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Adaptive Maternal Effects Shape Offspring Phenotype and Survival in Natal Environments

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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 seminatural 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.

Keywords: intergenerational plasticity, activity, density-dependent effects, habitat quality, personality, common lizards.

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 to adjust 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. In *Anolis* lizards, for instance, 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 behaviors (i.e., orientation toward the predator) in offspring

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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. Seminatural 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, and predation risk influence juvenile locomotion, basking behavior, 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 peat bog to 30% woodland habitats (Rutschmann et al. 2016), and densities vary within (Bestion et al. 2015*a*) and between (Massot et al. 1992; Meylan and Clobert 2004) populations. 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 seminatural 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. Both vegetation structure and population density 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 postnatal environmental determinants (Le Galliard et al. 2004, 2006; Bestion et al. 2014; Teyssier 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 behavioral, 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 from compensating 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). In *Uta stansburiana* lizards, for instance, larger juveniles survived better particularly when the competition for food was strong (Ferguson and Fox 1984).

We took advantage of a study of common lizards in 2010 in which lizards were released into 15 Metatron mesocosms varying with respect to vegetation cover. In the spring of 2011, we captured gravid females from the mesocosms and monitored their reproduction and offspring natal phenotype in the laboratory. Then we investigated the 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). Furthermore, 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 survival and growth in habitats varying with respect to vegetation cover and population density. We expected more active offspring to survive better in habitats with denser vegetation, as they are able to compensate for 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 the prehibernation season for females producing offspring with a phenotype matching the expected one in their future environment through anticipatory maternal effects.

Material and Methods

Species and Study Site

Common lizards (*Zootoca vivipara* Jacquin, 1787) emerge from hibernation in March, mate soon after, and lay around five soft-shelled eggs (range, 1–12) after 2 months of gestation. Offspring hatch within 1 h 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 × 10-m seminatural mesocosms (Legrand et al. 2012), each of which is fully enclosed by tarpaulins buried 30 cm into the ground and nets aboveground, containing diverse natural vegetation (37 ± 9 plant species), invertebrate communities (16 ± 3 invertebrate families), and microhabitats (Bestion et al. 2015*b*). We took advantage of lizards captured in eight natural populations of the Cevennes Mountains in Mont Lozère (Lozère, France; 44°47′N, 3°44′E) that 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 homogenizing 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 with ArcGIS, as was the total percentage of bare ground. 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% ± 6% SD; fig. S1). Such vegetation cover was related to mean vegetation height, plant richness, and synusial diversity as well as bare ground cover (app. 1). A follow-up experiment showed that the vegetation cover was positively linked to invertebrate diversity within the mesocosms, was negatively related to temperature in the vegetation layer, and was relatively stable at timescales corresponding to lizard life expectancy (app. 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 (app. 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 tree or shrub vegetation cover, although some populations were located near 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 of 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 4 days before measuring activity to allow acclimation to the laboratory conditions, and all of the lizards were released back to their original mesocosms in early May (i.e., on average 1 month before females laid eggs). This allowed minimizing the effect of this laboratory stay on maternal effects, although it could reduce the likelihood of observing 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 odors for activity assays. Ultraviolet (Zoo Med ReptiSun 5.0 UVB 36-W) and incandescent (25-W) lamps 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*).

At the end of May, just before the parturition of the first female, we recaptured all of the individuals. Females

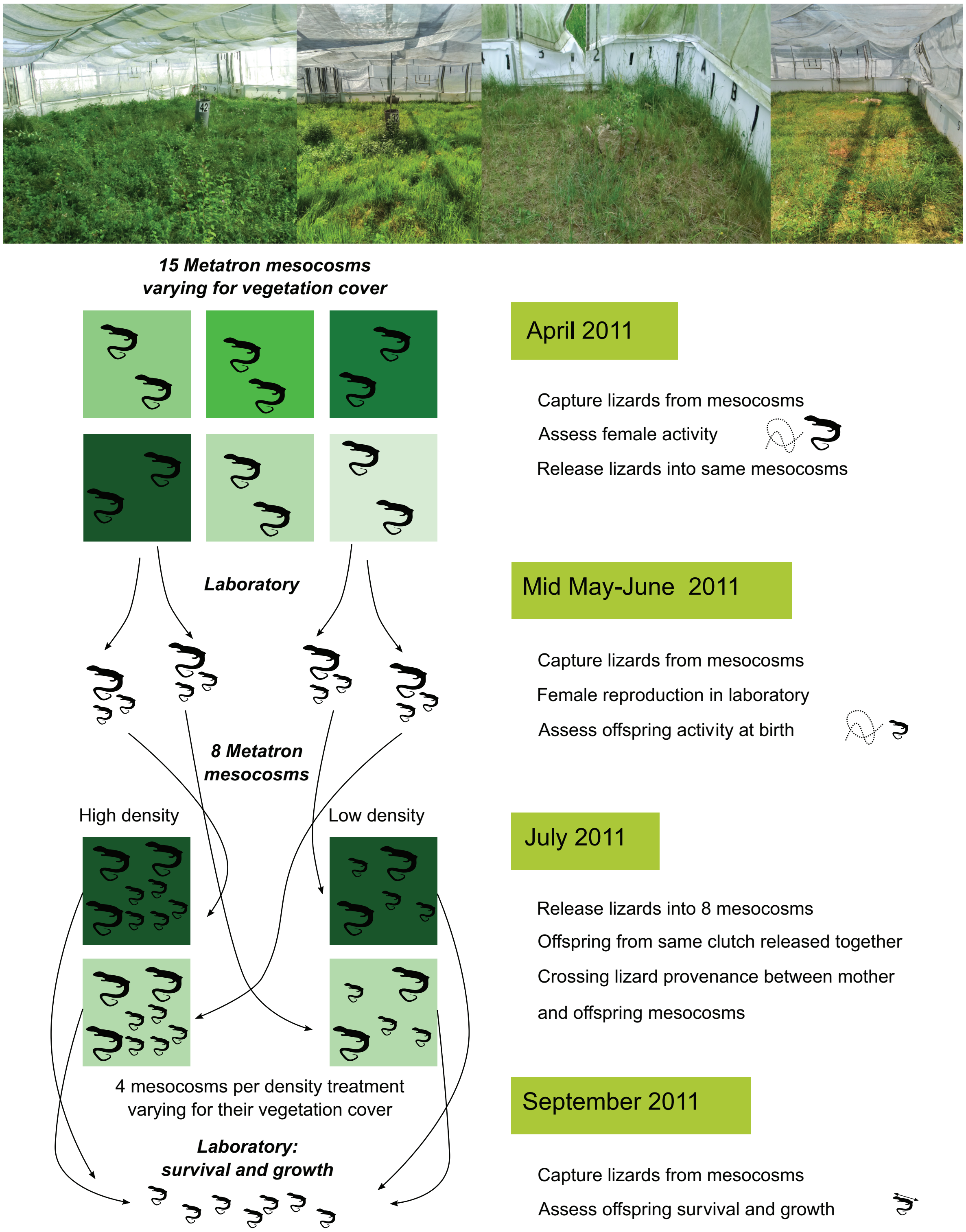

Figure 1: Flow diagram of the experimental design.

laid eggs in the terraria from May 20 to June 30. They produced on average 6 ± 0.26 eggs (mean ± SEM), of which 5 ± 0.31 were viable offspring. Offspring were measured for body length, sexed, and 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 odors) over 2 days. For offspring, we used only a novel environment and a social "mixed-odor" context to allow testing offspring over 1 day. Combining activities measured in different contexts allowed the evaluation of overall activity independent of a particular context (e.g., avoiding the risk of confounding activity tendency with the exploratory tendency of a novel environment). In common lizards, activity levels from similar assays have been shown to be correlated with survival (Le Galliard et al. 2015), female mate choice (Teyssier et al. 2014), and antipredator strategy (Bestion et al. 2014, 2015*a*) and are therefore ecologically relevant.

Assays were conducted in a controlled temperature room (20°C) in 35 × 18 × 23-cm terraria. For the novel environment assay, a PVC opaque wall divided each terrarium 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 terrarium was fitted with a heat source (i.e., bulb). The night before the assays, we acclimatized individuals in the small compartment for at least 12 h, with a heat source for 30 min the morning of the assay. Fifteen minutes before the assay, we turned off the light in the acclimatization compartment and turned on the light above the shelter in the large ("novel") compartment. Turning off the light in the home compartment allowed decreasing interindividual variation in basking motivation. After acclimation, we removed the separation between compartments and measured the time spent moving for 10 min using The Observer software (ver. 2.0). After the assay, we divided terraria in three compartments with PVC walls and put individuals in the middle compartment with a shelter until the next behavioral 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 the presence of female or male odors (for females) or of mixed male and female odors (for offspring). The odor was collected by cutting one or two pieces of absorbent paper from a housing terrarium, with each piece being used once for a focal mother and three times for offspring. We used 75 females and 57 males as odor donors, excluding mothers as donors for their own offspring to avoid specific responses to maternal cues. Females were tested with one randomly assigned odor (male or female) in the morning and the other in the afternoon. Offspring were tested in the afternoon with the odor mix. Offspring from a single clutch were tested using different odor mixes, and a given odor mix was never used more than twice per clutch. Pieces of papers were put under shelters, with one piece with odor in one side compartment and one without odor (collected from vacant terraria) in the other side compartment as a control. After 10 min, we removed the walls separating compartments, let individuals familiarize with the odors for 10 min, and then measured time spent moving for 10 min.

We estimated general activity levels from the time spent moving during the three different types of assays using principal component (PC) analysis. The first PC axis explained 53% of the variance in females and 50% in offspring and was positively related to time 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 = 0.13–0.43, $P < .001$) and not repeatable among the two contexts for offspring (ICC = 0, 95% confidence interval = 0–0.13, $P = .50$). 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 vs. afternoon). As we were not able to measure the repeatability of PC axes over time, we used a database of 4,339 observations of activity measured every year through life on 1,596 lizards inhabiting the Metatron between 2011 and 2020 (Bestion et al. 2015*b*) and found a repeatable activity throughout lifetime in a model including year as a covariate (ICC = 0.21, 95% confidence interval = 0.16–0.25, $P = 1 \times 10^{-23}$).

Genetic Data and Paternity Analyses

Lizard DNA was extracted from tail tips with the QIAquick 96 purification kit (Qiagen) following the 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 (ver. 3.0; Teyssier et al. 2014). This allowed creating a pedigree with a total of 351 individuals, 246 dam-offspring links, and 190 sire-offspring links and with 47% of full-sib clutches and 53% of half-sib clutches. 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. 2015*b*) to assess trait heritability.

Offspring Survival and Growth Rates

In early July, we released all lizards (i.e., offspring, mothers, males, and yearlings) into eight mesocosms of varying vegetation cover (41% ± 5.1% SD; range, 36%–50%). Individuals of different age and sex where distributed to create four high-density mesocosms (12 females, eight males, and three yearlings; 37 ± 2 offspring from 9 ± 1 clutches) and four low-density mesocosms (eight females, five males, and two 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 with respect to 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 with those of their mothers and other clutches were released into different environments compared with 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: $F_{1,6} = 0.02$, $P = .90$; high density: 41.6% ± 5.9% [range, 37%–50%]; low density: 41.1% ± 5.4% [range, 36%–48%]).

In late September, we captured all of the survivors to assess survival and growth rate during three capture-recapture sessions. Each capture session lasted 1 h per enclosure. Lizards were identified, measured, and released. The cumulative probability of capture was 93% (Bestion et al. 2015*b*), and individuals that were never captured were considered 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 (ver. 4.0.5). Data and code are available on Zenodo (https://doi.org/10.5281/zenodo.6619408; Bestion et al. 2022).

General Statistical Approach. We studied these questions with generalized (with a binomial distribution for offspring survival and a Poisson distribution for maternal fitness) and general (all other traits) linear mixed models with maximum likelihood using the lme4 package. We created a global model including fixed predictors (centered and scaled) and random intercepts, and we 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 the Akaike information criterion corrected for small sample size (AICc; Burnham et al. 2002) and averaged best models (within $\Delta\mathrm{AICc} < 2$) following Grueber et al. (2011). We present conditional averages for the averaged models. We further fitted a model containing all of 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 1,000,000 iterations with a 3,000 burn-in and a 1,000 thinning.

In a third step, we refitted the main models with the 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 whether 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-min 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: $F_{1,266} = 1.06$,

$P = .303$; females: $F_{1,160} = 0.79$, $P = .375$; males: $F_{1,103} = 0.09$, $P = .764$) or between vegetation cover and exploratory tendency (all: $F_{1,149} = 0.11$, $P = .745$; females: $F_{1,104} = 0.21$, $P = .644$; males: $F_{1,42} = 0.01$, $P = .923$).

Second, we checked whether vegetation cover affected female body length and activity at the time of the experiment in the spring of 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 (V_R) variances. We first used noninformative priors (V = 1, nu = 0.002), but we also reran analyses with two sets of informative priors as well as 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 the 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, birth date (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 $\Delta\mathrm{AIC} < 2$ 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 noninformative priors 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 noninformative priors (V = 1, nu = 1,000, 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 for density, we focused on vegetation cover and categorized mesocosms into dense-vegetation (vegetation cover >40%, four mesocosms) and sparse-vegetation (<40%, four mesocosms) habitats. We first tested for an interaction between offspring centered and scaled traits and vegetation category on survival (table S10) and then modeled survival for each vegetation category depending on centered and scaled activity, body length, and birth date, 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 difference, 6.8%;

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

Response variable, independent variable	Estimate	95% CI	Effective sample size	P
Body length:				
Fixed effects:				
Intercept	**23.083**	**22.608 to 23.452**	**1,000**	**.001**
Maternal vegetation cover	−.001	−.402 to .423	1,000	.988
Maternal activity	.116	−.110 to .359	1,000	.306
Maternal body length	**.550**	**.294 to .771**	**1,000**	**.001**
Maternal vegetation cover × maternal activity	**.406**	**.127 to .673**	**863**	**.006**
Maternal vegetation cover × maternal body length	.179	−.065 to .438	1,182	.162
Random effects:				
V_A	1.364	1.100 to 1.646	…	…
V_E	.315	.005 to .888	…	…
V_R	.012	.000 to .140	…	…
Activity:				
Fixed effects:				
Intercept	.007	−.209 to .190	1,000	.904
Maternal vegetation cover	**.243**	**.043 to .432**	**1,000**	**.020**
Maternal activity	−.052	−.222 to .124	1,000	.520
Maternal body length	−.035	−.229 to .121	838	.676
Maternal vegetation cover × maternal activity	.101	−.085 to .305	1,000	.320
Random effects:				
V_A	.533	.180 to 1.227	…	…
V_E	.009	.000 to .084	…	…
V_R	.442	.001 to .708	…	…

Note: Shown is an 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 effects variables were not correlated (generalized variance inflation factor <1.1) and were centered 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 ($P < .05$). CI = credible interval.

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 of 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 with 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 zero if vegetation cover in the habitats of the mother and offspring are similar, mimicking environmental predictability. We then modeled maternal fitness as a function of the match of maternal anticipatory effect for activity, plus maternal body length

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

Response variable, independent variable	Estimate	SE	z	P	RI
Survival:					
Intercept	−.02	.25	.10	.921	
Vegetation cover	.41	.21	1.88	.060	1.00
Activity profile	**.42**	**.15**	**2.89**	**.004**	**1.00**
Body length	.23	.16	1.42	.155	.68
Vegetation cover × activity profile	**.33**	**.17**	**1.97**	**.049**	**1.00**
Sex	−.36	.30	1.21	.226	.29
Vegetation cover × body length	.12	.17	.68	.495	.11
Density treatment	.13	.42	.30	.767	.11
Density treatment × body length	.53	.34	1.57	.117	.11
Birth date	−.09	.15	.62	.537	.10
Growth:					
Intercept	**19.28**	**1.46**	**13.04**	**<.001**	
Birth date	**−1.29**	**.34**	**3.77**	**<.001**	**1.00**
Activity profile	−.54	.29	1.83	.068	.81
Body length	−.43	.33	1.30	.192	.23
Density treatment	2.32	2.55	.90	.366	.14
Vegetation cover	1.15	1.26	.90	.368	.14

Note: Shown are model averages of generalized (binomial family; survival) or linear (growth) mixed models. 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, birth date, and sex, plus random mother and mesocosm identities ($N_{\text{group}} = 60$ mothers for survival and 48 for growth, $N_{\text{group}} = 8$ mesocosms for both survival and growth, and $N = 246$ offspring for survival, 117 surviving offspring for growth; tables S12–S13). Numeric independent fixed effects variables were not correlated (generalized variance inflation factor <1.2) and were centered 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 effects of 0.39 and 3.25 SD, respectively, for survival and growth. Confirmatory models with $\Delta\text{AIC} < 4$ (table S8) or with an animal model including additive genetic effect and environmental effect (table S9) gave similar results. In bold: significant effects ($P < .05$). RI = relative importance.

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 $r = 0.05$, 95% confidence interval = -0.07 to -0.18, $t = 0.45$, df = 244, $P = .397$). 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 (95% credible interval = 0.002–0.588) using noninformative priors (up to 0.192 with informative priors) and a maternal effect of 0.125 (95% credible interval = 0.005–0.278; table S4). Body length had a heritability of 0.010 (95% credible interval = 0–0.194) but a large nongenetic maternal inheritance of 0.641 (95% credible interval = 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 (95% credible interval = 0.091–0.350), with a maternal effect of 0.102 (95% credible interval = 0.044–0.171), and heritability of body length was 0.237 (95% credible interval = 0.169–0.303), with a maternal effect of 0.436 (95% credible interval = 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 favor 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 (tables 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 (tables 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 (tables 1, S5–S7).

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

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

Vegetation type, variable	Estimate ± SE	β ± SE	z	P
Dense vegetation:				
Intercept	.197 ± .199	.080 ± .081	.986	.324
Activity	**.783 ± .248**	**.319 ± .101**	**3.156**	**.002**
Body length	.204 ± .205	.083 ± .084	.994	.320
Birth date	−.231 ± .208	−.094 ± .085	−1.111	.266
Sparse vegetation:				
Intercept	−.404 ± .440	−.209 ± .227	−.918	.359
Activity	.116 ± .198	.060 ± .102	.585	.559
Body length	.273 ± .208	.141 ± .107	1.312	.189
Birth date	.167 ± .215	.086 ± .111	.775	.438

Note: The offspring data set is separated into dense vegetation (vegetation cover >40, $N = 119$ offspring) and sparse vegetation (vegetation cover <40, $N = 127$ offspring). Shown are results from generalized linear models investigating survival as a function of activity, body length, and birth date, plus random mother identity and mesocosm identity. Numeric fixed effects variables investigated were not correlated (generalized variance inflation factor for the three variables <1.2) and were centered and scaled. Logistic coefficients were recalculated to average gradient vectors β_{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 explained 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 ($P < .05$).

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 (tables 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 (tables 2, S8, S9). Growth was not influenced by vegetation cover or population density but was negatively related to birth date, and it tended to be negatively related to activity profile (tables 2, S8, S9).

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 better fitness, corroborating the adaptiveness of maternal effects suggested by the survival analysis. To test this prediction, we 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).

Discussion

Abiotic and biotic conditions, such as vegetation structure, population density, and thermal conditions, influence species performance (Heatwole 1977; Cody 1981; Wasiolka et al. 2009; Bestion et al. 2015*b*; Paterson and Blouin-Demers 2018), driving individuals toward locally adapted phenotypes through selection or plasticity. Anticipatory maternal effects are an efficient mechanism to plastically and rapidly adjust the phenotype of the offspring to their environment, 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 the 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,

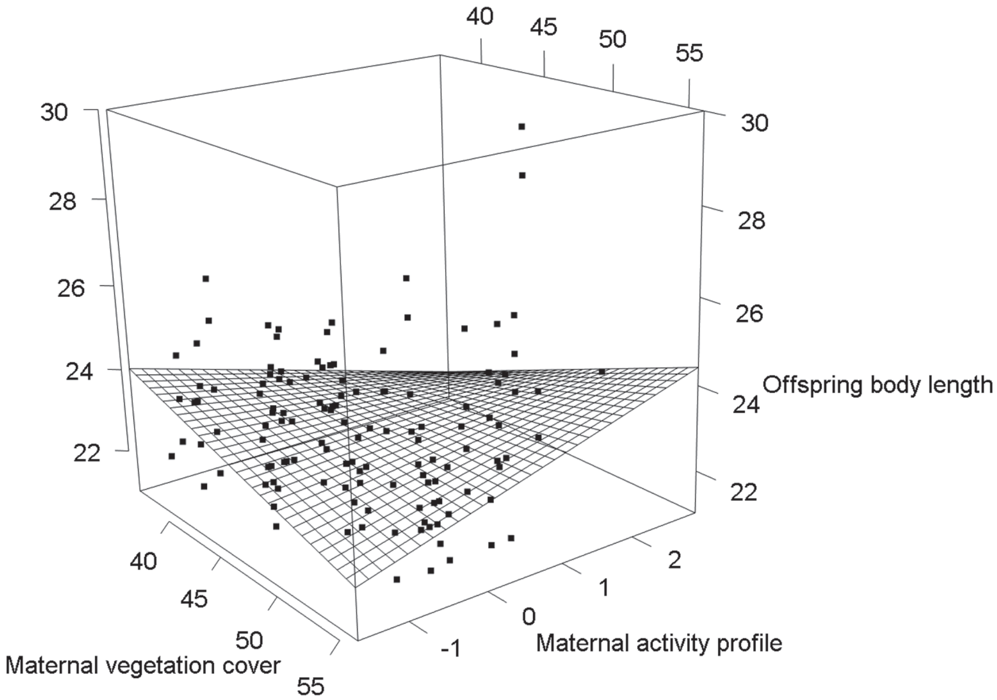

Figure 2: Body length of offspring depended on their maternal activity profile and the vegetation cover in maternal habitats. In denser habitats, less active females produced smaller offspring than their more active counterparts, while in sparse habitats they produced bigger offspring than their more active counterparts. The surface was derived from the table 1 model. $N = 246$.

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 adaptive anticipatory maternal effects in response to vegetation structure in common lizards.

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 favored 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). Furthermore, 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 aggression 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 yearlings 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 in behavioral 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—that is shaping offspring phenotype through maternal effects. In particular, activity levels and body length were strongly influenced by vegetation cover in maternal habitats. Other studies in common lizards have found that maternal environment during gestation influence offspring phenotype, including effects of

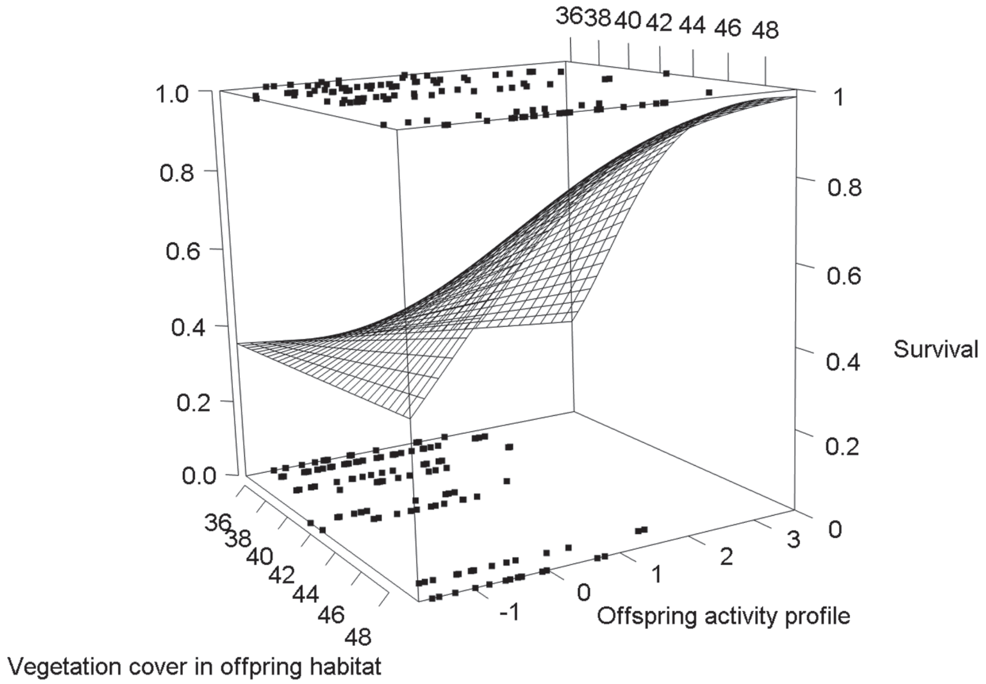

Figure 3: Survival probability of offspring depended on their activity at birth and the vegetation cover in their introduction habitat. More active offspring survived better than their less active counterparts in dense vegetation habitats, while activity had no affect on survival in sparse vegetation. The surface was derived from the table 2 model. $N = 246$.

predation risk and maternal stress hormones on offspring morphology, behavior, 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 behavioral 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 behavior.

Although anticipatory maternal effects are often assumed to be adaptive, they do not always increase offspring fitness (Marshall and Uller 2007). Yet most studies of anticipatory parental effects fail to consider environmental predictability and to adequately test their adaptiveness (Burgess and Marshall 2014). The use of a seminatural experimental system permitted 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 favorable 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 favorable environments 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% and 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 (app. 1). Denser vegetation is indeed linked to higher prey diversity and availability (app. 1), to 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

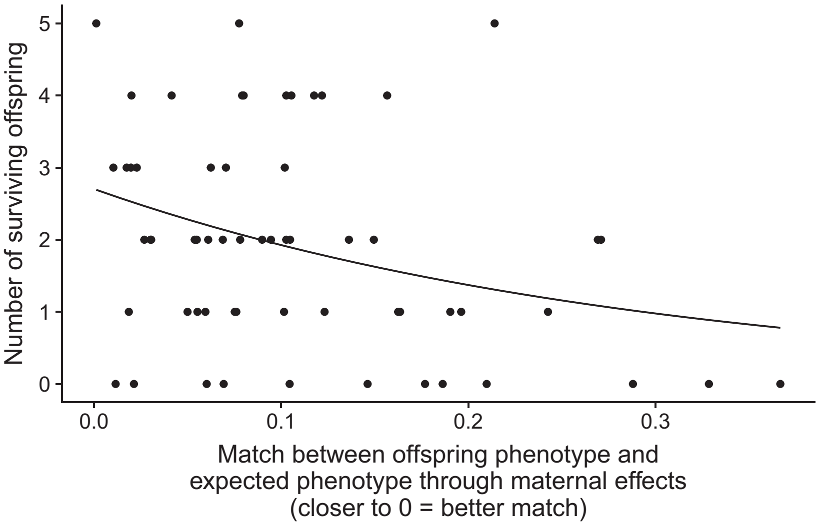

Figure 4: Maternal fitness was related to the match between offspring phenotype and expected phenotype in their living environments through maternal effects. The match between offspring observed phenotype and the expected phenotype in their future environment through anticipatory maternal effects was the absolute difference between log-transformed mean offspring activity and offspring log-transformed activity expected in offspring mesocosms through anticipatory maternal effects. Females that 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 the table S11 model), suggesting that maternal effects were adaptive. $N = 60$ females.

foraging (Beauchamp 2000), particularly for prey that are 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 (app. 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 of *Anolis sagrei* showing that mothers maintained with high prey availability produced offspring that survived 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 favored 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, the positive activity-survival relationship in dense vegetation observed in the present study does not support this last hypothesis. These hypotheses assume a consistent interindividual variation in activity, with a low within-individual variation (i.e., low behavioral flexibility). Studies of common lizards, including the present study, have found that activity levels consistently vary among individuals throughout life, 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 behavioral plasticity, which might have influenced our results. For example, a study of sand lizards has shown that lizards were able to shift from a sit-and-wait foraging tactic to an active 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 forage actively 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 behavioral 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 the predation-dependent mate choice and maternal effects in common lizards (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 the absence of actual predators to prevent lethal assessment errors (Johnson et al. 2013). In fat sand rats, for instance, increasing vegetation cover changed vigilance and foraging tactics, likely because of increased perceived predation risk (Tchabovsky et al. 2001). Because more active individuals are more conspicuous to predators, if lizards perceive sparse vegetation cover habitats to confer a higher risk of predation, it is possible that more active lizards, with an increased threat of predation, might modify their behavior 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 among 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 (app. 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 of thermal syndromes in lizards show the opposite relationships between activity and thermal needs (Goulet et al. 2017; 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 those with a "cold" thermal type (Michelangeli et al. 2018).

Conclusion

We have experimentally demonstrated anticipatory maternal effects adjusting offspring phenotype to their natal habitat and increasing their early-life survival prospects, suggesting that adaptive anticipatory maternal effects shape 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

J.C. designed the study; F.Z. and S.Z. provided the lizards; A.B. measured vegetation cover; O.G. maintained the Metatron; J.C., A.T., M.Ra., O.C., and E.B. captured the lizards; J.C., A.T., and M.Ra. performed the behavioral

experiments; M.Ri. and A.T. performed the genetics extraction and M.Ri. performed the paternity analysis; E.B. and J.C. analyzed the data and wrote the article; and M.Ri., F.Z. and S.Z. contributed to revisions.

Data and Code Availability

Data and code can be found on Zenodo (http://doi.org/10.5281/zenodo.6619408; Bestion et al. 2022).

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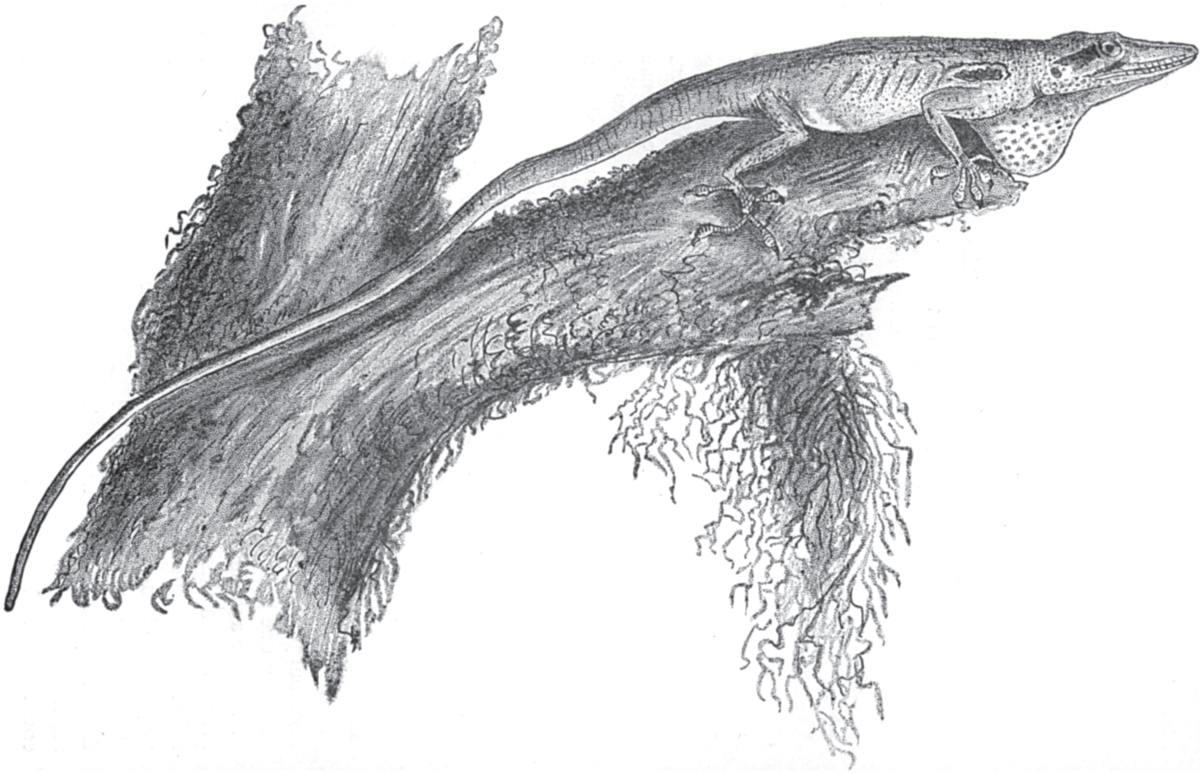

"Under all circumstances lizards are interesting creatures, meet them where we may. . . . There is something very mysterious, at times, in their very look, their dignified mien, their almost provoking silence; this is changed in us to a sense of curious interest that is quickened as the reptile assumes its livelier air, darts along the tree branch that it may be on, or shoots with the rapidity of an arrow up the trunk of some old tree." From "Observations on the Habits of the American Chameleon (*Anolis principalis*)" by R. W. Shufeldt (*The American Naturalist*, 1883, 17:919–926).