roe deer are faced with (Gaillard 1996, Hamel et al. 2009), was lower and varied twice as much at Chizé (mean = 14.92 kg, CV = 0.11) as at Trois-Fontaines (mean = 17.44 kg, CV = 0.06). Moreover, a recent immunological analysis supports the high energetic stress at Chizé (Gilot-Fromont et al. 2012). Consistent with these between-population differences, the effects of environmental conditions in early life on late growth of females were more pronounced at Chizé than at Trois-Fontaines.

Sex-specific sensitivity to early-life conditions

In support of the low level of polygyny in roe deer, there is only a weak sexual size dimorphism and both sexes have similar early life-history traits like birth mass and early growth (Gaillard et al. 1993b) and similar survival up to one year of age (Gaillard et al. 1997). However, despite the weak intensity of sexual selection, there are some marked between-sex differences in roe deer life history. Only males are territorial, with a long territory tenure that spans over half the year. Contrary to females, males thus allocate energy to patrol, mark, and defend their territories. Hence, annual adult survival in roe deer is much less in males than in females (Gaillard et al. 1993a). Moreover, recent investigations of sex-specific mass-size allometry in roe deer have reported between-sex differences in ontogeny, structural size, and physiological condition (Hewison et al. 2011). We found that, contrary to females, there was no direct influence of early environmental conditions on adult body mass of males in the two studied populations. While the absence of statistically significant direct effects of early conditions on male adult mass at Trois-Fontaines could be due to a lack of statistical power, similar sample sizes for both sexes at Chizé led to similar between-sex differences involving a lack of direct effects in males. Such between-sex differences could result from sex-specific growth duration and timing of first reproduction. Female roe deer reach their asymptotic body

mass more rapidly than males in both populations (Hewison et al. 2011). For instance, males gained an additional 1.5–2.0 kg between 1.5 and 2.5 years of age, whereas females only gained 0.6 kg at Chizé (Hewison et al. 2011). This difference in body growth between sexes is likely due to the earlier occurrence of the trade-off between growth and energy allocation to reproduction for females than for males. At both sites, most females are pregnant for the first time at 2 years of age (Gaillard et al. 2003a) while males become territorial and mate for the first time at 3 years of age (Vanpé et al. 2009). The longer duration of body growth in males confers on them a greater flexibility to deviate from their initial growth trajectory compared to females. For instance, individuals may accelerate body growth when environmental conditions improve after a period of food restriction (compensatory growth sensu Bohman 1955). In contrast, such an opportunity to deviate from the initial growth trajectory is reduced for roe deer females because of reproductive constraints that shorten the growth period.

In conclusion, environmental conditions in early life have long-lasting effects on body growth in female roe deer. Moreover, the difference in productivity between the two study areas modulates the magnitude of these effects. Sex-specific long-lasting effects of early-life conditions on growth are likely related to differences of growth duration between males and females, and thereby to between-sex differences in the timing of first reproduction. While the causal mechanisms underlying these effects are not yet known, they are consistent with the idea that environmental stress during the crucial period of early life can permanently affect the body structure, physiology, and metabolism of mammals. Further studies are now needed to determine whether direct effects of early conditions on body mass during adulthood result from developmental constraints or correspond to adaptive developmental plasticity.

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SUPPLEMENTAL MATERIAL

Appendix A

Estimates of the temporal autocorrelation for weather variables and population size at Chizé and Trois-Fontaines, France ([Ecological Archives E094-164-A1](#)).

Appendix B

Parameter estimations and plot representations of variations in adult body mass of roe deer at Chizé, France ([Ecological Archives E094-164-A2](#)).

Appendix C

Parameter estimations and plot representations of variations in adult body mass of roe deer at Trois-Fontaines, France ([Ecological Archives E094-164-A3](#)).

Appendix D

Graphical representations of direct and indirect effects of environment in early life on adult body mass of roe deer at Chizé, France ([Ecological Archives E094-164-A4](#)).