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Adaptive maternal effects shape offspring phenotype and survival in natal environments

Elvire Bestion^{1*}, Aimeric Teyssier^{2,3}, Marylin Rangassamy^{2,4}, Olivier Calvez¹, Olivier Guillaume¹, Murielle Richard¹, Amandine Braem¹, Felix Zajitschek^{1,5}, Susanne Zajitschek^{1,6} & Julien Cote²

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¹ *Station d'Ecologie Théorique et Expérimentale, CNRS, UAR 2029, Moulis 09200, France*

² *Laboratoire Evolution et Diversité Biologique, CNRS, Université Toulouse III Paul Sabatier, IRD, UMR5174, Toulouse, France*

³ *Terrestrial Ecology Unit, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium*

⁴ *Laboratoire d'Ethologie Expérimentale et Comparée, Université Paris 13 Nord, Paris, France*

⁵ *School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia*

⁶ *School of Biological and Environmental Sciences, John Moore's University, James Parsons Building Byrom Street, Liverpool, L3 3AF, United Kingdom*

* Corresponding author: Elvire Bestion, elvire.bestion@sete.cnrs.fr

ORCID IDs: 0000-0001-5622-7907 (EB), 0000-0003-2275-9651 (AT), 0000-0002-2733-0056 (OG), 0000-0003-2135-8194 (MRi), 0000-0001-6010-6112 (FZ), 0000-0003-4676-9950 (SZ), 0000-0002-4453-5969 (JC)

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Abstract

Maternal effects can give newborns a head start in life by adjusting natal phenotypes to natal environments. Yet their strength and adaptiveness are often difficult to investigate in natural populations. Here, we studied anticipatory maternal effects and their adaptiveness in common lizards in a semi-natural experimental system. Specifically, we investigated how maternal environments (i.e. vegetation cover) and maternal phenotype (i.e. activity levels and body length) can shape offspring phenotype. We further studied whether such maternal effects influenced offspring survival in natal environments varying with respect to vegetation cover, conspecific density, and, consequently, maternal fitness. More active females from dense vegetation habitats produced bigger offspring than their less active counterparts, the contrary being true for sparse vegetation habitats. Moreover, females from dense vegetation habitats produced more active offspring and more active offspring survived better in dense vegetation habitats, resulting in greater maternal fitness through maternal effects. These results suggest adaptive anticipatory maternal effects, induced by vegetation structure and mediated by activity levels that may shape early life prospects in natal environments.

Introduction

Natal phenotypes are crucial in shaping the ability of newborns to cope with their environment and to survive into adulthood. However, the adaptiveness of phenotypes may vary with ecological conditions encountered at birth. For example, larger juveniles can be better competitors, grow faster and survive better than smaller juveniles but these benefits can be cancelled out or magnified with predation risk (Ferguson and Fox 1984; Sogard 1997). While quickly assessing natal environments and plastically adjusting their phenotype to those environments is crucial for fitness early in life, it entails costs in time and energy.

Lifetime plasticity alone might not suffice to rapidly cope with challenging natal environments. Transgenerational plasticity may help adjusting the phenotype and increase performance even before or at birth (Sheriff et al. 2017). Maternal effects arise when maternal environments or maternal phenotypes influence offspring phenotypes beyond the direct effects of transmitted genes (Marshall and Uller 2007). They have been shown in a wide variety of species, with complex ecological and evolutionary implications (Mousseau and Fox 1998; Badyaev and Uller 2009; Yin et al. 2019; Tariel et al. 2020). When maternal and offspring environments are similar, maternal effects provide information on the natal environment to offspring before birth and may lead to better-adapted phenotypes in these environments. For instance, in *Anolis* lizards, low prey availability in the offspring environment led to reduced survival, but this effect was reduced through maternal effects when prey availability was low in maternal environments as well (Warner et al. 2015). However, maternal effects can also be maladaptive, as in three-spined sticklebacks in which maternal exposure to predation risk prevented antipredator behaviours (i.e. orientation towards the predator) in offspring and thus led to higher predation rates (McGhee et al. 2012). Such maladaptive maternal effects were attributed to a developmental exposure to elevated levels of stress hormones known to have deleterious effects on offspring (McGhee et al. 2012). The adaptiveness of maternal effects however depends on the predictability of the environment. When maternal and offspring environments are similar, anticipatory maternal effects, in which mothers ‘anticipate’ the natal environment to produce offspring with the appropriate phenotype, should yield greater fitness (Marshall and Uller 2007), while their adaptiveness could be much lower in less predictable environments. Semi-natural experiments may serve to investigate how anticipatory maternal effects affect juvenile fitness in different environments.

Here we studied how vegetation structure in maternal habitats can adaptively modify natal juvenile phenotype through maternal effects in common lizards (*Zootoca vivipara*). Common lizards are live-bearers with no parental care but with important maternal effects influencing offspring phenotype. Maternal hormonal levels, ectoparasite loads, nutritional status, thermal and water conditions as well as predation risk influence juvenile locomotion, basking behaviour, activity, morphology and dispersal (Sorci et al. 1994; Massot and Clobert 2000; Meylan and Clobert 2004; Bestion et al. 2014; Rozen-Rechels et al. 2018). As only 50% of juveniles survive their first summer (Meylan and Clobert 2005), juveniles have little time to plastically adjust to their environment and maternal effects might thus be a determining factor for juvenile fitness. Common lizards live in generally dense vegetation habitats, and the density of lizards is generally high (Massot et al. 1992). Habitat types vary from peatbog to 30% woodland habitats (Rutschmann et al. 2016) and densities vary within (Bestion et al. 2015a) and between populations (Massot et al. 1992; Meylan and Clobert 2004). As lizard fitness varies with vegetation structure, with lower survival in sparser vegetation environments (Josserand et al. 2017), maternal effects related to vegetation cover in the maternal habitat are expected to influence offspring fitness.

We used semi-natural mesocosms (the Metatron, (Legrand et al. 2012)) to experimentally investigate how vegetation cover in maternal habitats shapes offspring natal

phenotype and success in habitats varying for vegetation cover and population density. Vegetation structure and population density both influence prey availability (Spiller and Schoener 1988; Asteraki et al. 2004; Wasiolka et al. 2009) and may subsequently influence competition strength, hunting strategies and fitness outcomes (Mugabo et al. 2011). We focused on body length and activity level because both traits are good predictors of competitive abilities and life history traits (Le Galliard et al. 2004, 2013, 2015) and have genetic and pre- and post-natal environmental determinants (Le Galliard et al. 2004, 2006; Bestion et al. 2014; Teysier et al. 2014). Maternally driven changes in activity and body length in offspring could therefore lead to different success depending on population density and vegetation cover. In particular, activity levels are part of a syndrome encompassing behavioural, life-history and physiological traits in various species (Biro and Stamps 2008, 2010; Réale et al. 2010). Within a species, more active individuals often have a higher metabolic rate, higher food intake, and higher growth and are often more aggressive, bolder, and more competitive (Biro and Stamps 2008, 2010). Such higher activity and metabolic rate can be positive in high quality environments such as in habitats with high vegetation cover and abundant food, but might be detrimental when low food availability prevents individuals to compensate for higher energy expenditure (Biro and Stamps 2008, 2010). In zebra finches, foraging activity was related to basal metabolic rates, with high basal metabolic rates having positive effects on body mass change in treatments with high food availability and negative effects in treatments with low food availability (Mathot et al. 2009). Regarding body size, bigger individuals should survive better (Smith et al. 1989), particularly in habitats with strong competition for resources (e.g., high population density (Calsbeek and Smith 2007), low food availability (Ferguson and Fox 1984), and sparse vegetation). For instance in *Uta stansburiana* lizards, larger juveniles survived better particularly when the competition for food was strong (Ferguson and Fox 1984).

We took advantage of a study on common lizards in 2010, in which lizards were released into 15 Metatron mesocosms varying for vegetation cover. In spring 2011, we captured gravid females from the mesocosms and monitored their reproduction and offspring natal phenotype in the laboratory. Then, we investigated adaptiveness of maternal effects by releasing offspring into eight mesocosms in a crossed design with varying levels of vegetation cover and population density. First, we investigated whether offspring natal phenotypes resulted from heritable genetic effects and/or maternal effects mediated by vegetation cover. We used animal models to investigate heritability and to separate genetic from maternal effects. We expected the benefits of high activity levels to outweigh the costs in dense vegetation, leading mothers to produce more active offspring in dense vegetation habitats (i.e anticipatory maternal effects). Further, in dense vegetation, highly active females might be able to access more resources and therefore produce bigger offspring than their less active counterparts. We also expected activity and body length to be heritable, allowing for a response to selection on those traits. Second, we investigated whether offspring body length and activity affected their survival and growth in habitats varying for vegetation cover and population density. We expected more active offspring to survive better in habitats with denser vegetation, as they are able to compensate they high energy expenditure. We also expected bigger offspring to survive better with a stronger effect in habitats with sparse vegetation and high population densities. Finally, we investigated whether potential anticipatory maternal effects would lead to greater maternal fitness in more predictable environments. We expected a higher number of offspring would survive to pre-hibernation season for females producing offspring with a phenotype matching the expected one in their future environment through anticipatory maternal effects.

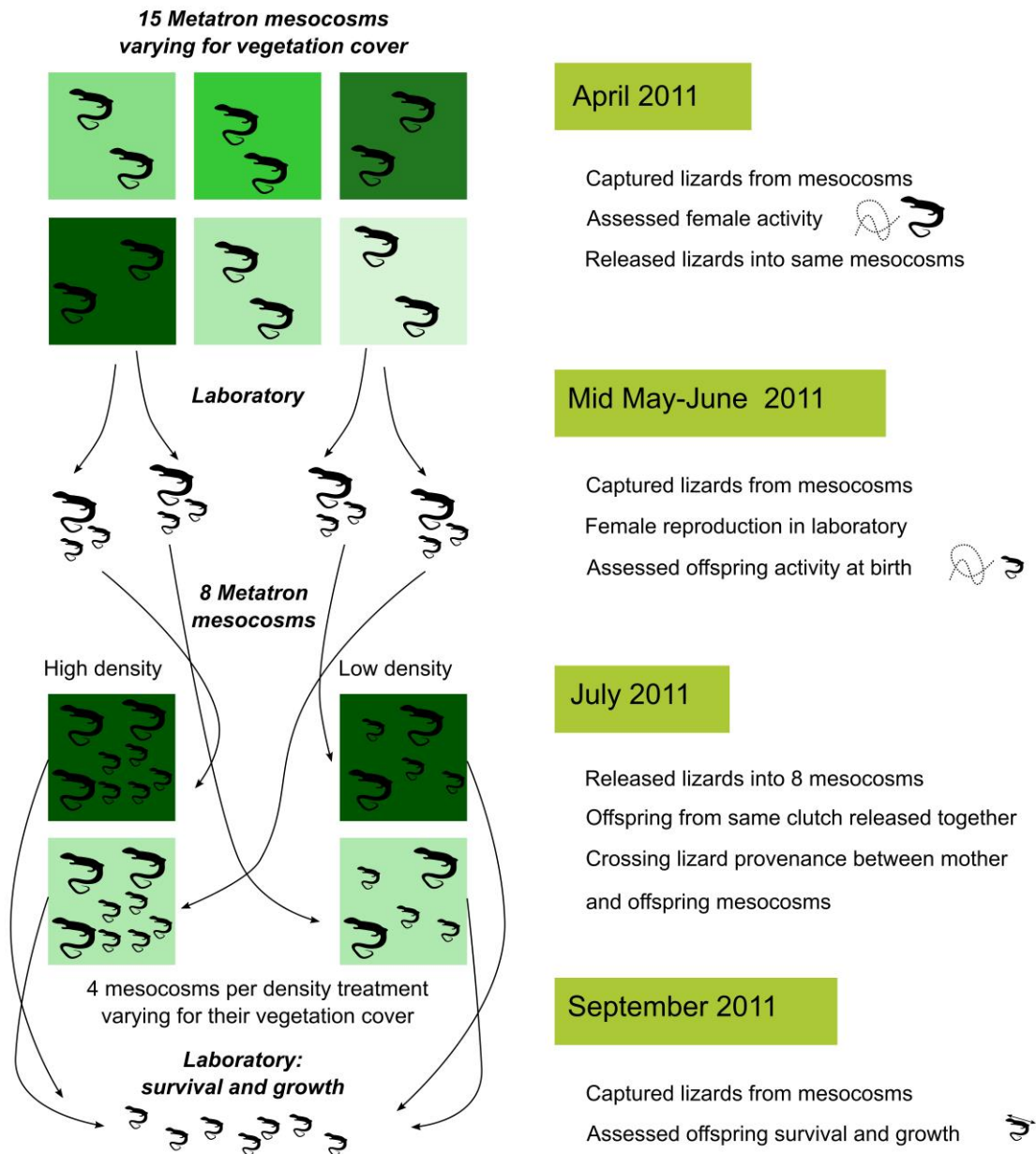
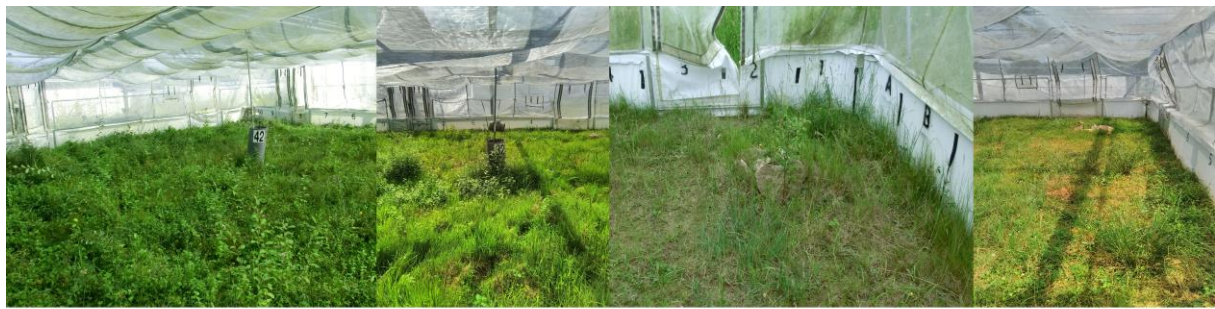


Figure 1: Flow diagram of the experimental design

Material and methods

Species and study site

Common lizards (*Zootoca vivipara*; Jacquin 1787) emerge from hibernation in March, mate soon after, and lay around 5 soft-shelled eggs (range 1-12) after two months of gestation. Offspring hatch within 1 hour of egg laying and are immediately independent.

Experiments were conducted at the Station of Theoretical and Experimental Ecology (Ariège, France, 43°01' N, 1°05' E). We used the Metatron, a system of 10 x 10 m semi-natural mesocosms (Legrand et al. 2012), each of which is fully enclosed by tarpaulins buried 30 cm into the ground and nets above-ground, containing diverse natural vegetation (37 ± 9 plant species), invertebrate communities (16 ± 3 invertebrate families), and micro-habitats (Bestion et al. 2015b). We took advantage of lizards captured in 8 natural populations of the Cevennes mountains in the Mont Lozère (Lozère, France, 44°47'N, 3°44'E), which had been marked by toe clipping, measured for body length and assessed for exploratory tendencies for the purpose of another experiment and released into 15 Metatron mesocosms in 2010, while homogenising the populations of origins.

Between April and June 2011, we surveyed plant communities within each mesocosm, recording species present and vegetation cover. Within each mesocosm, the vegetation was divided into a number of synusiae (i.e. a one-layered, floristically, physiognomically and ecologically homogeneous concrete plant community in which plants are living under uniform environmental conditions, (Gillet and Julve 2018)). The percentage of the ground covered by each synusia was measured, as well as the total percentage of bare ground with ArcGis. The overall vegetation cover was measured as the mean of the vegetation cover over all synusiae weighted by the total ground cover. Thus, mesocosms with a higher vegetation cover had a higher percentage of ground covered by vegetation as well as a more diverse cover in terms of functional diversity. The herbaceous layer covered between 37% and 56% of each mesocosm ($45 \% \pm 6$ SD, Fig S1). Such vegetation cover was related to mean vegetation height, plant richness and synusial diversity as well as bare ground cover (Appendix 1). A follow-up experiment showed that the vegetation cover was positively linked to invertebrate diversity within the mesocosms, negatively related to temperature in the vegetation layer, and was relatively stable at time scales corresponding to lizard life expectancy (Appendix 1). Overall, our metric of vegetation cover is a good metric for the structure of the environment, coherent with natural habitats in which invertebrate communities and microclimate are related to plant communities (Appendix 1) and is thus likely to be ecologically meaningful for the lizards.

The mesocosms contained only an herbaceous layer, with no shrub or tree layer, mainly consisting of plants representative of wet meadows. Natural habitats in Mont Lozère consist of wet meadows and peat bogs with sparse trees or shrubs vegetation cover, although some populations were located nearby forests. Thus, the vegetation inside the Metatron is representative of the vegetation type commonly found in the original lizard habitat. Ideally, the adaptiveness of anticipatory maternal effects should be tested in the individuals' native environments. Difficulties in testing *in natura* preclude the observation of such effects in natural habitats, but mesocosms that are similar to the natural habitat provide the opportunity to investigate these maternal effects if they exist.

Experimental design

The experiment was conducted between April and September 2011 (Fig. 1). From mid-April, we captured all the lizards (75 females, 57 males and 23 yearlings) present in the 15 mesocosms to assess female activity profiles. Captures were done within the first month of gestation to reduce the effect of gestation on activity. Lizards were housed in the laboratory for

four days before measuring activity to allow acclimation to the laboratory conditions, and all the lizards were released back to their original mesocosms early May, i.e. on average one month before females laid eggs. This allowed minimizing the effect of this laboratory stay on maternal effects, although it could reduce the likelihood to observe effects of maternal environment. Lizards were housed in individual terraria containing 3 cm of soil, a shelter (piece of egg carton), a water dish and a piece of absorbent paper to collect odours for activity assays. Ultraviolet (Zoomed Reptisun 5.0 UVB 36W) and incandescent lamps (25W) provided light and heat for thermoregulation from 9:00 to 12:00 and from 14:00 to 17:00. Lizards were fed daily with one cricket (*Acheta domesticus*).

End of May, just before the parturition of the first female, we recaptured all the individuals. Females laid eggs in the terraria from May 20th to June 30th. They produced on average 6 ± 0.26 eggs (mean \pm SEM), of which 5 ± 0.31 were viable offspring. Offspring were measured for body length, sexed, marked by toe-clipping and a tail tip was taken for paternity analyses. Three days after birth, we assessed offspring activity, and released the offspring into new mesocosms in a crossed design the day after.

Activity profile

We measured activity levels in mothers in three different contexts: a novel environment and two social contexts (with female or male odours) over two days. For offspring, we only used a novel environment and a social “mixed-odour” context to allow testing offspring over one day. To combine activities measured in different contexts allowed to evaluate an overall activity independently of a particular context (e.g. avoid the risk to confound activity tendency to the exploratory tendency of a novel environment). In common lizards, activity levels from similar assays have been shown to be correlated to survival (Le Galliard et al. 2015), female mate choice (Teyssier et al. 2014) and anti-predator strategy (Bestion et al. 2014, 2015a) and are therefore ecologically relevant.

Assays were conducted in a controlled temperature room (20°C) in 35×18×23cm terraria. For the novel environment assay, a PVC opaque wall divided the terraria into a small and a large compartment (1/3:2/3) with a shelter (piece of egg carton) in each compartment. Each side of the terraria was fitted with a heat source (i.e. bulb). The night before the assays, we acclimated individuals into the small compartment for at least 12h, with a heat source for 30 min the morning of the assay. Fifteen minutes before the assay, we turned off the light in the acclimation compartment and turned on the light above the shelter in the large (“novel”) compartment. Turning off the light in the home compartment allowed decreasing inter-individual variation in basking motivation. After acclimation, we removed the separation between compartments and measured the time spent moving for 10 minutes using “The Observer” software v. 2.0. After the assay, we divided terraria in 3 compartments with PVC walls and put individuals in the middle compartment with a shelter until the next behavioural assay, which would take place either the following morning for females, or in the afternoon for offspring. A heat source was provided either until 17:00 for females, or until the next assay for offspring.

For the social context assays, we measured the time spent moving in presence of female or male odours (for females) or of mixed male and female odours (for offspring). The odour was collected by cutting 1-2 pieces of absorbent paper from a housing terrarium, each piece being used once for a focal mother and thrice for offspring. We used 75 females and 57 males as odour donors, excluding mothers as donors for their own offspring to avoid specific responses to maternal cues. Females were tested with one randomly assigned odour (male or female) in the morning and the other in the afternoon. Offspring were tested in the afternoon with the odour mix. Offspring from a single clutch were tested using different odour mixes and a given odour mix was never used more than twice per clutch. Papers were put under shelters, a paper

with odour in one side compartment and a paper without odour, collected from vacant terraria, in the other side compartment as a control. After 10 minutes, we removed the walls separating compartments, let individuals familiarize with the odours for 10 minutes and then measured time spent moving for 10 minutes.

We estimated general activity levels from the time spent moving during the three different types of assays using principal component analysis. The first PC axis explained 53 % of the variance in females and 50% in offspring and was positively related to times spent moving in assays (Table S1). Time spent moving was repeatable among the three contexts for females (intraclass correlation coefficient [ICC] = 0.28, 95% confidence interval [CI] = [0.13,0.43], $p < 0.001$) and not repeatable among the two contexts for offspring (ICC = 0 [0, 0.13], $p = 0.50$). The lack of repeatability in offspring is likely explained by a high sensitivity of offspring to contexts or to the time of assays (i.e. morning versus afternoon). As we were not able to measure the repeatability of PC axes over time, we used a database of 4339 observations of activity measured every year through life on 1596 lizards inhabiting the Metatron between 2011 and 2020 (Bestion et al. 2015b) and found a repeatable activity throughout lifetime in a model including year as a covariate (ICC = 0.21 [0.16, 0.25], $p = 1e-23$).

Genetic data and paternity analyses

Lizard DNA was extracted from tail tips with QIAquick 96 Purification Kit (QIAGEN) following manufacturer's instructions after a proteinase K digestion. Individuals were genotyped using eight microsatellite markers (Richard et al. 2012). We checked for perfect match between offspring and their mother and assessed paternities using CERVUS v.3.0 (Teyssier et al. 2014). This allowed creating a pedigree with a total of 351 individuals, 246 dam-offspring links, 190 sire-offspring links, and with 47 % of full-sib clutches and 53 % of half-sib. The pedigree was used in the animal models to calculate additive genetic, maternal and environmental variances of offspring traits. Because such a pedigree might be too small to properly estimate heritability, we also used a larger database of observations of activity and body length measured at birth on lizards inhabiting the Metatron between 2011 and 2020 (Bestion et al. 2015b) to assess trait heritability.

Offspring survival and growth rates

Early July, we released all lizards (i.e. offspring, mothers, males and yearlings) into eight mesocosms of varying vegetation cover ($41 \% \pm 5.2 \% \text{ SD}$, range 36-50 %). Individuals of different age and sex were distributed to create 4 high density mesocosms (12 females, 8 males, 3 yearlings, 37 ± 2 offspring from 9 ± 1 clutches) and 4 low density mesocosms (8 females, 5 males, 2 yearlings, 27 ± 2 offspring from 6 ± 1 clutches) matching densities used in similar experiments (Cote et al. 2008). Following a crossed design, offspring from a clutch were released together into mesocosms different from those of their mothers, varying for their vegetation cover and density treatments. This allowed a continuous variation of the predictability of the environment such that some clutches were released into environments with similar vegetation cover compared to those of their mothers, and other clutches were released into different environments compared to maternal habitats. This led the absolute difference between vegetation covers in maternal habitats and in offspring habitats (i.e. the predictability of vegetation cover), to vary among offspring (median: 6.8 %, range: 0-19.5 %). Mesocosms of the same density treatment did not differ statistically for vegetation cover but still showed some variation within treatments (effects of density treatment: $F_{1,6} = 0.02$, $p = 0.90$, HD: $41.6 \pm 5.9 \%$, range: 37-50 %, LD: $41.1 \pm 5.4 \%$, range: 36-48 %).

In late September, we captured all the survivors to assess survival and growth rate during 3 capture-recapture sessions. Each capture session lasted one hour per enclosure. Lizards were identified, measured and released. The cumulative probability of capture was 93 % (Bestion et

al. 2015b) and individuals never captured were considered as dead. Growth was calculated as the difference between body length in September and at birth.

Statistical analyses

We first checked that there was no relationship between mother traits (i.e. activity and body length) and vegetation cover. We then studied (1) whether offspring natal phenotypes were heritable and varied with maternal vegetation cover and traits with anticipatory maternal effects, (2) whether offspring natal phenotypes affected their survival and growth in mesocosms varying for vegetation cover and population density, and (3) whether potential anticipatory maternal effects affected maternal fitness depending on the experimentally manipulated environmental predictability. Analyses were done in R v 4.0.5. Data and code are available on Zenodo: <http://doi.org/10.5281/zenodo.6619408> (Bestion et al. 2022).

General statistical approach

We studied these questions with generalised (with a binomial distribution for offspring survival and a Poisson distribution for maternal fitness) and general linear mixed models (all other traits) with maximum likelihood using the *lme4* package. We created a global model including fixed predictors (centred and scaled) and random intercepts, and derived all possible models with fixed effects with the dredge function from the *MuMIN* package. We checked global models for residuals' normality and homoscedasticity or overdispersion and the absence of collinearity between predictors through variance inflation factors (Zuur et al. 2010), which were all well below 2. We selected best fitting models using AICc (Burnham et al. 2002) and averaged best models (within $\Delta\text{AICc} < 2$) following (Grueber et al. 2011). We present conditional averages for the averaged models. We further fitted a model containing all the predictors present in the averaged model and calculated marginal and conditional R^2 (Nakagawa and Schielzeth 2013) and standard deviations from the random components. Models included a combination of maternal mesocosm identity, maternal identity and offspring mesocosm identity as random intercepts when appropriate (see detailed statistical analyses).

For offspring traits and fitness, we then refitted the models containing all fixed variables maintained in the averaged model with *MCMCglmm* to include genetic information from the pedigree through an animal effect (Riska et al. 1985; Wilson et al. 2010), running 1000000 iterations with a 3000 burnin and a 1000 thinning.

In a third step, we refitted the main models with maternal natural population of origin to check for effects of potential differences in evolutionary history.

Relationship between vegetation cover and female traits

We first checked whether there was a relationship between the phenotype of the lizards, at release into the mesocosm in 2010, and vegetation cover, to check if potential differences between populations would bias our results. For the purpose of another unpublished experiment in 2010, lizards' body length was measured and exploratory tendencies in a novel environment assessed in the laboratory, before release in the mesocosms. The lizards were assessed for time spent moving in two 5-minutes assays in terraria in two different novel environments. The exploratory tendency was the average of the time spent moving in the two experiments. There was no relationship between vegetation cover and body length (all individuals: $F_{1,266} = 1.06$, $p = 0.303$, females: $F_{1,160} = 0.79$, $p = 0.375$, males: $F_{1,103} = 0.09$, $p = 0.764$) and between vegetation cover and exploratory tendency (all: $F_{1,149} = 0.11$, $p = 0.745$, females: $F_{1,104} = 0.21$, $p = 0.644$, males: $F_{1,42} = 0.01$, $p = 0.923$).

Second, we checked whether vegetation cover affected female body length and activity at the time of the experiment in Spring 2011 with a global model including vegetation cover, and for female activity, their body length, plus random mesocosm identity (N= 75).

This was not the case, as female activity level and body length did not depend on vegetation cover in their habitats (Table S2) and there was no relationship between female activity level and body length (body length not kept in best models for activity level, Table S2). Including the natural population of origin had no impact on the main fixed effects, with very similar results between models (Table S3) and population of origin represented a very low proportion of the explained variance (between 0 and 0.19 SD). Thus, it is likely that there was no selective or plastic response of those phenotypic traits to vegetation cover and unlikely that effects of vegetation cover on offspring would be linked to a difference in maternal phenotype between enclosures.

Offspring natal phenotypes: heritability and maternal effects of vegetation cover

Sixty mothers produced 246 offspring. We first checked for potential correlations between activity and body length with Pearson correlations.

Second, we estimated the heritability (h^2) and maternal effects (m^2) of body length and log-transformed activity with animal models, where we included animal and mother identities from the pedigree as well as maternal mesocosm identity as random effects in *MCMCglmm* to decompose additive (V_A), maternal (V_M), environmental (V_E , corresponding to the mesocosm identity) and residual variances (V_R). We first used non-informative priors ($V=1$, $\nu=0.002$), but we also reran analyses with two sets of informative priors, and also with a larger database spanning multiple years (Table S4).

Third, we studied the effect of maternal traits and vegetation cover on offspring body length and log-transformed activity. Full models included vegetation cover in maternal mesocosm and its two-way interactions with maternal body length and activity plus random mother and maternal mesocosm identities (Table S5). Then we reran these analyses with the fixed parameters maintained in the averaged model in the previous step with *MCMCglmm*, including animal identity from a pedigree and maternal mesocosm identity as random effects and using noninformative priors to check whether these effects were maintained when controlling for genetic background (Table 1). We did not include maternal identity in the model so as to avoid capturing variance due to the interaction between maternal traits and habitat vegetation cover in the V_M term. However, we redid the models including V_M with similar results (Table S6). We also refitted the *lmer* models with maternal natural population of origin to check for effects of potential differences in evolutionary history (Table S7). Including the population of origin had no impact on the main fixed effects, with very similar results between models and no variance explained by population of origin.

Impact of offspring natal phenotypes and their survival and growth in varying habitats

Models for survival (on 246 offspring) and growth (on 117 surviving offspring) included the density and vegetation cover in offspring mesocosms, offspring activity profile and body length, sex, the two-way interactions between the two environmental traits and between each environmental trait and each offspring trait, birthdate (particularly important to control for growth), and random mother identity and offspring mesocosm identity (Table 2). Because of the large list of possible models, the models within $\Delta AIC < 2$ represented a low cumulated AIC weight. We thus redid the analyses with a second ΔAIC threshold of 4 to check for consistency (Table S8). As for natal phenotypes, we reran the analyses with an animal model including animal identity from a pedigree and offspring mesocosm identity and using non-informative prior to check whether potential effects were maintained when controlling for genetic

background (Table S9). Note that as survival was a binary trait, we used modified non-informative priors ($V = 1$, $\nu = 1000$, $\alpha.\mu = 0$, $\alpha.V = 1$).

We then calculated selection gradients on the traits using linear mixed models of offspring survival in habitats with different vegetation cover. Given the results on density, we focused on vegetation cover and categorized mesocosms into dense-vegetation (vegetation cover $> 40\%$, 4 mesocosms) and sparse-vegetation habitats ($< 40\%$, 4 mesocosms). We first tested for an interaction between offspring centred and scaled traits and vegetation category on survival (Table S10) and then modelled survival for each vegetation category depending on centred and scaled activity, body length and birthdate plus random mother identity and offspring mesocosm identity (Table 3). Selection gradients were transformed from logistic regression coefficients to average gradient β_{avggrad} following (Janzen and Stern 1998) and scaled by mean fitness.

Impact of anticipatory maternal effects on maternal fitness

We investigated whether potential anticipatory maternal effects affected maternal fitness (i.e. total number of offspring surviving to September). Because we released offspring in environments that varied in their similarity to maternal vegetation cover (median: 6.8 % difference, range: 0-19.5 %), offspring phenotype varied for their match to the optimal phenotype expected by anticipatory effect in the living environment they were released in. The highest phenotypic matching would result from maternal and offspring environments being identical (i.e. full predictability) and from maternal environment explaining all the phenotypic variance in offspring (i.e. fully efficient anticipatory maternal effect). If maternal effects are adaptive, we expect maternal fitness to be higher when the offspring phenotypes match the expected optimal phenotype. Thus, we created a metric measuring the match between offspring phenotype and the expected phenotype in the offspring living environment through anticipatory effects. To do so, we measured the absolute difference between the mean observed offspring phenotype of a clutch and the phenotype of offspring expected in a fully predictable environment (i.e. mothers and offspring environments are identical regarding vegetation cover) and with a fully efficient anticipatory effect (i.e. maternal vegetation cover explaining all of the phenotypic variance in offspring). To calculate the expected optimal phenotype, we used the models assessing anticipatory maternal effects (Table S11), in which the offspring phenotype depends on maternal vegetation cover. With these models, we predicted what the optimal offspring phenotype, entirely shaped by adaptive maternal effects, should be, if mothers and offspring inhabited the same environment. To do so, we used the predict function with the model by replacing maternal vegetation cover by offspring vegetation cover. Thus, the difference between observed and expected phenotype measures whether offspring are in an optimal situation for adaptive anticipatory maternal effects to arise (i.e. predictable environment and strong influence of maternal effects on offspring phenotype). This difference indeed varies experimentally with the chosen mesocosms for offspring and should be close to 0 if vegetation cover in the habitats of the mother and offspring are similar, mimicking environmental predictability. We then modelled maternal fitness as a function of the match of maternal anticipatory effect for activity, plus maternal body length and random maternal and offspring mesocosm identities for the 60 females that produced viable offspring.

Results

Offspring natal phenotypes

Activity and body length were not correlated in offspring (Pearson's $r = 0.05$ [-0.07,-0.18], $t = 0.45$, $df = 244$, $p = 0.397$). Second, we calculated the heritability of those traits, to understand the potential maternal and genetic effects on those phenotypic traits. Offspring activity profile had a heritability of 0.150 [0.002, 0.588] using non-informative priors (up to 0.192 with

informative priors), and a maternal effect of 0.125 [0.005, 0.278] (Table S4). Body length had a heritability of 0.010 [0, 0.194] but a large non-genetic maternal inheritance of 0.641 [0.464, 0.754] (Table S4). Using a larger database of juveniles maintained in the Metatron between 2011 and 2020, heritability of activity was 0.220 [0.091, 0.350], with a maternal effect of 0.102 [0.044, 0.171], and heritability of body length was 0.237 [0.169, 0.303] with a maternal effect of 0.436 [0.331, 0.515] (Table S4).

We first predicted that higher activity levels should be beneficial in dense vegetation habitats and that selection should then favour mothers producing more active juveniles in those habitats. Natal activity profile was indeed positively related to vegetation cover in maternal habitats, but not to maternal phenotype, in models controlling or not for additive genetic variance (Table 1, S5-S7). Our second prediction was that more active females produce bigger offspring in dense vegetation habitats and conversely smaller offspring in sparse vegetation habitats. We found that body length depended on the interaction between vegetation cover and maternal activity (Table 1, S5-S7). In dense vegetation, more active mothers produced bigger offspring than less active ones, while the pattern was reversed in sparse vegetation (Fig. 2). Natal body length was further positively related to maternal body length (Table 1, S5-S7).

Table 1: Impact of maternal traits and vegetation cover on offspring traits at birth

Response variable	Independent variable	Estimate	95 % Credible Interval	effective sample size	p-value
Body length	fixed effects				
	Intercept	23.083	[22.608,23.452]	1000	0.001
	Maternal vegetation cover	-0.001	[-0.402,0.423]	1000	0.988
	Maternal activity	0.116	[-0.110,0.359]	1000	0.306
	Maternal body length	0.550	[0.294,0.771]	1000	0.001
	Maternal vegetation cover:Maternal activity	0.406	[0.127,0.673]	863	0.006
	Maternal vegetation cover:Maternal body length	0.179	[-0.065,0.438]	1182	0.162
	random effects				
	V _A	1.364	[1.100,1.646]		
	V _E	0.315	[0.005,0.888]		
V _R	0.012	[0.000,0.140]			
Activity	fixed effects				
	Intercept	0.007	[-0.209,0.190]	1000	0.904
	Maternal vegetation cover	0.243	[0.043,0.432]	1000	0.020
	Maternal activity	-0.052	[-0.222,0.124]	1000	0.520
	Maternal body length	-0.035	[-0.229,0.121]	838	0.676
	Maternal vegetation cover:Maternal activity	0.101	[-0.085,0.305]	1000	0.320
	random effects				
V _A	0.533	[0.180,1.227]			
V _E	0.009	[0.000,0.084]			
V _R	0.442	[0.001,0.708]			

Animal model of (1) offspring body length as a function of maternal activity, body length and their interaction with vegetation cover as fixed effects and animal identity from a pedigree and maternal mesocosm as random effects, and (2) offspring log-transformed activity as a function

of maternal body length and the interaction between maternal activity and vegetation cover as fixed effects and animal identity from a pedigree and maternal mesocosm as random effects to control for additive genetic variance (V_A) and environmental effect (V_E corresponding to the mesocosm effect, V_R = residual variance). Numeric independent fixed-effect variables were not correlated (generalized variance inflation factor [GVIF] <1.1) and were centred and scaled. The choice of fixed effects corresponded to the effects retained in the best averaged model in Table S5. Confirmatory models including V_M (Table S6) and natural population of origin (Table S7) give very similar results. In bold: significant fixed effects ($p < 0.05$)

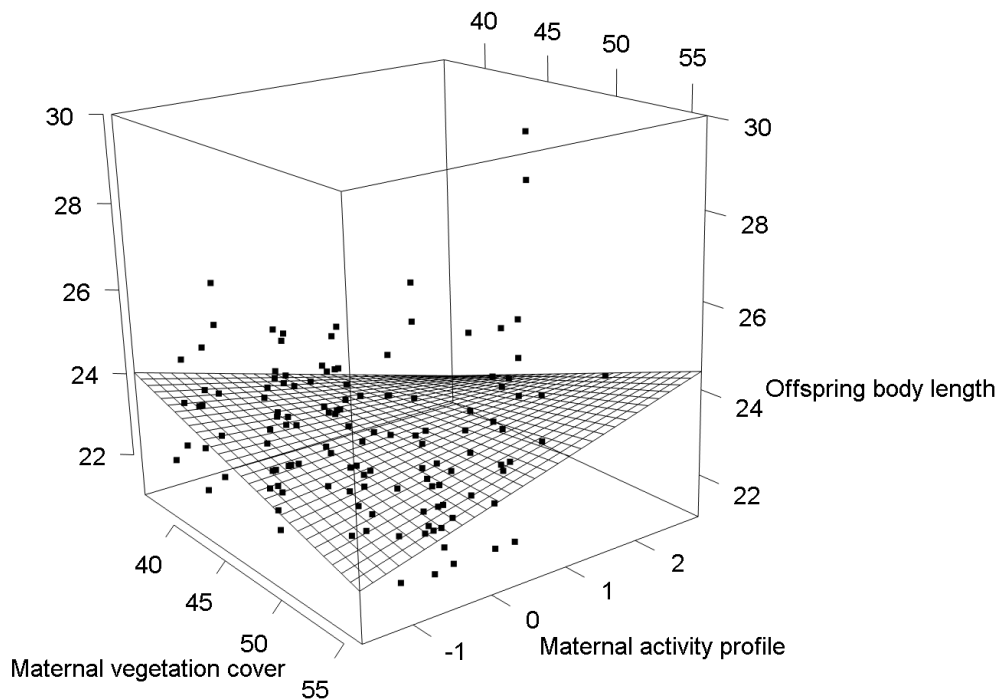


Figure 2: offspring body length depended on their maternal activity profile and the vegetation cover in maternal habitats

In denser habitats, less active females produced smaller offspring than their more active counterparts, while in sparse habitats they produced bigger offspring than their more active counterparts. The surface was derived from Table 1 model. $N = 246$.

Offspring survival and growth

We predicted that offspring survival and growth would be related to their activity and body length, depending on the environmental conditions. Specifically, we predicted that high levels of activity would be beneficial in dense vegetation habitats only. This prediction was validated, as offspring survival depended on the interaction between their natal activity profile and vegetation cover in their habitat (Table 2, S8-S9). Survival was positively related to offspring activity in dense vegetation habitat, but not in sparse vegetation (Fig. 3) resulting in a selection gradient for activity in dense vegetation habitat only (Table 3, S10). A second prediction was that larger individuals would survive and grow better, and that these benefits would be more pronounced in sparse vegetation habitats with denser populations (i.e. poor quality environments). This prediction was not validated as neither body length nor population density influenced survival (Table 2, S8-S9). Growth was not influenced by vegetation cover or

population density, but was negatively related to birthdate and tended to be negatively related to activity profile (Table 2, S8-S9).

Table 2: Impact of offspring traits and vegetation cover and population density in their introduction habitat on summer survival and growth.

Response variable	Independent variable	Estimate	SE	z-value	p-value	RI
Survival	Intercept	-0.02	0.25	0.10	0.921	
	Vegetation cover	0.41	0.21	1.88	0.060	1.00
	Activity profile	0.42	0.15	2.89	0.004	1.00
	Body length	0.23	0.16	1.42	0.155	0.68
	Vegetation cover:Activity profile	0.33	0.17	1.97	0.049	1.00
	Sex	-0.36	0.30	1.21	0.226	0.29
	Vegetation cover:Body length	0.12	0.17	0.68	0.495	0.11
	Density treatment	0.13	0.42	0.30	0.767	0.11
	Density treatment:Body length	0.53	0.34	1.57	0.117	0.11
	Birthdate	-0.09	0.15	0.62	0.537	0.10
Growth	Intercept	19.28	1.46	13.04	<0.001	
	Birthdate	-1.29	0.34	3.77	<0.001	1.00
	Activity profile	-0.54	0.29	1.83	0.068	0.81
	Body length	-0.43	0.33	1.30	0.192	0.23
	Density treatment	2.32	2.55	0.90	0.366	0.14
	Vegetation cover	1.15	1.26	0.90	0.368	0.14

Model averages of generalized (binomial family; survival) or linear mixed models (growth). Global models included offspring activity and body length and their two-way interactions with vegetation cover and population density in its habitat, the two-way interaction between vegetation cover and population density, birthdate, sex plus random mother and mesocosm identities ($N_{group} = 60$ mothers for survival and 48 for growth, $N_{group} = 8$ mesocosms for both survival and growth, and $N = 246$ offspring for survival, 117 surviving offspring for growth, Table S12-S13). Numeric independent fixed-effect variables were not correlated ($GVIF < 1.2$) and were centred and scaled. Submodels containing all of the variables and interactions maintained in the averaged models explained 13 and 21 % of R^2_m and 21 and 68 % of R^2_c , with random mother identity effects of 0 and 1.15 SD and random mesocosm identity effect of 0.39 and 3.25 SD respectively for survival and growth. Confirmatory models with $\Delta AIC < 4$ (Table S8) or with an animal model including additive genetic effect and environmental effect (Table S9) gave similar results. In bold: significant effects ($p < 0.05$). RI = relative importance.

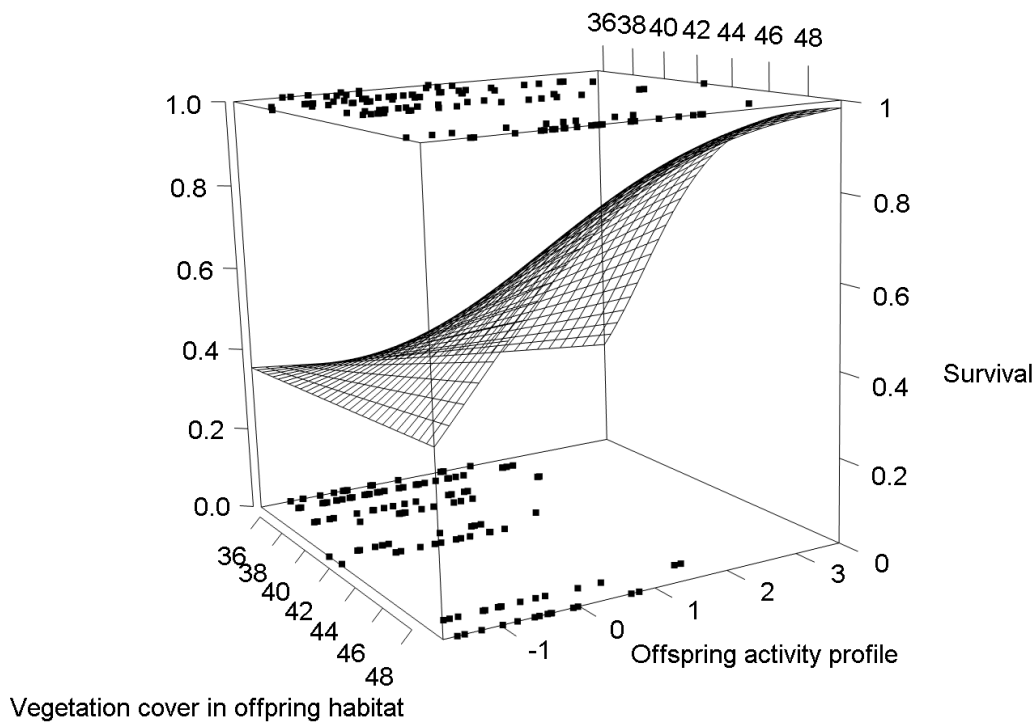


Figure 3: Offspring survival probability depended on their activity at birth and the vegetation cover in their introduction habitat.

More active offspring survived better than their less active counterparts in dense vegetation habitats while activity had no affect survival in sparse vegetation. The surface was derived from Table 2 model. $N = 246$.

Maternal fitness and environmental predictability

Finally, we predicted that adaptive maternal effects should increase maternal fitness when the environment is predictable and the anticipatory effect is efficient. As we released offspring in environments that varied for their similarity to the maternal environment in terms of vegetation cover, we expected that mothers that produced a phenotype close to the expected optimal phenotype in offspring living environment would have a better fitness corroborating the adaptiveness of maternal effects suggested by the survival analysis. To test this prediction, we thus calculated the absolute difference between the mean observed offspring phenotype of a clutch and the optimal phenotype of offspring expected through fully efficient anticipatory effects in a fully predictable environment. By doing so, the difference between observed and predicted phenotype measures whether offspring phenotype is close to the optimal phenotype expected through anticipatory effects in the living environment, with values close to zero being a good match. We found that mothers producing offspring with an activity level close to the activity expected in the offspring habitat through anticipatory effects had a greater number of offspring surviving to September (Fig 4, Table S11).

Table 3: Survival selection gradients on offspring phenotypic traits depending on vegetation cover

Vegetation type	Variable	Estimate \pm SE	$\beta \pm$ SE	z-value	p-value
Dense vegetation	Intercept	0.197 \pm 0.199	0.080 \pm 0.081	0.986	0.324
	Activity	0.783 \pm 0.248	0.319 \pm 0.101	3.156	0.002
	Body length	0.204 \pm 0.205	0.083 \pm 0.084	0.994	0.320
Sparse vegetation	Birthdate	-0.231 \pm 0.208	-0.094 \pm 0.085	-1.111	0.266
	Intercept	-0.404 \pm 0.440	-0.209 \pm 0.227	-0.918	0.359
	Activity	0.116 \pm 0.198	0.060 \pm 0.102	0.585	0.559
	Body length	0.273 \pm 0.208	0.141 \pm 0.107	1.312	0.189
	Birthdate	0.167 \pm 0.215	0.086 \pm 0.111	0.775	0.438

Offspring dataset is separated into dense vegetation (vegetation cover > 40, $N = 119$ offspring) and sparse vegetation (vegetation cover < 40, $N = 127$ offspring). Results from generalized linear models investigating survival as a function of activity, body length and birthdate plus random mother identity and mesocosm identity. Numeric fixed-effect variables investigated were not correlated (GVIF for the three variables < 1.2) and were centred and scaled. Logistic coefficients were recalculated to average gradient vectors $\beta_{avggrad}$ according to the methods of Janzen and Stern (1998). The models explained 16 % and 4 % of R^2_m and 17 % and 19 % of R^2_c , respectively, for dense and sparse vegetation; the random mother effect explained 0.11 and 0.0 SD and the random mesocosm effect 0.0 and 0.78 SD, respectively, for dense and sparse vegetation. As predicted in Table S10, there is a difference between selection gradients for activity in sparse and dense vegetation cover. In bold: significant effects ($p < 0.05$).

Discussion

Abiotic and biotic conditions, such as vegetation structure, population density, or thermal conditions, influence species performance (Heatwole 1977; Cody 1981; Wasiolka et al. 2009; Bestion et al. 2015b; Paterson and Blouin-Demers 2018), driving individuals towards locally adapted phenotypes through selection or plasticity. Anticipatory maternal effects are an efficient mechanism plastically and rapidly adjusting the phenotype of the offspring to their environment, and therefore increasing maternal fitness, particularly in heterogeneous and predictable environments (Burgess and Marshall 2014). Here, we show that the vegetation structure in maternal environments shapes offspring phenotype depending on mothers' own phenotypic traits. Females in denser vegetation habitats produce juveniles with higher activity levels, a repeatable and partially heritable trait, than females in sparse vegetation habitats. Moreover, offspring survival is related to their activity level depending on the environmental conditions. More active offspring survive better than less active ones in dense vegetation habitats, but not in sparse vegetation, resulting in a selection gradient of 0.32 ± 0.10 in dense vegetation habitats. Finally, when mothers produce offspring with phenotypes close to the phenotype expected through maternal effects in offspring habitats, maternal fitness is greater. Combined with the effects on offspring survival, these results suggest adaptative anticipatory maternal effects in response to vegetation structure in common lizards.

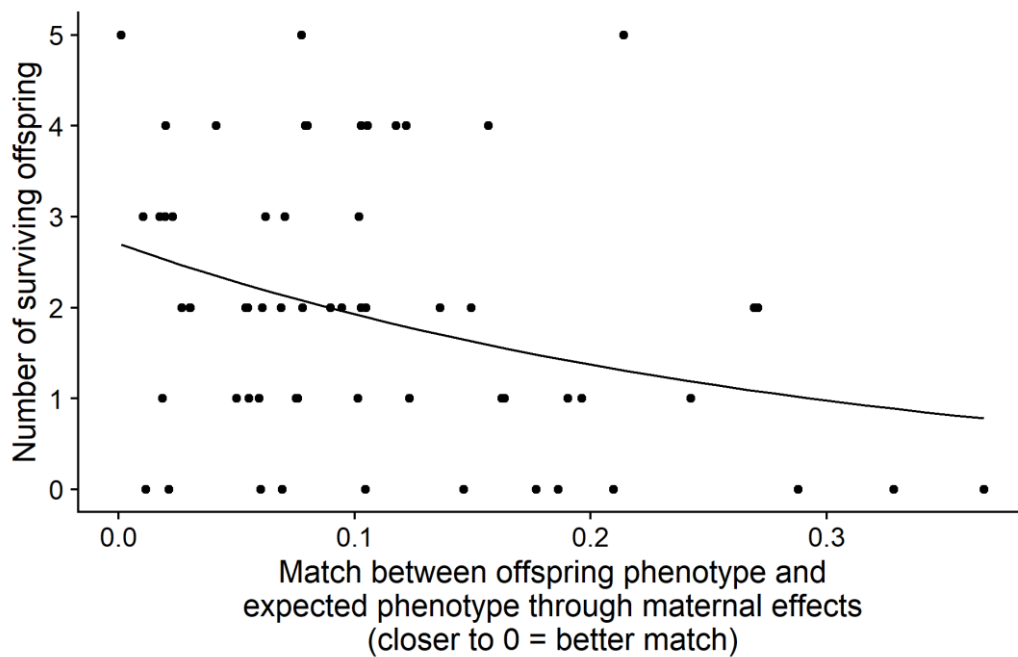


Figure 4: Maternal fitness was related to the match between offspring phenotype and expected phenotype in their living environments through maternal effects

The match between offspring observed phenotype and the expected phenotype in their future environment through anticipatory maternal effects was the absolute difference between log-transformed mean offspring activity and offspring log-transformed activity expected in offspring mesocosms through anticipatory maternal effects. Females who produced offspring whose phenotype was closer to the phenotype expected in the offspring habitat (better match, small difference between predicted and observed offspring activity, expected in predictable environments and when maternal effects have a strong influence on offspring fitness) had a higher number of surviving offspring (line derived from Table S11 model), suggesting that maternal effects were adaptive. $N = 60$ females.

Interestingly, although maternal effects influenced offspring body length depending on vegetation cover and female traits, those effects did not seem adaptive. We expected that in dense vegetation habitats, more active mothers would be favoured, and would be able to produce better quality offspring (i.e. bigger offspring) with better survival prospects. Although more active mothers did indeed produce bigger offspring in dense vegetation habitat, offspring body length had only a weak effect on survival and no effect on growth. This was surprising as other studies have found selection on body size (Ferguson and Fox 1984; Calsbeek and Smith 2007). Further, while we were expecting low offspring survival with high population densities, particularly when prey availability was low (i.e. sparse vegetation) (Meylan et al. 2007; Mugabo et al. 2013; Le Galliard et al. 2015), population density did not influence offspring survival and growth. The effects of population density on offspring life history however vary with external and internal factors (Cote et al. 2008; Le Galliard et al. 2015) and the negative impact may arise at older ages through aggressions by adults (Mugabo et al. 2010, 2011). If negative impacts arise at older ages, is it also possible that selection on body size only acts later, on yearling or adults, where competitiveness is of greater importance.

A recent meta-analysis has shown the importance of maternal effects in determining the variance of a trait, with mean estimates of maternal effects m^2 determining 10.8 % of all

phenotypic variance, while additive genetic effects h^2 explained 21.6 % of the variation (Moore et al. 2019). However, the importance of maternal effects relative to additive genetic effects depended on the trait studied, with a greater importance in morphological traits than behavioural or physiological traits (Moore et al. 2019). Our results are in line with these, with a higher importance of maternal effects in body length than in activity. In addition to estimating the strength of maternal effects, our study identified a specific environmental factor, the vegetation structure in maternal habitats, which is shaping offspring phenotype through maternal effects. Particularly, activity levels and body length were strongly influenced by vegetation cover in maternal habitats. Other studies on common lizards have found that maternal environment during gestation influence offspring phenotype, including effects of predation risk and maternal stress hormones on offspring morphology, behaviour and dispersal (Meylan et al. 2002; Meylan and Clobert 2005; Uller and Olsson 2006; Bestion et al. 2014). Such acute stressors are often a strong driver of maternal effects (Sheriff 2015), in particular predation risk, which has been found to elicit strong morphological and behavioural responses including on activity in various species (Tariel et al. 2020). Here, we show that a more subtle chronic stressor, maternal habitat structure, is also able to affect offspring natal morphology and behaviour.

Although anticipatory maternal effects are often assumed to be adaptive, they do not always increase offspring fitness (Marshall and Uller 2007). Yet, most studies on anticipatory parental effects fail to consider environmental predictability and to adequately test their adaptiveness (Burgess and Marshall 2014). The use of a semi-natural experimental system allowed us to overcome this barrier, allowing an orthogonal design between maternal and offspring environment, and the measure of offspring and maternal fitness proxies. We showed that when the anticipatory maternal effects lead to a close match between the observed offspring phenotype and the expected phenotype in the offspring living environments, in fully predictable environments and with fully efficient anticipatory effects, maternal fitness is greater, suggesting the adaptiveness of maternal effects in activity levels. Interestingly, our experiment uncovered an asymmetry in the effect of anticipatory maternal effects depending on the type of environment. Indeed, while in sparsely vegetated habitats activity had no effect on survival, in dense vegetation habitats activity had a strong positive effect on survival. This suggests that maternal effects would have a stronger positive effect in favourable conditions than in harsh conditions. This is in line with the results of a meta-analysis that suggested that vertebrates benefit more from transgenerational effects in more favourable than in more stressful environments (Yin et al. 2019; Sánchez-Tójar et al. 2020; Zhang et al. 2020).

In our study, relatively small differences in vegetation cover (between 36-50 %) had a measurable effect on maternal effects, as well as on lizard survival depending on their phenotype. Such effects suggest that vegetation cover is a useful metric of habitat complexity that has important ecological impacts on lizards. However, vegetation cover could instead be a proxy of one or several other important ecological factors (Appendix 1). Denser vegetation is indeed linked to higher prey diversity and availability (Appendix 1), easier hiding from predators, or to different thermal characteristics. Our main hypothesis for the effect of vegetation cover on survival relates to prey availability and hunting strategies. Higher activity levels may help offspring to capture prey faster through active foraging (Beauchamp 2000), particularly for prey energetically rewarding but difficult to capture, such as orthopterans (Avery 1966; Paulissen 1987; Fuller and Joern 1996; González-Suárez et al. 2011). This might particularly be true when prey are less abundant and diverse, as in sparse vegetation (Appendix 1, (Wasiolka et al. 2009)). However, highly active foragers may compensate high energetic expenditures only when prey are abundant by consuming more energetically rewarding or more numerous prey (Biro and Stamps 2008, 2010). When prey are less densely distributed and less diverse, as in sparse vegetation, highly active individuals may not compensate high energetic expenditures while less active individuals may opt for an energy saving sit-and-wait hunting

strategy. It would equalize fitness benefits between highly active and less active individuals and explain the observed activity- and context-dependent survival. These results are consistent with a study on *Anolis sagrei* showing that mothers maintained with a high prey availability produced offspring surviving better in habitats with high prey availabilities than with low prey availabilities, while no such effect was observed when maternal prey availability was low (Warner et al. 2015). The hypothesis that highly active individuals are favoured in dense vegetation habitats might further be strengthened if differences in activity relate to diet breadth. Less active sit-and-wait individuals might have a more generalist diet while their more active foraging counterpart might have a more specialist diet (Bolnick et al. 2003) which might increase the costs for highly active individuals in sparse vegetation with less diverse prey. Common lizards actually display intraspecific variation in diet specialization depending on environmental conditions and dietary specialists have lower survival in warmer challenging environments (Bestion et al. 2019). Alternatively, denser vegetation could also hinder lizards' ability to catch prey, as found in fish where swimming speed and number of prey captured decreased with submerged vegetation density (Priyadarshana et al. 2001). Thus, the energetic costs of high activity levels would outweigh the benefits in dense vegetation. However, positive activity-survival relationship in dense vegetation observed in the present study does not support this last hypothesis. These hypotheses assume a consistent inter-individual variation in activity, with a low within-individual variation (i.e. low behavioural flexibility). Studies on common lizards, including the present study, have found that activity levels consistently vary among individuals throughout lifetime, with a repeatability between 0.2 and 0.3, and are involved in a pace-of-life syndrome (Le Galliard et al. 2013). Such results suggest that there is a moderate interindividual consistency of activity levels, coherent with our heritability estimates, but leave significant room for behavioural plasticity, which might have influenced our results. For example, a study on sand lizards has shown that lizards were able to shift from a sit-and-wait foraging tactic to an actively foraging tactic, depending on vegetation cover (Wasiolka et al. 2009). While this species usually opts for a sit-and-wait foraging tactic, lizards started to actively forage in habitats with very sparse vegetation habitats and low prey densities. This suggests that high levels of activity may be beneficial in sparse vegetation habitats, which might at first glance disagree with the lack of relationship between survival and activity in sparse vegetation in the present study. However, estimates of energetic expenditures or fitness are needed to evaluate the overall benefits of behavioural shifts in sand lizards. Wasiolka et al.'s (2009) study further reveals a significant degree of flexibility in activity-related foraging tactics and adds a potential explanation to our results. In sparse vegetation habitats, less active sit-and-wait individuals would start to forage more, thus reducing the variation in activity levels and its effect on survival.

Another driver of variability in activity profile might be predation risk, as activity levels mediate the time spent visible to predators (Wooster and Sih 1995), influence, in common lizards, the predation-dependent mate choice and maternal effects (Bestion et al. 2014; Teyssier et al. 2014) and may therefore shape selection gradients on activity. Vegetation cover could hence have an effect through conspicuousness of lizards to predators. Although there was no predator in this experiment, vegetation structure might influence the perceived predation risk in natural habitats and the use of this environmental cue might still be maintained in absence of actual predators to prevent lethal assessment errors (Johnson et al. 2013). For instance, in fat sand rats, increasing vegetation cover changed vigilance and foraging tactics, likely due to increased perceived predation risk (Tchabovsky et al. 2001). Because more active individuals are more conspicuous to predators, if lizards perceived sparse vegetation cover habitats as a higher risk of predation, it is possible that more active lizards, with an increased threat of predation, might modify their behaviour in these habitats (Wooster and Sih 1995; Teyssier et

al. 2014). This change in activity pattern may have led to the observed lack of effect of activity on survival in sparse vegetation cover habitats.

Finally, a last hypothesis has to do with the thermal characteristics of the environment. Although there was no relationship between air temperature, hygrometry and vegetation cover, denser vegetation however affected thermal microhabitat conditions, with lower average ground temperature and lower thermal variability within the mesocosms (Appendix 1). If activity is related to lower thermal needs, it could lead to better outcomes of less active lizards in dense vegetation cover. However, studies on thermal syndromes on lizards show opposite relationships between activity and thermal needs (Goulet et al. 2016; Michelangeli et al. 2018), and thus do not support this hypothesis. Indeed, in *Lampropholis delicata* lizards, individuals with a “hot” thermal type performed optimally at higher temperatures, had faster sprint speeds and were more active, explorative and bold relative to “cold” thermal types (Michelangeli et al. 2018).

Conclusion

We experimentally demonstrated anticipatory maternal effects adjusting offspring phenotype to their natal habitat and increasing their early-life survival prospects, suggesting adaptive anticipatory maternal effects shaping offspring prospects in natal habitats. We found that differences in vegetation structure led to maternal effects on activity and body size, although only the effects on activity were found to be adaptive. Effects of vegetation cover on offspring phenotype and fitness are believed to relate to differences in prey availability between habitats, although other hypotheses, such as differences in perceived risk of predation or thermal characteristics, have been raised.

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Statement of Authorship: JC designed the study, FZ and SZ provided the lizards, AB measured vegetation cover, OG maintained the Metatron, JC, AT, MRa, OC and EB captured the lizards, JC, AT, MRa performed the behavioural experiments, MRi and AT performed the genetics extraction and MRi performed the paternity analysis, EB and JC analysed the data and wrote the article, MRi, FZ and SZ contributed to the revisions.

Competing interests: the authors declare no competing interests

Data availability statement: Data and code can be found on zenodo at <http://doi.org/10.5281/zenodo.6619408>.

Ethics statement: Experiments were conducted at the Station d'Ecologie Théorique et Expérimentale (Ariège, France, 43°01' N, 1°05' E) in accordance with French ethics regulations (permits number APAFIS#15897-2018070615164391 v3 and APAFIS#19523-201902281559649 v3, laboratory animal use agreement B09583). We used lizards captured in

8 natural populations of the Cevennes mountains in the Mont Lozère (Lozère, France, 44°47'N, 3°44'E, capture licence 2010-189-16 DREAL).

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