

Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard

Marianne Mugabo · Olivier Marquis ·
Samuel Perret · Jean-François Le Galliard

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Abstract Food availability is a major environmental factor that can influence life history within and across generations through direct effects on individual quality and indirect effects on the intensity of intra- and intercohort competition. Here, we investigated in yearling and adult common lizards (*Zootoca vivipara*) the immediate and delayed life-history effects of a prolonged food deprivation in the laboratory. We generated groups of fully fed or food-deprived yearlings and adults at the end of one breeding season. These lizards were released in 16 outdoor enclosures together with yearlings and adults from the same food treatment and with food-deprived or fully fed juveniles, creating four types of experimental populations. Experimental populations were then monitored during 2 years, which revealed complex effects of food on life-history trajectories. Food availability had immediate direct effects on morphology and delayed direct effects on immunocompetence and female body condition at winter emergence. Also, male annual survival rate and female growth rate and body size were affected by an interaction between direct effects of food availability and indirect effects on asymmetric competition with juveniles. Reproductive outputs were insensitive to past food availability, suggesting that female common lizards do not solely

rely on stored energy to fuel reproduction. Finally, food conditions had socially-mediated intergenerational effects on early growth and survival of offspring through their effects on the intensity of competition. This study highlights the importance of social interactions among cohorts for life-history trajectories and population dynamics in stage-structured populations.

Keywords Food deprivation · Allocation strategies · Asymmetric competition · Density dependence · *Zootoca vivipara*

Introduction

Food availability can have major consequences for life history by affecting the intrinsic quality of individuals. For instance, food deprivation during sexual maturation can have long-term consequences for fecundity, body size and survival (e.g. Beckerman et al. 2003). Likewise, adverse food conditions during the breeding season can compromise the fecundity, immunity, survival and future reproduction of individuals (e.g. Brommer et al. 2004; Koskela et al. 1998; Martin et al. 2007; Saino et al. 1999) and can also influence the performances of their descendants through intergenerational effects (e.g. Plaistow et al. 2006). In some species, poor nutrition during the inter-breeding period may further compromise the restoration of body fat reserves, structural growth, survival until the next breeding and the energy available for future reproduction (Drent and Daan 1980). The extent to which conditions during breeding and inter-breeding periods are influential depend on resource allocation strategies since income breeders rely on resources acquired recently whereas capital breeders rely on stored energy (Drent and Daan 1980).

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M. Mugabo (✉) · O. Marquis · J.-F. Le Galliard
CNRS, UMR 7625, Laboratoire Ecologie et Evolution,
Université Pierre et Marie Curie, 7 Quai St. Bernard,
75005 Paris, France
e-mail: mmugabo@snv.jussieu.fr

S. Perret · J.-F. Le Galliard
CNRS/ENS UMS 3194, CEREEP-Ecotron IleDeFrance,
École Normale Supérieure, 78 rue du Château,
77140 St-Pierre-lès-Nemours, France

By potentially influencing both the quality and the number of survivors, food availability can affect competition within a population (Beckerman et al. 2003; de Roos et al. 2003; Mugabo et al. 2010; van de Wolfshaar et al. 2008). For example, intraspecific competition is strongly influenced by the size distribution of competitors (Bystrom and Andersson 2005; Claessen et al. 2000). Therefore, the competitive interactions within and between cohorts of individuals should be influenced by food conditions experienced in the past if these have lasting effects on size distribution. It is well known that competition plays a major role in life-history evolution and significantly influences the dynamics of size and stage-structured populations (e.g. Bystrom and Andersson 2005; Claessen et al. 2000; de Roos et al. 2003; van de Wolfshaar et al. 2008). Surprisingly, however, little is known about the effects of past environmental conditions on the intensity and the outcome of intraspecific competition and the consequences of this for life-history variation in structured populations (Mugabo et al. 2010).

Using the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model system, we investigated life-history effects of food deprivation experienced at the end of the reproductive period and aimed to identify the underlying mechanisms of life-history variation. As many ectotherms, the common lizard can use stored energy to fuel its reproduction (Bleu et al., unpublished data; Avery 1975), but some data indicate that recently acquired resources may also be influential (Avery 1975; Massot and Clobert 1995). To unravel immediate and delayed life-history effects, we manipulated food availability in the laboratory of yearling and adult males and females. Fully fed and food-deprived lizards were then released separately in outdoor enclosures and experimental populations were monitored during 2 years, thus spanning two breeding seasons. Natural populations of the common lizard are checked by density dependence and asymmetric competition between juveniles, yearlings and adults has been reported (Lecomte et al. 1994; Massot et al. 1992; Mugabo et al. 2010). To unravel how asymmetric interactions between juveniles on one side and adults and yearlings on the other side influence food-mediated life-history effects, adults and yearlings from each food treatment were released in outdoor enclosures with fully fed or food-deprived juveniles from the laboratory in a full-factorial design.

In the manipulated cohort of juveniles, we demonstrated earlier that food deprivation in the laboratory had direct immediate negative effects on structural growth but positive long-lasting effects on immunocompetence (Mugabo et al. 2010). Also, food deprivation had indirect delayed effects on the growth, body size, early survival and future reproduction of juveniles mediated by an interaction between its direct effects on individual quality and its

indirect effects on the intensity of intercohort social interactions combined with density dependence on body size. In populations with fully fed yearlings and adults, fully fed juveniles maintained their body size advantage over food-deprived juveniles until the yearling stage, and fully fed females also benefited from a reproductive advantage as they produced more and larger offspring than food-deprived females despite similar body size at adulthood. However, fully fed lizards suffered from a lower survival at the juvenile stage than food-deprived lizards. In sharp contrast, in populations with food-deprived yearlings and adults, food-deprived juveniles overcompensated during the following spring for their limited growth early in life. This compensatory growth at the juvenile stage enabled them to reach a larger body size at adulthood and to produce more offspring than fully fed juveniles but was associated with a reduction of juvenile survival (Mugabo et al. 2010).

Here, we hypothesise that food deprivation at the yearling and adult stages has strong immediate effects on body condition and to a lesser extent on body size since size growth is limited in adults (Andrews 1982). Contrary to results obtained in juveniles (Mugabo et al. 2010), males and females should differ in their sensitivity to food conditions because sexes have different energetic requirements and resource allocation strategies at the yearling and adult stages (González-Suárez et al. 2011; Le Galliard et al. 2005). In particular, we predict stronger direct delayed effects of food deprivation in females than in males since this sex invests more in reproduction (e.g. Aubret et al. 2002). As previously reported for the manipulated cohort of juveniles (Mugabo et al. 2010) and as expected for size-structured populations (see above), life-history variation in yearlings and adults could depend on food conditions experienced by the juveniles with which they interact. For instance, faster growth in juveniles could be associated with a larger niche overlapping with yearlings and adults and affect performances of the latter through exploitative competition (Bystrom and Andersson 2005). If so, we expect males to be less sensitive to competition than females as they are socially dominant over females and juveniles (Lecomte et al. 1994).

Materials and methods

Model species

Zootoca vivipara is a small (adult snout–vent length, SVL: 50–75 mm) ovoviviparous lizard inhabiting humid habitats across northern Eurasia. This lacertid species is characterized by a 3- to 4-year life expectancy, continuous growth and plastic life history that is sensitive to food availability

(Le Galliard et al. 2005; Mugabo et al. 2010). Natural populations are structured in three stage classes: juveniles (newborn individuals), yearlings (1- to 2-year-old individuals) and adults. In our study site, males start to emerge from hibernation around the beginning of March, followed shortly by juveniles and by females few weeks later. Reproductive investment (i.e. spermatogenesis and vitellogenesis) occurs within few weeks after winter emergence and the mating period starts shortly after emergence of females (Bauwens et al. 1989; Bauwens and Verheyen 1985). From June to July, females lay an average of five non-calcified eggs (range 1–12). Offspring hatch shortly after parturition and are immediately autonomous. Lizards enter hibernation in October.

Experimental design

From 16 June 2006 to 19 September 2006, we manipulated in the laboratory the daily food consumption of 263 yearling and adult lizards during 50 days. We fed lizards with a combination of larvae of the cricket *Acheta domesticus* and of the moth *Pyralis farinalis* obtained from Kreca (Ermelo, Holland). We used two food treatments adjusted by food consumption data of wild common lizards (Avery 1971). In the “high food” treatment group (HF), individuals were fully fed with an average of 200 mg day⁻¹ whereas in the “low food” treatment group (LF) lizards were maintained under a dietary restriction with an average of 100 mg day⁻¹. Prey items were weighed each day prior to feeding and non-consumed prey were removed each week. Animals were captured in outdoor enclosures at the Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP, northern France, 48°17'N, 2°41'E; $n = 214$) and in two natural populations (Mont Lozère, 44°27'N, 3°44'E; $n = 49$). Half the individuals from each origin were randomly assigned to each food treatment and adult females were manipulated from the day after parturition. Before the beginning of the food manipulation, all individuals were marked by toe clipping, sexed, measured for snout–vent length (to the nearest mm) and weighed (to the nearest mg). Food treatment groups of adults and yearlings did not differ initially in SVL, body condition (estimated from an analysis of covariance of body mass including SVL as a covariate) or sex ratios (ANOVA, all $P > 0.45$). During the manipulation, lizards were kept in individual cages under standardised conditions with optimal thermal and humidity conditions.

At the same time, we manipulated in the laboratory the daily food consumption of 460 juvenile lizards during 50 days from their birth day (detailed procedures are described in Mugabo et al. 2010). Juvenile food treatments did not differ initially in SVL, body condition or sex ratios (ANOVA, all $P > 0.80$) but body size was significantly

higher in the HF treatment group than in the LF treatment group after the manipulation ($F_{1,357} = 77.28$, $P < 0.0001$, as previously reported in Mugabo et al. 2010).

At the end of the laboratory manipulation, yearling and adult lizards were measured for body size (SVL) and body mass and then released in 16 outdoor enclosures each 10 by 10 m and located in a natural meadow at the CEREEP. Yearlings and adults from each food treatment (hereafter named “main food treatment”) were released with food-deprived or with fully fed juveniles (hereafter named “juvenile food treatment”), generating four different types of experimental populations with four replicates each (i.e. “fully fed” populations in which all lizards have been fully fed, “food-deprived” populations, and two types of mixed populations; see Fig. 1b in Mugabo et al. 2010). Outdoor enclosures were randomly selected for each treatment group and initial populations had similar age and sex structure (4–5 adult females, 3 adult males, 4–6 yearling females, 4–5 yearling males, and 28–34 juveniles). Outdoor enclosures provided lizards with natural food supply, shelters and basking sites, and were protected by nets to avoid avian predation.

Measurements of life-history traits and immunocompetence

Populations were monitored during three successive capture sessions to obtain data of growth in SVL, body condition, survival, reproduction and immunocompetence of yearlings and adults. Capture sessions were from 2 to 5 April 2007 ($n = 110$), from 15 to 31 May 2007 ($n = 112$) and from 19 May to 5 June 2008 ($n = 56$). Growth rates in SVL were calculated as the change in SVL divided by the time interval (number of days elapsed between the initial measurement and the focal measurement minus the number of days spent in hibernation and emergence, assumed to be from 1 October to 15 March in the study site). We estimated annual survival probabilities in 2007 and in 2008 between release in summer 2006 and May 2007 and between May 2007 and May 2008, respectively. Survival probabilities were directly obtained from recapture data since the catchability (i.e. capture probability) in our experimental system is very close to 1 at this time of the year (Le Galliard et al. 2005). In late spring 2007 and 2008, all females were maintained until parturition in the laboratory to assess their reproductive characteristics. Five of the 69 females recaptured in May 2007 and 2 of the 43 females recaptured in May 2008 were not gravid. Reproductive characteristics of gravid females were estimated by measuring fecundity (total number of eggs) and postpartum body condition.

We also assessed immunocompetence of manipulated lizards in late spring 2007 and 2008. Immunocompetence

was measured by the skin-swelling in response to the injection of a mitogen, the phytohaemagglutinin (PHA), as described by Mugabo et al. (2010). The skin-swelling was calculated as the difference in thickness of the leg (mm) between 12 h before and after the injection. This procedure triggers a haemagglutination and lymphoproliferation and evaluates the ability of an individual to mount an inflammatory response (Vinkler et al. 2010, and references therein).

In addition, we gathered data on intergenerational effects of food availability by measuring the SVL at birth of offspring produced by manipulated lizards during the first and second year of the study, and by measuring the body growth and juvenile survival of the cohort of offspring produced during the first year of the study. Numbers of released adults and yearlings, of released juveniles and of offspring born during the experiment were recorded for each population at each capture session to test for density dependence.

Statistical analyses

We analysed immediate effects of food availability on body condition and SVL at the end of the manipulation with linear models. Explanatory variables included main food treatment (i.e. food treatment of yearlings and adults), sex, age class (yearling and adult classes), and their first-order interactions, as well as additive effects of date at the beginning of the manipulation and geographical origin.

We used mixed-effects linear models to analyse the delayed effects of food treatments on growth rates in SVL, SVL, body condition, female reproductive characteristics and immunocompetence. These models included fixed effects of (1) main food treatment in interaction with juvenile food treatment to account for the manipulation of juveniles, (2) second-order interactions with sex to test for sexual differences of sensitivity to food treatments, (3) initial age class (yearling or adult) and first-order interactions with food treatments, and (4) additive effects of date at the beginning of the manipulation and geographical origin. A first-order interaction between SVL and sex was included when analysing body condition to control for sex-specific slopes between body mass and SVL. A fixed effect of initial SVL was included when analyzing growth rates to control for decelerating growth curves (Andrews 1982) and the number of activity days was included when analyzing SVL to control for differences in release and capture dates. Fecundity generally increases with female SVL (Avery 1975). We therefore tested for effects of treatments on fecundity without and with additive effects of SVL. The random part of all these

models included an effect of enclosure identity. We used the restricted maximum likelihood approach of the *lme* procedure to estimate model parameters and test statistics following Pinheiro and Bates (2000). Minimum adequate models were selected by removing non-significant terms in a backward procedure using marginal *F* tests. Assumptions of normality were fulfilled, but Bartlett tests detected variance heterogeneity in some analyses. In these cases, we accounted for heterogeneous variances with a *varIdent* function in *lme* (chapter 5.2 in Pinheiro and Bates 2000).

Annual survival probabilities in 2007 and 2008 were analysed with mixed-effects logistic regressions including a logit link and binomial error terms. Models included fixed effects of (1) main food treatment, juvenile food treatment, sex, initial age class and their first-order interactions, (2) additive effects of initial SVL centred at its grand mean (linear and quadratic effects) to evaluate selection on body size, and (3) additive effects of geographical origin and date at the beginning of the manipulation. The random part of all these models included an enclosure effect. Model parameters were estimated with a Laplace approximation of the maximum likelihood in *lmer* and fixed effects were tested with Wald *Z* tests (Bolker et al. 2009). A minimum adequate model was obtained by backward elimination of non-significant terms.

We used similar mixed-effects models to analyse intergenerational effects of food treatments on SVL at birth of offspring born during the experiment and on annual growth rate and survival of offspring born in 2007. These models included additive effects of (1) date of birth of the offspring, (2) clutch size corrected for female's SVL (residuals of linear regression of clutch size against SVL) when analysing SVL at birth of juveniles, and (3) SVL at birth of the offspring when analysing growth rate (linear effect) and probability of annual survival (linear and quadratic effects). Clutch size was included to control for the classical trade off between offspring quantity and offspring size in lizards (Olsson and Shine 1997). The random part of all these models included a clutch identity effect nested in an enclosure effect.

Whenever significant effects of food treatments were observed, we tested for density-dependent effects. When analysing delayed effects of food treatments, we used current numbers of yearlings and adults and numbers of juveniles from each population as covariates. When analysing intergenerational effects on the growth rates and survival of offspring produced in 2007, we used numbers of offspring and numbers of older conspecifics. All models were implemented in R 2.10.1 software (<http://cran.r-project.org/>) and estimates are provided with standard errors.

Results

Immediate effects on morphology

Dietary restriction had immediate, negative effects on the body condition and SVL at the end of the laboratory experiment (Table 1; Fig. 1a). Body condition was influenced by an interaction between main food treatment and age class (Table 1). The effect of main food treatment on body condition was stronger in adults than in yearlings (Fig. 1a). In addition, SVL at the end of the manipulation was about 1 mm larger in fully fed than in food-deprived lizards (Table 1). Sex affected both traits independently of main food treatment (main food treatment × sex: *F* tests, all *P* > 0.09; see Table 1 for details on sexual differences). Variability in body condition was also greater for adults than for yearlings (Bartlett’s *K*-squared = 17.72, *df* = 1, *P* < 0.0001, variance ratio = 1.53; Fig. 1a).

Delayed effects on life history and immunocompetence

Delayed effects on morphology

Body condition at winter emergence in April 2007 was affected by an interaction between main food treatment and sex (*F*_{1,87} = 13.88, *P* = 0.0003). LF females were less corpulent than HF females (post-hoc test: *F*_{1,13} = 12.15, *P* = 0.004) whereas in males body condition was similar between food-treatment groups (*F*_{1,13} = 0.13, *P* = 0.72; Fig. 1b). In addition, body condition at winter emergence was significantly higher (*F*_{1,87} = 18.15, *P* = 0.0001; Fig. 1b; sex-specific slopes between body mass and SVL:

*F*_{1,83} = 0.69, *P* = 0.41) but less variable (Bartlett’s *K*-squared = 5.68, *df* = 1, *P* = 0.02, variance ratio = 0.77) in males than in females.

Annual growth rates during the first year of the field experiment and SVL in May 2007 were both affected by a three-way interaction between main food treatment, juvenile food treatment and sex (respectively: *F*_{1,90} = 11.19, *P* = 0.001 and *F*_{1,90} = 7.08, *P* = 0.009). When maintained with HF juveniles, HF females grew to be larger than LF females (post-hoc tests for growth rate: *F*_{1,6} = 11.96, *P* = 0.01; for SVL: *F*_{1,6} = 5.41, *P* = 0.06; Fig. 2) whereas the opposite was observed when females were maintained with LF juveniles (growth rate: *F*_{1,6} = 13.57, *P* = 0.01; SVL: *F*_{1,6} = 6.44, *P* = 0.04; Fig. 2). These effects were not observed in males (growth rate and SVL, main × juvenile food treatment: *F*_{1,7} = 1.11, *P* = 0.33 and *F*_{1,7} = 0.11, *P* = 0.75). Growth rate was marginally higher in LF than in HF males (*F*_{1,9} = 3.78, *P* = 0.08) and SVL was similar between LF and HF males (*F*_{1,9} = 0.41, *P* = 0.54; Fig. 2). Numbers of conspecifics in May 2007 did not explain this variation of annual growth rate and SVL in males and females.

During the second year of the experiment, annual growth rate and SVL were no longer affected by the three-way interaction (respectively: *F*_{1,38} = 3.57, *P* = 0.07; *F*_{1,37} = 1.79, *P* = 0.19) nor by main food treatment effects (respectively: *F*_{1,10} = 0.01, *P* = 0.95; *F*_{1,11} = 0.75, *P* = 0.41). However, the pattern of body growth and SVL for females was very similar to the one of the first year (Fig. 2), suggesting that we lacked power to detect a significant effect. In both years, females grew more and were larger than males (*F* tests, all *P* < 0.0001) and growth rates decreased with initial SVL (*F* tests, all *P* < 0.0001).

Table 1 Immediate effects of food availability on body condition and SVL (mm) at the end of the manipulation in yearling (*n* = 144) and adult (*n* = 119) common lizards (*Zootoca vivipara*)

Effects	Estimate ± SE	<i>F</i> _{ndf,ddf}	<i>P</i> value
Body condition (body mass controlled for SVL)			
Intercept	0.12 ± 0.07	<i>F</i> _{1,255} = 3.01	0.08
SVL (mm)	0.10 ± 0.01	<i>F</i> _{1,255} = 241.37	<0.0001
Sex	M: 0.47 ± 0.05	<i>F</i> _{1,255} = 84.74	<0.0001
SVL × sex	M: 0.02 ± 0.01	<i>F</i> _{1,255} = 5.86	0.02
Main food treatment	LF: −0.44 ± 0.07	<i>F</i> _{1,255} = 37.36	<0.0001
Age class	Y: −0.59 ± 0.09	<i>F</i> _{1,255} = 45.93	<0.0001
Main food treatment × age class	LF-Y: 0.26 ± 0.08	<i>F</i> _{1,255} = 9.57	0.002
Origin	C: 0.22 ± 0.08	<i>F</i> _{1,255} = 6.69	0.01
SVL (mm)			
Intercept	59.05 ± 0.56	<i>F</i> _{1,258} = 10882.84	<0.0001
Main food treatment	LF: −1.08 ± 0.40	<i>F</i> _{1,258} = 7.29	0.007
Sex	M: −3.96 ± 0.48	<i>F</i> _{1,258} = 88.01	<0.0001
Age class	Y: −9.93 ± 0.48	<i>F</i> _{1,258} = 420.06	<0.0001
Origin	C: 6.23 ± 0.63	<i>F</i> _{1,258} = 98.70	<0.0001

LF Low food treatment, M males, Y yearlings, C origin CEREEP

Fig. 1 **a** Immediate effects of main food treatment on body condition in female and male adult and yearling common lizards (*Zootoca vivipara*) and **b** delayed effects on body condition at winter emergence in females and in males. Data are given as mean values per food-treatment group in each stage \pm SE. *Black symbols* HF main food treatment, *white symbols* LF main food treatment

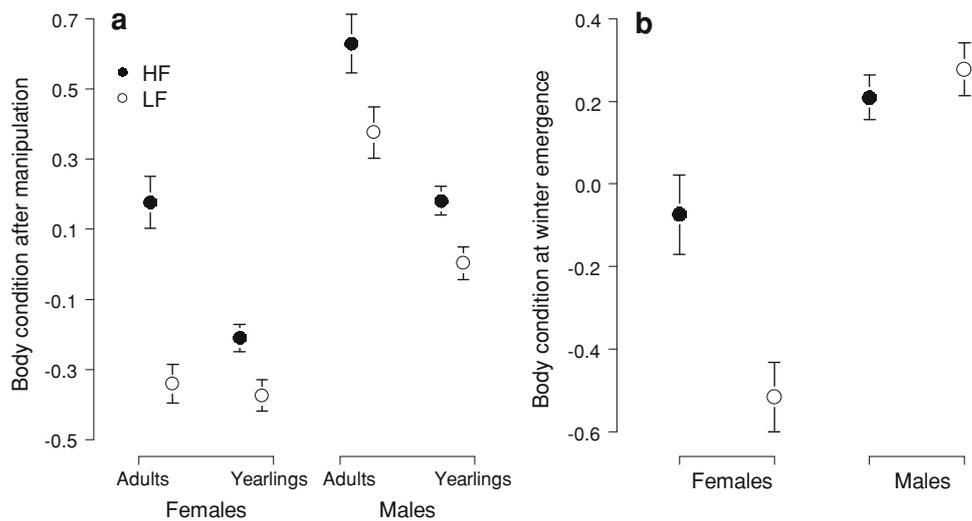
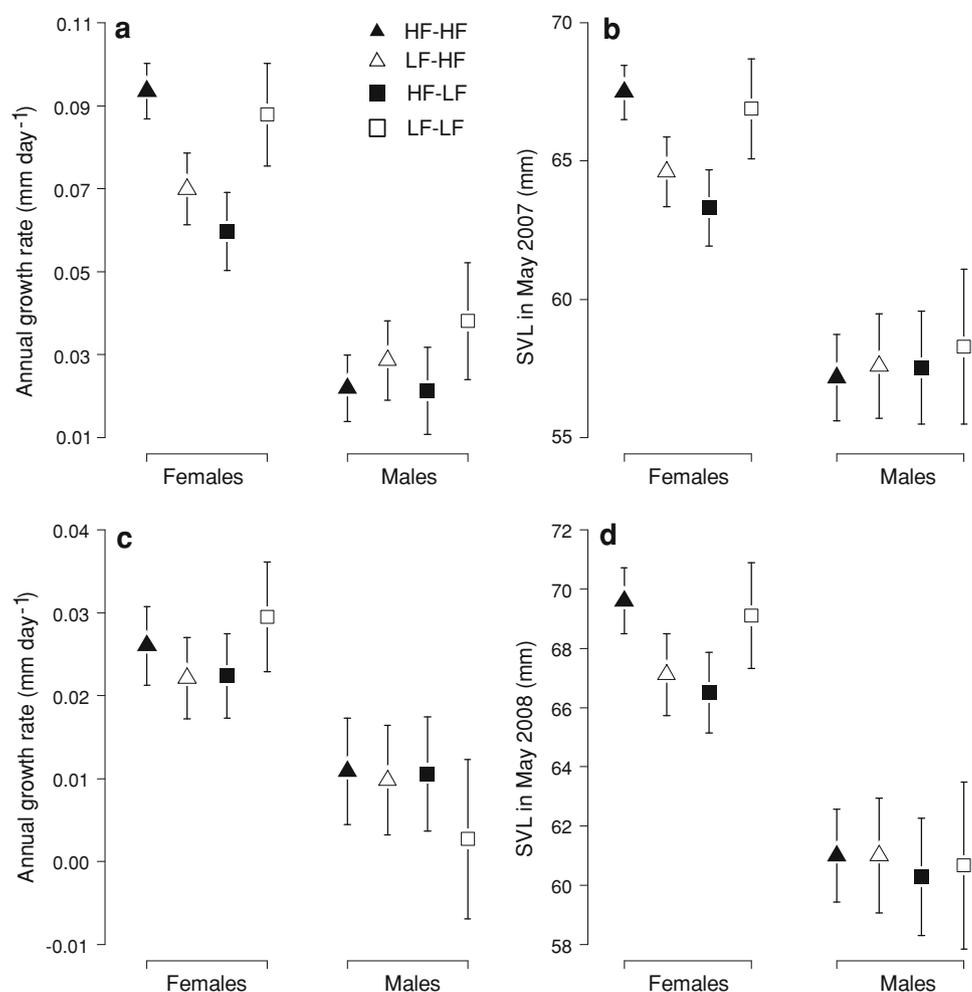


Fig. 2 Delayed effects of main food treatment and juvenile food treatment on the annual growth rates and SVL of females and males during **a, b** the first and **c, d** the second year of the experiment. **a–d** Estimates were obtained from linear mixed effect models with fixed effects of main food treatment, juvenile food treatment, sex and their second-order interactions, and **a, c** additive effects of initial SVL centred at its grand mean. **c** The negative values of annual growth rate are due to measurement errors (± 1 mm in adults). *Black symbols* HF main food treatment, *white symbols* LF main food treatment, *triangles* HF juvenile food treatment, *squares* LF juvenile food treatment

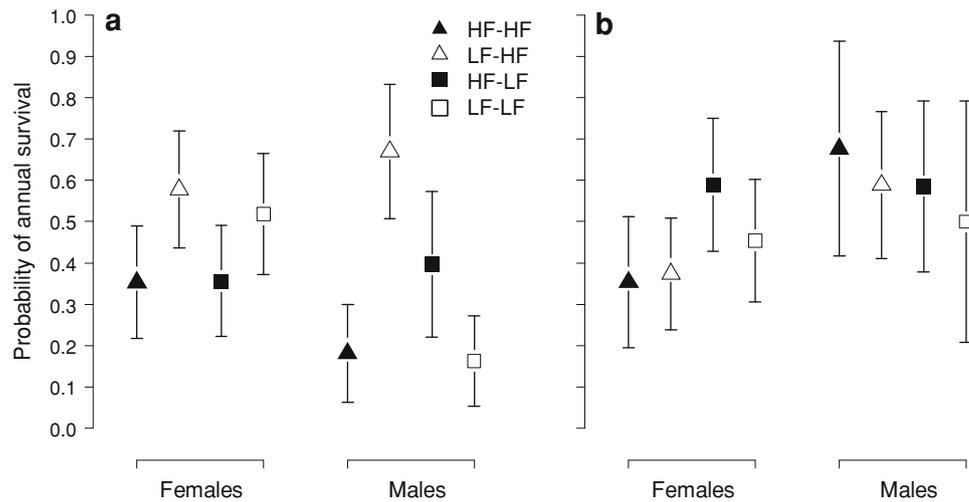


Delayed effects on annual survival

Probability of annual survival during the first year of the experiment was affected by an interaction between main

food treatment, juvenile food treatment and sex ($Z = -2.64, P = 0.008$). Annual survival was affected by an interaction between main food treatment and juvenile food treatment only in males (in females: $Z = -0.21, P = 0.83$;

Fig. 3 Delayed effects of main food treatment and juvenile food treatment on the probability of annual survival of females and males during **a** the first and **b** the second year of the experiment. Estimates were obtained from generalised mixed effect models with main and juvenile food treatment and their interaction as fixed factors. Symbols as in Fig. 2



in males: $Z = -2.23$, $P = 0.02$). Fully fed males but not females had a lower annual survival rate than food-deprived males when maintained with fully fed juveniles (post-hoc tests in males: $Z = 2.08$, $P = 0.04$; in females: $Z = 1.00$, $P = 0.32$) but not in populations with food-deprived juveniles (post-hoc tests in males: $Z = -1.09$, $P = 0.27$; in females: $Z = 0.91$, $P = 0.36$; Fig. 3a). Annual survival during the first year was higher in yearlings than in adults (yearlings = 0.48 ± 0.07 , adults = 0.32 ± 0.08 ; $Z = 2.67$, $P = 0.008$), with no significant influence of body size (SVL: $Z = 1.77$, $P = 0.08$; SVL²: $Z = 0.47$, $P = 0.64$). During the second year of the experiment, annual survival rates were not affected by food treatments (Wald Z tests, all $P > 0.11$) and males and females had similar survival rates ($Z = 1.38$, $P = 0.17$; Fig. 3b).

Delayed effects on reproduction

Fecundity recorded in 2007 was not affected by food treatments, despite a strong positive effect of body size (fecundity not controlled for SVL: F tests, all $P > 0.14$; fecundity controlled for SVL: F tests, all $P > 0.08$; SVL: $F_{1,51} = 33.12$, $P < 0.0001$). Similarly, fecundity in 2008 was not affected by food treatments when controlling or not for SVL of females (F tests, all $P > 0.10$). In addition, postpartum body condition in 2007 and 2008 was not affected by food treatments (F tests, all $P > 0.11$). Postpartum body condition was lower in yearlings than in adults in 2007 ($F_{1,49} = 17.61$, $P = 0.0001$) but not in 2008 ($F_{1,18} = 2.56$, $P = 0.13$).

Delayed effects on immune performances

Main food treatment marginally affected immune performances in 2007 ($F_{1,14} = 3.83$, $P = 0.07$) and had no effect

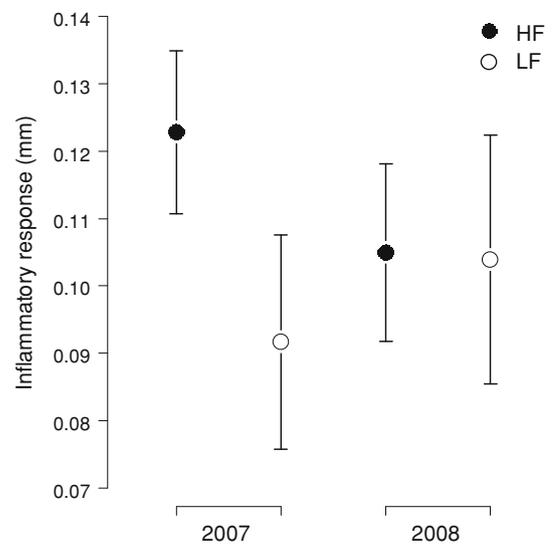


Fig. 4 Delayed effects of main food treatment on inflammatory response in 2007 and 2008. Data are given as mean values per group \pm SE

in 2008 ($F_{1,10} = 0.15$, $P = 0.70$). In 2007, HF lizards displayed a higher inflammatory response than LF lizards (Fig. 4). Immune performances in 2007 and 2008 were not correlated [Pearson’s product moment correlation: $r = 0.03$ ($-0.29, 0.34$), $P = 0.87$] and did not differ between sexes and age classes (F tests, all $P > 0.13$).

Intergenerational effects

The SVL at birth of offspring born from manipulated lizards in 2007 and in 2008 was not affected by food treatments (F tests, all $P > 0.16$; Fig. 5a). SVL at birth decreased with clutch size in 2007 ($F_{1,44} = 10.14$, $P = 0.003$) but not in 2008 ($F_{1,13} = 2.11$, $P = 0.17$) and was lower for male offspring (in 2007: $F_{1,249} = 92.36$,

$P < 0.0001$; in 2008: $F_{1,162} = 57.76$, $P < 0.0001$). In addition, growth rate of offspring born in 2007 during their first year of life was not affected by food treatments (Fig. 5b), irrespective of whether we controlled for density-dependence (F tests, all $P > 0.23$) or not (F tests, all $P \geq 0.1$). Growth rate of offspring decreased with the number of older conspecifics (slope: -0.0014 ± 0.0003 , $F_{1,11} = 28.00$, $P = 0.0003$) and female offspring grew faster than males ($F_{1,80} = 14.55$, $P = 0.0003$).

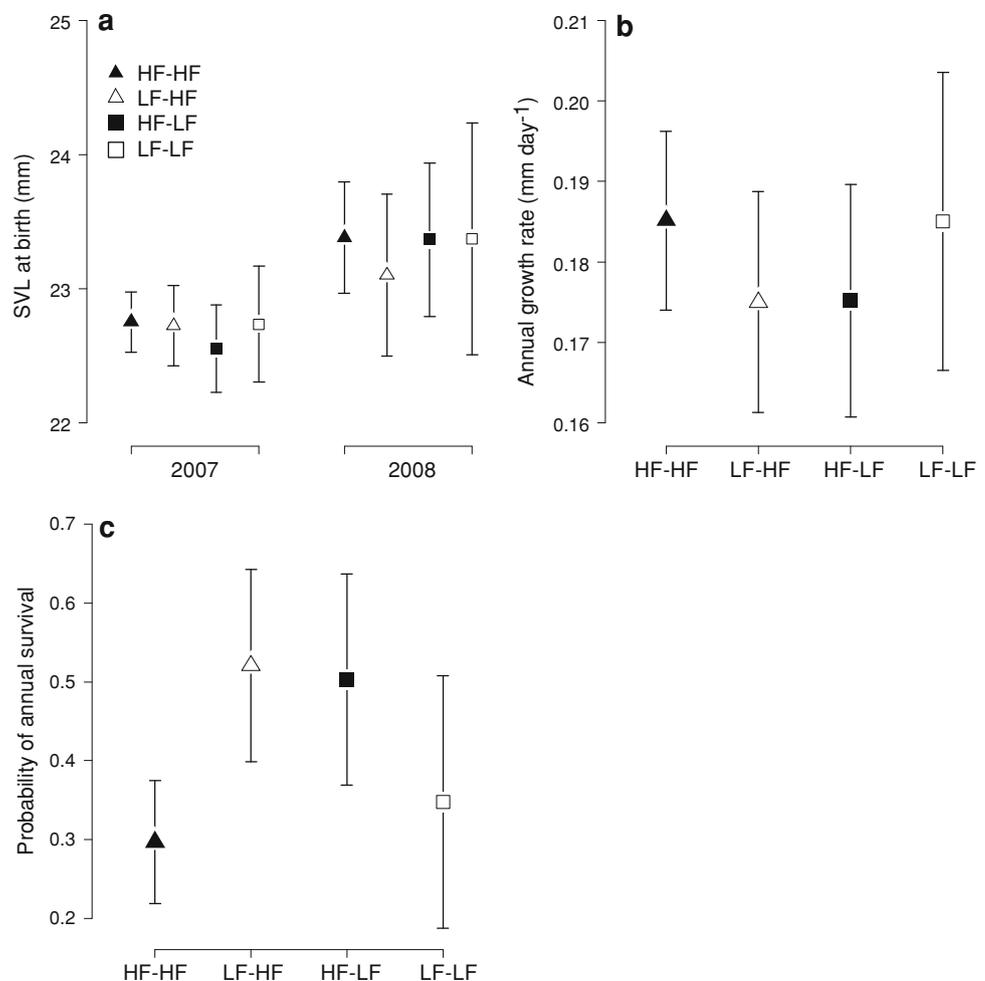
In contrast, annual survival of offspring born in 2007 was affected by a two-way interaction between main food treatment and juvenile food treatment ($Z = -2.34$, $P = 0.02$). When maintained with HF juveniles, offspring born from HF females had a lower survival than those born from LF females ($Z = 2.07$, $P = 0.04$) whereas such a difference was reversed but not significant when offspring were maintained with LF juveniles ($Z = 1.26$, $P = 0.21$; Fig. 5c). We found no effect of cohort densities, SVL at birth (linear and quadratic) and date of birth on offspring survival (Wald Z tests, all $P > 0.26$), but male offspring survived better than females ($Z = 2.03$, $P = 0.04$).

Discussion

Immediate effects of food availability on morphology

A prolonged food deprivation during the summer had immediate negative effects on body condition and body size of yearlings and adults, which emphasises a classical reduction of body fat reserves, muscular mass and structural growth at low food availability (Kooijman 2000). These immediate effects of food deprivation on body condition were stronger in adults than in yearlings. During the food manipulation, yearlings and adults received the same amounts of food. Yet, yearlings were substantially smaller than adults and thus had less energetic requirements for maintenance than adults (Kooijman 2000), which allowed them to capitalise more efficiently on available resources. Furthermore, the immediate effects of food deprivation were similar in males and females despite the existence of substantial sexual differences in body size and body condition (males are smaller but more corpulent than females) and thus in body composition (e.g. in muscles and

Fig. 5 Intergenerational effects of main food treatment and juvenile food treatment on **a** the SVL at birth of offspring born in 2007 and 2008, **b** on the annual growth rate and **c** annual survival probability of offspring born in 2007 during their first year of life. **a**, **b** Estimates (\pm SE) were obtained from linear mixed effects models including main food treatment, juvenile food treatment and their interaction as fixed factors. **c** Estimates (\pm SE) were obtained from generalised mixed effects models including main food treatment, juvenile food treatment and their interaction as fixed factors. Symbols as in Fig. 2



body fat; Kratochvil et al. 2003). This result indicates that male and female lizards have a similar flexibility of their energy allocation strategy to body condition and structural growth at that time of the year. This is surprising because female common lizards spend large amounts of energy in vitellogenesis and gestation and body size is important for their fecundity, whereas energetic investment of males in production of gametes is less important (Avery 1975; Nagy 1983). We would therefore expect stronger sensitivity of growth allocation in females than in males. However, male mating behaviors can be costly in this species. Mating activity (e.g. mate searching and acquisition and multiple copulations) may limit the food intake of males (González-Suárez et al. 2011) and male–male aggressions have been reported in a mating experiment (Fitze et al. 2008). Body size is also an important determinant of the mating success of male common lizards (Fitze and Le Galliard 2008). In addition, males emerge from hibernation a few weeks before females and expose themselves to adverse food and climatic conditions where body fat reserves and muscular mass are critical for survival. Therefore, male and female common lizards may experience similar selection for an optimal body condition and body size (Schwarzkopf 1994), thus explaining their parallel flexibility to food availability.

Direct delayed effects of food availability on life history

In accordance with our expectations, some lasting effects of food deprivation were seen for body condition in females, indicating that males but not females were able to fully compensate before hibernation for the immediate effects of food deprivation. Since males and females did not differ in their immediate sensitivity to food deprivation, this result suggests that sexes differed in their acquisition and/or allocation of energy before and during wintering. For example, food-deprived yearling and adult males may have limited compensatory responses in females through dominance in competition for food (Lecomte et al. 1994; Massot et al. 1992). However, even in females, main effects of food deprivation did not last until the end of spring following winter emergence, since food-deprived and fully fed females had similar fecundity and postpartum body condition during the 2 years of the experiment. This ability to compensate for a lower body condition at the onset of reproduction and to invest similar amounts of energy in reproduction throughout life demonstrates that, as in female geckos (Kubicka and Kratochvil 2009), female common lizards can use energy acquired during vitellogenesis to fuel reproduction, i.e. an income breeder strategy. This result agrees with a study by Avery (1975) which suggested that female common lizards invest in egg

production energy acquired during vitellogenesis and to a lesser extent stored energy.

Socially mediated delayed effects of food availability on life history

During the first year of the field experiment, annual growth rates and body size of females and annual survival rates of males were affected by an interaction between food conditions they experienced in the past and food conditions experienced by juveniles from the same population. Altogether, these results indicate that the delayed life-history effects of food deprivation for yearlings and adults depended on social interactions with juveniles and not on intracohort interactions (traits were insensitive to cohort densities). Comparable socially-mediated life-history effects were found for juveniles, except that no sexual differences were detected (see Mugabo et al. 2010, and the “Introduction”). Yet, substantial life-history differences existed between the adults and yearlings on one hand and the juveniles on the other, suggesting that different mechanisms may be involved.

A similar pattern of survival was observed for juveniles and for yearling and adult males but not for females. In the common lizard, yearling and adult males and juveniles have similar activity periods that differ from the activity period of females. Males and juveniles emerge from hibernation in late winter, a few weeks before yearling and adult females, when environmental conditions are suboptimal and risks of starvation are high (Bauwens et al. 1989; Bauwens and Verheyen 1985). This difference of phenology may explain why annual survival of females was not affected by food treatments. In “fully fed” populations (i.e. HF-HF treatment group), fully fed yearling and adult males and juveniles suffered from a lower survival than after a food deprivation. This result suggests that the intensity of competition was increased when both juveniles and older lizards experienced favourable past food conditions. Since males are socially dominant over females and juveniles (Lecomte et al. 1994) and since females were not affected, we hypothesised that this increased competition gave rise to survival costs within the few weeks after winter emergence of juveniles and males and before emergence of females. We also speculate that a combination of two mechanisms may have contributed to this high level of competition between juveniles and yearlings and adults in “fully fed” populations compared to other populations (Mugabo et al. 2010). First, large juveniles should be more affected by competition with older conspecifics than small juveniles due to a larger niche overlapping. Second, large and corpulent yearlings and adults may compete more with juveniles than small and thin individuals due to the higher social rank and to the energetic requirements associated

with a larger body mass (Kooijman 2000). Exploitative competition (Bystrom and Andersson 2005) more than an increase of aggressive behaviours (Claessen et al. 2000) or a change in resource exploitation behaviours (Lecomte et al. 1994) could be responsible for the mortality of juveniles and yearling and adult males. Indeed, juveniles from “fully fed” populations did not suffer from more aggression or predation attempts than juveniles from other populations (estimated by tail loss; Mugabo et al. 2010). However, behavioural data combined with estimates of food consumption and resource availability would be needed to validate these hypotheses. In “food-deprived” populations (i.e. LF-LF treatment group), food-deprived juveniles (Mugabo et al. 2010) but not adult and yearling males suffered from a significant reduction in survival relative to fully fed lizards. In these populations, Mugabo et al. (2010) observed that juveniles showed a strong overcompensatory growth, whereas males only showed a marginal compensatory growth in this study. Thus, some physiological costs of compensation (reviewed in Metcalfe and Monaghan 2001) rather than ecological costs of competition could be responsible for the lower survival of food-deprived juveniles in these populations (Mugabo et al. 2010).

Similar patterns of growth rates and body size were observed for juveniles and for yearling and adult females but not for males. Two non-exclusive mechanisms could explain this. First, investment in structural growth may be too limited in reproductive males to be substantially affected by competition with juveniles (Andrews 1982; Schwarzkopf 1994). Second, when environmental conditions were more favourable for body growth (i.e. from April–May to September), male performances may have been insensitive to competition due to their social dominance (Lecomte et al. 1994). When maintained with food-deprived conspecifics (i.e. LF-LF treatment group), both food-deprived old females (this study) and food-deprived juveniles (Mugabo et al. 2010) displayed overcompensatory growth. In these populations, a limited level of competition for food between juveniles and yearling and adult females may have provided favourable conditions for compensatory responses to occur. In sharp contrast, when maintained with fully fed conspecifics (i.e. HF-HF treatment group), both fully fed females (this study) and fully fed juveniles (Mugabo et al. 2010) benefited from a “silver spoon effect” on body size, i.e. long-term fitness advantages of past favourable conditions (Grafen 1988). They reached a higher body size than food-deprived females and juveniles and fully fed females even displayed higher growth rates. In juveniles, we hypothesised previously that competition with fully fed yearlings and adults prevented food-deprived juveniles from compensating for their limited growth early in life (Mugabo et al. 2010). Fully fed

juveniles thus maintained the body size advantage they acquired in the laboratory over food-deprived juveniles. Here, we suggest that fully fed females were able to maintain higher growth rates than food-deprived females even after the food manipulation because of their higher competitive abilities than juveniles (Lecomte et al. 1994). Another possibility is that juveniles invest more energy in structural growth whereas older individuals invest more energy in body condition (Andrews 1982). In contrast to juveniles, fully fed females did accumulate additional stored energy during the food manipulation and were able to reinvest a substantial part of this energy in structural growth during the following spring. This result raises the need for a better understanding of energy allocation strategies in this species (Kooijman 2000).

Female fecundity during the first year of the experiment was similar between treatment groups, despite the existence of significant differences in body size and significant effects of body size on reproductive outputs. This result differs from what was observed in the manipulated cohort of juveniles (Mugabo et al. 2010). Contrary to juveniles, fast growth in yearling and adult females facilitated by full feeding may entail reproductive costs rather than survival costs, e.g. a negative trade-off between growth rate and future reproduction (Heino and Kaitala 1999; Schwarzkopf 1994). Altogether, these results demonstrate that females are not more affected than males by competition with juveniles but that sensitivity of life-history traits to competition with juveniles is contrasted between sexes. Differences in phenology and in energy acquisition and allocation could explain this heterogeneity between sexes and traits.

Direct delayed effects of food availability on immunocompetence

In sharp contrast with life-history traits, immunocompetence was affected by lasting effects of the main food treatment but was insensitive to juvenile food treatment. Such a discrepancy was also observed in the manipulated cohort of juveniles (see Mugabo et al. 2010) and suggests a decoupling between immunity and life-history variation in the common lizard. The lasting effects of food deprivation were opposite for yearlings and adults (this study) compared with for juveniles (Mugabo et al. 2010): food deprivation had marginal immunosuppressive effects in yearlings and adults after 1 year in the field, whereas food-deprived juveniles had higher immune responses during the 2 years of the field study. Developmental plasticity may be responsible for these age-specific effects of a food deprivation on immunocompetence (Bateson et al. 2004). Indeed, in developing individuals, food deprivation may alter the construction of the immune system leading to a

higher investment in immunity throughout life compared to individuals which experienced early good conditions (Birkhead et al. 1999; Tschirren et al. 2009). In grown and non-developing individuals, a decrease of energetic resources is expected to inhibit immune responses (Martin et al. 2007). In addition, differences of the inflammatory responses of yearlings and adults between the first and the second year of the field experiment could be explained by the activation of different components of the immune system between the first and the second encounter with PHA (e.g. activation of acquired immunity at the second encounter; Vinkler et al. 2010, and references therein).

Intergenerational effects of food availability

Intergenerational effects of the environment experienced by the mother have been described in many taxa (e.g. in humans, Lummaa and Clutton-Brock 2002; in squamates, Marquis et al. 2008; and in soil mites, Plaistow et al. 2006). Here, contrary to our expectations, quality at birth and early performances of offspring were not affected by past food conditions experienced by mothers. However, early performances of offspring were influenced by our treatments through similar, socially-mediated effects than the one detected for juveniles (Mugabo et al. 2010) and for adults and yearlings (this study). First, offspring early growth rate was negatively affected by the number of older conspecifics (i.e. manipulated adults, yearlings and juveniles) inside the population of birth. Second, offspring early survival varied similarly to survival in males and juveniles, suggesting an intergenerational effect of past food conditions through the intensity of intercohort competition. These results indicate that food conditions have the potential to influence the performances of individuals across generations not only through direct effects on the intrinsic quality of individuals (Plaistow et al. 2006) but also through indirect effects on their social environment.

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