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Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal

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Predation is a strong selective pressure generating morphological, physiological and behavioural responses in organisms. As predation risk is often higher during juvenile stages, antipredator defences expressed early in life are paramount to survival. Maternal effects are an efficient pathway to produce such defences. We investigated whether maternal exposure to predator cues during gestation affected juvenile morphology, behaviour and dispersal in common lizards (*Zootoca vivipara*). We exposed 21 gravid females to saurophagous snake cues for one month while 21 females remained unexposed (i.e. control). We measured body size, preferred temperature and activity level for each neonate, and released them into semi-natural enclosures connected to corridors in order to measure dispersal. Offspring from exposed mothers grew longer tails, selected lower temperatures and dispersed thrice more than offspring from unexposed mothers. Because both tail autotomy and altered thermoregulatory behaviour are common antipredator tactics in lizards, these results suggest that mothers adjusted offspring phenotype to risky natal environments (tail length) or increased risk avoidance (dispersal). Although maternal effects can be passive consequences of maternal stress, our results strongly militate for them to be an adaptive antipredator response that may increase offspring survival prospects.

1. Introduction

Predatory pressure is a strong selective force shaping the ecology and evolution of prey organisms [1,2]. Prey antipredator adaptations range from behavioural defences [3,4], morphological defences [5], to shifts in life-history traits [6,7]. Prey can notably respond to predation risk by altering their behaviour to be less susceptible to predation (e.g. increased vigilance levels [3], reduction of foraging time [4]) or by developing defences to deter predators (e.g. helmets [5]). Alternatively, individuals can elude predation risk by altering their habitat use [8] or dispersing away from predators [9–11]. Such defences are not mutually exclusive, as a single species/individual can display a panel of antipredator traits. For example, snails of the species *Helisoma trivolis* exposed to crayfish predators not only develop narrower shells but also change habitat use [8]. Producing such defences is costly and thus often subjected to trade-offs [1]. For example, perceived predation risk can lead individuals to leave high-quality habitats and settle in less suitable habitats [12]. Such changes may improve survival prospects but at a cost for life-history traits such as growth [13] or reproduction [14]. For many organisms, predation pressure can be higher in early stages of life [15]. Consequently, individuals usually express antipredator defences at birth or early in life (e.g. transparency in fish larvae [15], deeper tail fins in tadpoles [16]) and have an innate ability to identify predator cues that can even generate changes in morphology, behaviour or physiology later in life. For instance, in the common frog (*Rana temporaria*), predator cues from diving beetles at the egg stage induce changes in tadpole morphology [16].

One powerful mechanism allowing for antipredator defences to be expressed early on in life is maternal effects. Maternal effects arise when the phenotype of the offspring is influenced by the mother's internal state or external environment [17,18]. Maternal effects can allow individuals to acquire information on their natal environment prior to birth, as long as the maternal environment is a reliable predictor of offspring future environment. As such, through maternal effect, offspring are able to by-pass any delay in the plastic responses they might need to express at birth. Maternal effects can (i) adjust offspring's phenotype to the natal environment, or (ii) increase dispersal propensity from the risky habitat [19]. While several studies have shown the role of maternal effect in locally adapting offspring phenotype to predation risk (i.e. greater wing length in great tits [20], tighter shoaling behaviour in sticklebacks [21], longer time spent immobile in crickets [22]), to the best of our knowledge, evidence of predation risk induced maternal modification in offspring dispersal are very scarce (i.e. one study on insects [19]). Yet, documenting the modifications in dispersal behaviour owing to maternal exposure to predation risk is crucial to our understanding of dispersal evolution in predator–prey systems.

We investigated, in common lizards (*Zootoca vivipara*), the effects of maternal exposure to predator cues (odour of a saurophagous snake) during gestation on offspring adjustment to a risky environment (morphological and behavioural traits) and dispersal decisions and syndromes [23,24]. These maternal effects were studied at birth and carried over on a long period of development. The common lizard is a suitable model for this study as this species is live-bearing and does not provide parental care. Previous studies showed that gestation thus is the most likely period where information transfer from mother to offspring can occur [25–30]. In addition, it is known that both adult and naive common lizards reduce their activity and their basking behaviour in the presence of various predator cues, including saurophagous snake odour [31,32]. We therefore focused on activity and basking behaviour in offspring, as well as tail length for the effect of potential maternal effects. Indeed, predation risk experienced during gestation was shown to affect offspring tail length in an Australian skink; offspring from predator-exposed mothers had longer tails at birth [33]. Tail-autotomy is a widespread antipredator defence among most lizard families [34]. It allows lizards to escape the predator's grip by breaking, acting as a decoy while the lizard reaches a safe hide [35]. As a consequence, lizards with longer tails relative to their body length are less vulnerable to active hunting predators, as the chance that predators seize them by the tail is increased [36]. We finally recorded offspring dispersal propensity as an indicator of maternally induced predator avoidance strategy. We exposed gravid females to a predator cues treatment (i.e. snake olfactory cues) or to a control treatment (no snake cues) for one month. We predicted that our treatment would: (i) generate shifts in offspring's phenotypes that improved survival prospects in predator-rich environments. Offspring from mothers born to predator cues would hence display antipredatory morphological (i.e. longer tails) or behavioural shifts (lower activity and basking levels) or a combination of both; and (ii) conversely, although no study showed such effects on a vertebrate species (and only one on invertebrates), maternal exposure to predation cues should increase offspring dispersal propensity or dispersal success through disperser phenotypic specializations (i.e. dispersal syndrome, [23,24]) as an alternative strategy to avoid predation pressure.

2. Material and methods

(a) Study site and housing conditions

The study took place in the Station of Experimental Ecology in Moulis (France) using populations of common lizards maintained in semi-natural environments. Lizards were captured in the Cevennes mountains (France, 44°27′ N, 3°44′ E, Licence no. 2010-189-16 DREAL) in June 2011 and marked by toe clipping. Lizards were then released into the Metatron, a system of enclosures (10 × 10 m) made of natural lizard habitat (dense vegetation, hides and rocks [37]). Enclosures were delimited by tarpaulins buried 30 cm into the ground to prevent lizards from escaping and remove avian and terrestrial predation [37]. After emergence from hibernation in March 2012, 44 females and 22 males were captured for the experiment and maintained in laboratory for two weeks prior to mating. Lizards were individually housed in 25 × 15.5 × 15 cm terraria featuring 3 cm substrate, a piece of egg carton and a 5 cl Falcon tube for shelter. A light bulb (25 W) and an ultraviolet (UV) lamp (Zoomed Reptisun 5.0 UVB 36 W) provided light from 9.00 to 12.00 and from 14.00 to 17.00 as well as a heat source. Lizards were water sprayed three times a day. Food was offered daily (one cricket per lizard; *Acheta domestica*). In late March, females were mated with two males for the purpose of another experiment [32]. Females were kept with or without predator cues for 4 days and then mated sequentially with two males to study female mate choice depending on predation context. The short pre-mating treatments did not interfere with the results of this study (impact of mating treatment, *p*-value of more than 0.39 on all juvenile traits of interest). Out of 44 females, two did not mate during the trials and were therefore excluded from the results of the present experiment. On 18th April, females were transferred to four outdoor tanks (11 females per tank) where they were exposed to predator cues for one month (see below and the electronic supplementary material, S1 for a flow diagram of the experimental set-up). Females were kept in plastic cattle feeding tanks (Ø 1.7 m) containing 20 cm of soil litter, grass and two small dishes for water. Rocks and logs were placed at the centre of the tanks for lizards to bask and hide. Eleven 5 cl Falcon tubes hidden in the litter and three half flower pots provided additional refuges. The disposition of elements within the tank was the same in all tanks and tanks were placed in a large open area far from any buildings, so that external conditions were the same for all tanks. Each week, we provided 100 crickets, 200 mealworms and clean water to each tank. Two of the four tanks were free of predator cue, and two were treated with predator cues (see §2*b*).

(b) Predator cues

Predator chemical cues were collected from two adult green whip snakes (*Hierophis viridiflavus*). Neonate green whip snakes forage mainly on lizards, and reptiles account for nearly 20% of the adult diet [38]. Green whip snakes occur in the southern distribution of the common lizard (e.g. Massif central, Pyrenees) [39], however they are allopatric to the lizard population used in this experiment. This ensured that females had no prior experience of predation attempt by this species, circumventing the issue of differential responses owing to past experiences of predation. Moreover, it has been shown that common lizards are able to discriminate between predator and non-predator olfactory cues and display classical antipredator responses even if the predator species is allopatric to the population [40] such as green whip snakes in our study [32]. It is however difficult to ensure that, in our study, lizards display an antipredator reaction specific to this species and observed reactions can be general reactions to any saurophagous snakes. Finally, green whip snakes tend to stay within their home range during the lizard activity season [41]; therefore, it is likely that maternal predation risk is a good predictor of offspring predation risk, a condition for the potential maternal effects to be adaptive.

One adult snake was captured in the wild in April, and maintained in the laboratory for three weeks before being released and replaced by another adult snake (License 2012-10 DREAL). The snake was kept in a separate room in a plastic tub (50 × 40 × 10 cm) featuring a clean water bowl, a hiding spot and a light bulb for basking (40 W; set on a 12 L : 12 D cycle). In order to collect snake odours, we placed 40 small calcite tiles (3 × 3 × 0.6 cm) in the snake cage [32]. The tiles were left 3 days before being transferred into the lizards' tanks. Upon collection, tiles were gently rubbed against the snake belly and sides in order to saturate them with snake odour. Forty identical tiles, kept in a separate room, were used as control for the predator-free treatment. Every 3 days, tanks with predator cues treatments received 10 tiles collected from the snake terrarium, whereas control treatments received control, odour-free tiles. Tiles were used on a roll-over schedule (3 days in snake cages—or in the snake-free room for control tiles, 3 days in lizard tanks).

(c) Parturition

On 26th May, we brought all female lizards back to the laboratory to be kept in individual terraria in similar conditions as described above until parturition. Out of the 42 females, 25 gave birth to 127 juveniles (litter size: 5.1 ± 1.7) during June 2012 (13 and 12 females gave birth to 68 and 59 juveniles in the predator cues and control treatment, respectively). Such birth rate is comparable to natural population birth rates [42]. Just after parturition, offspring were marked, measured (snout–vent length and total length to the nearest millimetre), weighed (to the nearest 0.01 g), sexed and kept together without their mother in a terrarium. Three days after birth, we tested offspring preferred temperature (in the morning) and activity levels (in the afternoon, see §2*d*). Families were then released in the Metatron the day after (see §2*e*).

(d) Behavioural tests

All tests were performed in a controlled temperature room (20°C).

(i) Preferred temperature test

Tests were performed in eight 80 × 20 × 40 cm glass terraria. A light bulb (60 W) set at one end of the terrarium created a temperature gradient from 26.8 ± 0.2°C to 19.9 ± 0.1°C. All individuals were maintained without heat and light source on the morning of the test in the controlled temperature room (20°C). This ensured that there was no difference in heat needs among individuals previous to the experiment. The experiment proceeded as follows: each morning, one juvenile was placed into each testing terrarium in the coolest part of the temperature gradient. A video camera fitted above the terrarium and connected to a monitor located on the opposite side of the room was used to record juveniles positions every 30 s during a 30 min long trial. To ensure minimal disturbance, a thick curtain separated the testing from the recording part of the room. We calculated the mean position of lizards within the temperature gradient and derived average preferred temperature (see statistics).

(ii) Activity test

In the afternoon, we assessed activity levels in two different contexts in order to test for an individual ability to discriminate predator cues. Indeed, reduced activity is a typical antipredator response in this species [31]. Half of the offspring born to each mother were tested individually with predator cues, and the other half were tested without predator cues (i.e. split-litter design). Tests were performed in four 25 × 15.5 × 15 cm glass terraria. Each side of the terraria was fitted with a heat source and a shelter. Ten minutes before the test, a tile impregnated with snake odours (if the juvenile was tested in a predatory context) or a snake odour-free tile (otherwise) was slid under one of the shelters. Tile positions within the terraria were alternated. One juvenile was then placed in the middle of a terrarium for a 10 min acclimatization prior to testing. We then monitored juvenile behaviour for 10 min. Activity was estimated as the total amount of time spent walking during the experiment.

(e) Population monitoring

Along with lizards from another experiment, families were released in the Metatron in nine enclosures from 16th June to 15th July. Each population included six males, 10 females and their offspring (40 ± 3), conforming with densities observed in natural populations [42]. The 42 females and 127 juveniles from the present experiment were divided between the nine populations so that each enclosure contained around five females and 14 ± 3 juveniles, with at least one family from each treatment, and similar numbers of juveniles from each treatment. Each enclosure can be connected to a 19 m long S-shaped corridor with a pitfall trap at the end. This length equalled the minimal dispersal distance observed *in natura* in common lizards [43]. On 17th July, we opened all corridors to allow for juveniles to disperse. Pitfall traps were checked daily for dispersers from mid-July to mid-September. Dispersing individuals were identified and released thereafter in another enclosure. Then in mid-September we performed three capture–recapture sessions in the enclosures to assess lizard survival and growth rate. We measured snout–vent length, total length and weight on every surviving lizard.

(f) Statistical analysis

We modelled the impact of maternal exposure to predator cues on juvenile morphology (snout–vent length, relative tail length, body condition at birth and in September), behaviour (activity level, preferred temperature), dispersal, survival and growth. As tail length is correlated with snout–vent length [44], we used the residual values of the linear regression of tail length by snout–vent length as an index of relative tail length. This measure allowed us to study the length of the tail relative to the length of the body and was chosen because studies on South American lizards have shown that escape from predators was linked to the length of the tail relative to the body [36]. Five individuals were excluded from the summer results as their tails were missing. Body condition was calculated as the residual values of the linear regression of body mass by snout–vent length [45,46], and preferred temperature as the residual values of the linear regression of mean preferred temperature by maximal temperature in the gradient, allowing for control of variations of the temperature gradient between sessions. For an unknown reason, almost all individuals released in one of the nine Metatron enclosures died over the summer and thus were excluded from the summer data analysis. Dispersal probability was tested on the subset of 54 individuals that survived through the summer. Mortality in the first weeks of life is indeed high, thus analysing dispersal on all released individuals may underestimate dispersal tendencies and confound the residency with the death of lizards. However, refitting the analysis on the entire set of individuals did not change the results.

We performed generalized mixed models (dispersal and survival probabilities: binomial distribution), and linear mixed models (all other variables), using lmer procedure in R v. 2.15.2 [47,48].

Table 1. Impact of the maternal predator cues treatment during gestation on juvenile morphology, behaviour, growth, dispersal and survival. (Statistics of ΔAIC and likelihood ratio test compared two models, one with maternal predator cues treatment and one without predator cues treatment. GLMM with logit links were used for binomial factors such as dispersal and survival, other variables were modelled with linear mixed models. Simple models included only family as a random intercept (noted 1|F) a maternal tank identity random intercept (1|T, never in the best models) and a Metatron enclosure identity random intercept (1|E) or a combination of several random intercepts. Models including maternal treatment were labelled T + (1|F) or T + (1|E). When the best model was the model including treatment, we provided estimate and standard error of the effect of the predator cues treatment. We also estimated family effects as adjusted intraclass correlation coefficients and 95% CI using rpt.adj. See statistics for more details.)

			likelihood ratio test (d.f. = 1)		effect of maternal treatment		family effect
trait	**best model**	**ΔAIC**	**χ^2**	***p*-value**	**estimate**	**s.e.**	**ICC [95% CI]**
morphological traits							
snout–vent length at birth	(1|F)	1.09	0.91	0.34	—	—	0.58 [0.40,0.68]
body condition[a] (at birth)	(1|F)	1.75	0.25	0.62	—	—	0.38 [0.20,0.52]
relative tail length[b] (at birth)	T + (1|F)	0.87	2.87	0.09	0.84	0.47	0.18 [0.00,0.36]
snout–vent length (in Sept)	(1|E) + (1|F)	0.73	1.27	0.26	—	—	0.26 [0.00,0.58]
body condition[a] (in Sept)	(1|F)	0.30	1.70	0.19	—	—	0.32 [0.03,0.58]
relative tail length[b] (in Sept)	T + (1|F)	5.33	7.33	0.007	5.23	1.84	0.00 [0.00,0.00]
behavioural traits							
preferred temperature[c]	T + (1|F)	4.09	6.09	0.01	−0.79	0.32	0.00 [0.00,0.14]
summer fate							
dispersal probability	T + (1|E)	2.43	4.43	0.04	1.94	1.03	—
survival probability	(1|E)	2	0.02	0.90	—	—	—

[a] Calculated as the residuals of a linear model of body weight by snout–vent length.

[b] Calculated as the residuals of a linear model of juvenile tail length by snout–vent length.

[c] Calculated as the residuals of a linear model of juvenile mean preferred temperature by maximal temperature in the experimental room.

Models were built in the same way for each dependent variable except for activity. Variables were modelled as a function of both maternal treatment as a fixed effect and several random effects. Offspring family was modelled as a random intercept nested within the mother predator cues treatment, as siblings were not independent. We also added the identity of the tank in which the female spent the gestation period as a random intercept. Finally, we added the identity of the Metatron enclosure as a random intercept for models considering offspring traits in September to account for variation owing to potential differences among enclosures. Following Zuur *et al.* [49], we fitted full models with maternal treatment and either family random intercept only, enclosure random intercept only, maternal tank random intercept only, and every combination of random intercepts with a restricted maximum-likelihood approach. We compared models using the respective Akaike information criterion (AIC) and chose the best structure of the random component for each dependent variable (table 1). In each case, we then used these best models to test for the effect of maternal treatment. We compared a full model including both maternal treatment and random intercepts to a simpler model with random intercepts only through likelihood ratio tests. When the best model contained maternal treatment, we provided estimates and standard errors of the effect of the treatment. We also provided estimates of the family effect for every model including family as adjusted intraclass correlation coefficients (ICC) with 95% confidence interval (CI) using the rpt.adj from the rptR package, adjusting ICC for effects included in the final model [50]. For activity level at birth, the full model included juvenile predatory environment during the test as well as maternal treatment and their interaction as fixed effects, and best structure of random component included family. This full model was compared with all derived simpler models through AIC. As several models had close AICs, we then used a model averaging approach following Grueber *et al.* [51], as implemented in the MuMIn R package. Assumptions of linearity and homogeneity of variances on residuals from all models were checked visually.

3. Results

(a) Morphological responses

Juveniles born to mothers exposed to predator cues did not differ in their snout–vent length and body condition from neonates born to unexposed mothers, neither at birth (snout–vent length, exposed mothers: 21.7 ± 0.2, unexposed mothers: 22.1 ± 0.2; body condition, exposed mothers: 0.002 ± 0.003, unexposed mothers: −0.002 ± 0.004) nor in September (table 1, snout–vent length, exposed mothers: 47.4 ± 0.8, unexposed mothers: 49.2 ± 0.7; body condition, exposed mothers: 0.07 ± 0.06, unexposed mothers: −0.08 ± 0.07). However, juveniles born to mothers exposed to predator cues tended to have longer tails relative to body length at birth than juveniles born to unexposed mothers (table 1 and figure 1). In September, the difference of relative tail length between treatments was stronger and statistically significant (table 1 and figure 1).

(b) Behavioural responses

Juveniles born to mothers exposed to predator cues selected lower average temperatures than juveniles born to unexposed mothers (table 1 and figure 2). When tested without predator cues, juveniles born to both exposed and unexposed mothers did not differ in activity levels. However, juveniles born to

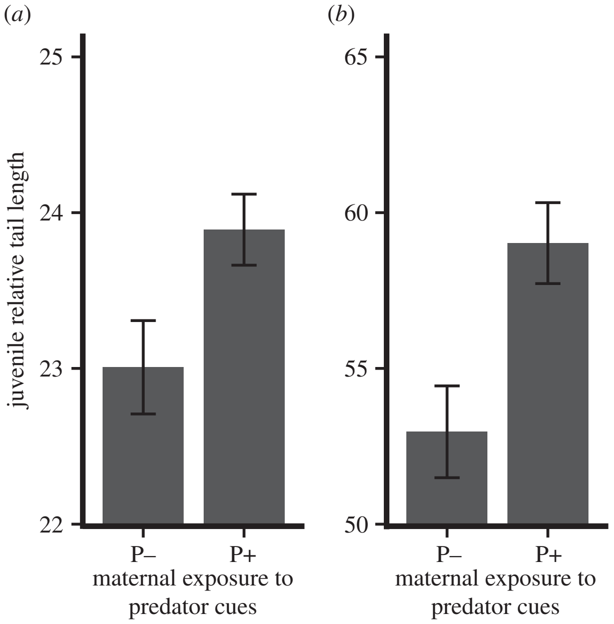

Figure 1. Mean juvenile relative tail length (mean ± s.e.) at birth (*a*) and in September (*b*) depending on maternal exposure to predator cues. Relative tail length is calculated as the residuals of the linear regression of tail length by snout–vent length, added to the mean juvenile tail length for clarity purposes. P−, juveniles born to mothers maintained without predator odour cues during gestation; P+, juveniles born to mothers with predator cues. Results at birth include 126 individuals, whereas results in September include 40 surviving juveniles with intact tails (five individuals had to be discarded as they had regenerated tails).

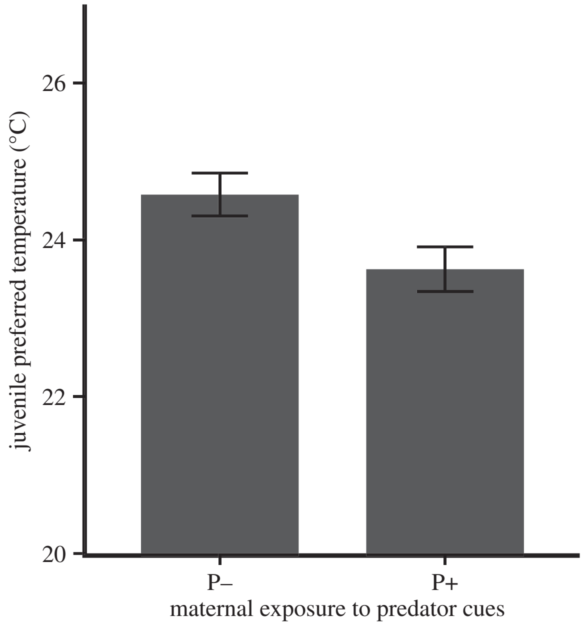

Figure 2. Mean juvenile preferred temperature (°C ± s.e.) depending on maternal exposure to predator cues. Preferred temperature is inferred from the mean position of the juvenile in a temperature gradient during a 30 min test. P−, juveniles born to mothers maintained without predator odour cues during gestation; P+, juveniles born to mothers maintained with predator cues.

exposed mothers had higher activity levels than juveniles born to unexposed mothers when tested in the presence of predator cues (maternal predator cues treatment: −5.39 ± 20.1, $p = 0.79$, relative importance (RI) = 0.41; juvenile exposure to predator cues: 3.18 ± 26.7, $p = 0.91$, RI = 0.41; interaction: 48.7 ± 23.8, $p = 0.04$, RI = 0.22; figure 3). Juveniles born to exposed mothers increased their activity when in the presence of predator cues, whereas juveniles born to unexposed mothers tended to decrease their activity (figure 3).

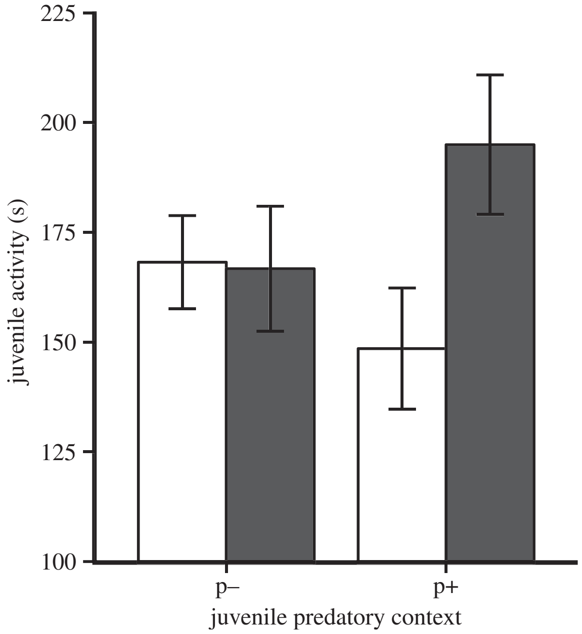

Figure 3. Mean juvenile activity (seconds ± s.e.) measured as the time spent walking over a 10 min period depending on both predatory context of the test (p−, juveniles tested without predator cues; p+, juveniles tested with predator cues) and maternal exposure to predator cues. White, juveniles born to mothers maintained without predator odour cues during gestation; grey, juveniles born to mothers maintained with predator cues.

(c) Summer dispersal, survival and growth

Juveniles born to mothers exposed to predator cues dispersed more than juveniles born to unexposed mothers (figure 4). Maternal exposure to predator cues had no effect of juvenile summer survival, nor on juvenile growth (table 1).

4. Discussion

Our study allowed us to estimate the impact of maternal exposure to predator cues on a large range of offspring phenotypic traits, both at birth and later in life. Female lizards maintained with predator cues during gestation produced juveniles with longer tails relative to their body, lower preferred temperature and different activity levels in the presence of predator cues than juveniles born to mothers unexposed to predator cues. Juveniles born to mothers exposed to predator cues also dispersed thrice more than juveniles born to unexposed mothers. Previous studies on other lizard species found that maternal predation risk had consequences on offspring morphology and predator recognition at birth [33], but did not look at carryover effects. To the best of our knowledge, this study is the first to investigate maternal effects on a long period of development and on a wide array of traits, coupling traits that involve juveniles' adjustment to a risky environment and traits that involve dispersal to search for a safer habitat.

Exposure to predator olfactory cues had no effect on the duration of the gestation period, nor on female reproductive

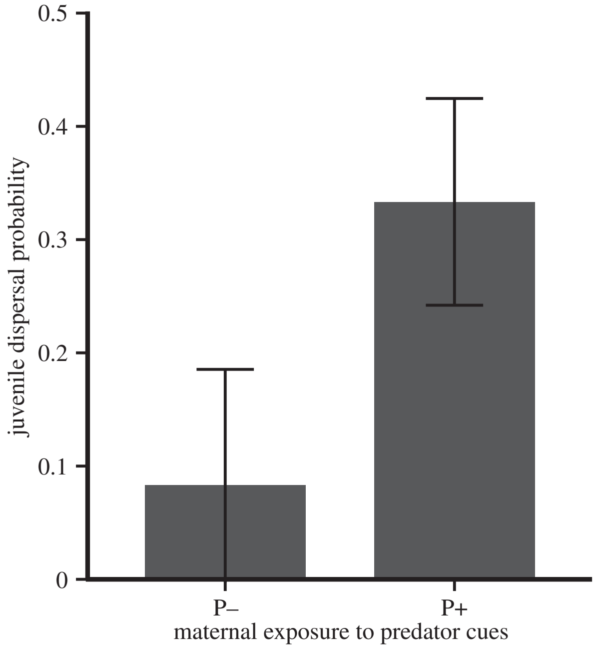

Figure 4. Juvenile dispersal probability (mean ± s.e.) depending on maternal exposure to predator cues. P−, juveniles born to mothers treated without predator odour cues during gestation; P+, juveniles born to mothers with predator cues.

investment (see the electronic supplementary material, S2), contrary to previous findings in other species [52]. Because the burden of carrying embryos [53] can make gravid females more susceptible to predation [54], it was proposed that gravid females may in turn hasten gestation to lower such costs under perceived risk of predation (as in the guppy [52]). On the other hand, gravid females may adopt cryptic behaviours and thus lower their susceptibility to predation [55]. Regardless of the lack of effect on female reproduction, our results strongly suggest that females were able to identify predator cues: not only did females lower their food intake (a classic antipredator response; E. Bestion, J. Cucherousset, A. Teyssier, J. Cote 2012, unpublished data) and grew longer tails than unexposed females (a costly antipredator strategy in lizards [56]; see the electronic supplementary material, S2), but also produced offspring with altered phenotypes.

Females exposed to predator cues during gestation produced offspring with longer tails relative to their body. Previous studies on lizards showed that tail length is partly heritable (broad sense heritability $h^2 = 0.51$ in common lizard, [44]; and on other lacertid species $h^2 = 0.46$, [57]). As suggested in these studies, heritability estimates may have confounded additive genetic effects and various potential maternal effects (e.g. population density, predation context). We found an important and lasting effect of maternal predatory context on relative tail length in common lizards which is likely to be an antipredator response mediated by maternal effects. These results are congruent with another study carried out on Australian lizards (*Pseudemonia pagenstecheri*), where neonates born to mothers exposed to snake chemical cues had longer tails at birth [33]. Our study adds to this previous result by demonstrating that morphological differences at birth can be carried on and become greater later in life. These morphological changes are likely to be adaptive antipredator defences. Indeed, tail length is correlated to stamina in lacertid lizards [57], an important antipredator trait. Moreover, a study on three South American lizard species found that their rate of escape from a Teiid predator was linked to the length of their tail relative to their body [36]. This Teiid predator has an active hunting strategy where it detects lizards by olfaction and directs its attack to the bulk of the lizard and often to the tail. As a consequence, lizards attacked on their tail had tails roughly 20% longer that lizards attacked on their body [36]. Another study on tropical lizards found that wide-foraging species had longer tails than their sit-and-wait foraging counterparts. This was attributed to the fact that predators which pursue these rapid species would presumably be faced with the tail of the lizard as it moved away, increasing the likeliness to be caught by the tail, whereas more cryptic sit-and-wait species will presumably be more detectable at close range, hence the predator will aim at the head [58]. These results collectively suggest that maternal effects on tail length are likely to be a widespread response to predation risk in lizards. Such morphological responses are similar to predator-induced transgenerational changes in other species such as longer wings in great tits [20] and deeper tail fins in frogs [59] to improve evasion from predators, or increased concentration of deterrent glucosinolates in plants [5] and helmeted morphs in *Daphnia* [5] to deter predators.

At birth, juveniles born to mothers exposed to predator cues also selected lower temperatures, reflecting a diminution in basking behaviour (less time spent in the hottest part of the temperature gradient). Previous studies found that when in the presence of predator cues, common lizards reduce their basking behaviour [31,60,61], presumably because lizards are particularly vulnerable to predation while basking in the open. Our study adds to these findings by demonstrating that maternal exposure to predator cues during gestation is sufficient to trigger a change in juvenile thermoregulation behaviour even in the absence of actual predation stimulus in the natal environment. Changes in preferred temperature represented 1 ± 0.3°C difference, which is likely to be an important difference for neonate lizards [62]. Contrary to expectations, maternal exposure to predator cues did not decrease juvenile overall activity levels. In fact, in the absence of predator cues, there was no difference in activity levels between juveniles born to exposed and unexposed mothers. Conversely, in the presence of predator cues, juveniles born to mothers exposed to predator cues increased their activity, displaying higher activity levels than juveniles born to unexposed mothers. Previous studies have shown that the response to predator cues is innate to common lizards, as naive juveniles respond to snake chemical cues in the same way that adults do [31]. Our results may provide an alternative explanation to this hypothesis. That is, mother experience of predation could change juvenile ability to respond to predation risk in their natal environment, as juveniles born to mothers exposed to predator cues responded more strongly to predator cues. Such greater sensitivity to predator scent was shown in Australian lizards: juveniles born to mothers exposed to snake predator cues exhibit higher tongue-flick rates when presented to predator cues than juveniles born to unexposed mothers [33]. Our results suggest that mothers exposure to predator cues generated behavioural differences at birth (i.e. basking behaviour, predator cue recognition) and morphological differences later in life (i.e. relative tail length) in juvenile lizards. These differences might reflect different antipredator strategies over the lifetime, as tails might be too short at birth to prevent predation by snakes. Later in life however, the difference in relative tail length between treatments was roughly 10%. At this stage, tail length represents more than half of the lizard total length. In anurans, tadpoles reared in the presence of predators used behavioural antipredator defences early in ontogeny (i.e. hiding and reduced activity), but relied on morphological adaptations (e.g. deeper tail fins) later on life [59]. However, although we expected all juveniles to reduce their activity levels in the presence of predator cues, as activity reduction is a widespread antipredator tactic (e.g. [1,63], see [31,32] for common lizard), offspring born to exposed mothers increased their activity in the presence of predator cues. This response was probably a flight response and may be linked to the increased dispersal shown by juveniles from exposed mothers.

Predator-induced dispersal has been documented separately in several species [9,10]. In plants, herbivory has been shown to influence seed dispersal: the proportion of floating seeds produced by an invasive weed was related to the damage caused to the plants by a specialist herbivore [64]. In aphids, the presence of predatory ladybirds enhanced the proportion of winged dispersal morphs at the next generation [19]. A review of stream insect response to predation showed however that increased or decreased emigration behaviours can be expected depending on the prey and predator species [63]. On the other hand, maternal effects have shown to influence offspring dispersal [25,65–68]. For example, a differential transfer of maternal yolk androgens in response to parasitism has been shown to modify offspring dispersal in great tits [65]. However this is, to the best of our knowledge, the first study to demonstrate maternal effects on offspring dispersal behaviour mediated by predation risk perceived during gestation in a vertebrate. Juveniles born to mothers exposed to predator cues dispersed thrice more than juveniles from unexposed mothers. This result seems intuitive, as fleeing from a supposed risky habitat appears as a safe response to predation risk. However, for this strategy to be adaptive, the costs of dispersal (e.g. energetic costs [69]) have to be lower than the expected benefits in terms of survival, this balance depending both on the context and on individual phenotype. Specifically, predation during transience is probably one of the major causes of mortality for dispersing individuals in animals [70]. A possible way to increase juvenile survival during transience is the concurrent manipulation of offspring dispersal and phenotype by mothers in order to create dispersal syndromes (i.e. phenotypic specializations in dispersers enhancing dispersal success [11,23,71,72]). Maternal exposure to predation risk should therefore generate specialized dispersal phenotypes in offspring. Indeed, we show that in offspring from exposed mothers, dispersing individuals had longer tails relative to their body than resident individuals (electronic supplementary material, S3), whereas the difference did not exist in juveniles from unexposed mothers. Our results suggest that maternal exposure to predator cues changed the trait associations in dispersing and resident individuals, creating different dispersal syndromes depending on the context.

In conclusion, our results suggest that adaptive antipredator defences may be induced by maternal exposure to predator cues. However, because we could not manipulate predator' presence in enclosures, whether the observed phenotypic changes may translate into higher survival probabilities to actual predation risk remains an open question. Yet, the specificity of the morphological and behavioural responses to the predator treatment and the relevance of the changes observed to the known antipredator defences in lizard species are strongly militating for an adaptive antipredator strategy. These responses do not constitute common maternal responses to any given stressor (e.g. parasitism [26], humidity [27], maternal corticosterone levels [28–30]). High maternal levels of hormone involved in stress response (i.e. corticosterone) has been shown to decrease juvenile activity [29], inconsistently increase basking behaviour [29], to have no effect on tail length [28,30] and to decrease offspring dispersal probability, at least in the common lizard [30]. Therefore, it seems that the present observed responses seem to be specific to predation risk even if they might share some mechanisms with the response to other stressors. Whatever the mechanism, and irrespective of the adaptive value of the response, we showed that exposure to predator cues during gestation is likely to affect juveniles future, and can modify population dynamics by increasing juvenile emigration from supposed dangerous habitats.

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