



## Original Article

# Maternal and personal information mediates the use of social cues about predation risk

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Organisms can gain information about predation risks from their parents, their own personal experience, and their conspecifics and adjust their behavior to alleviate these risks. These different sources of information can, however, provide conflicting information due to spatial and temporal variation of the environment. This raises the question of how these cues are integrated to produce adaptive antipredator behavior. We investigated how common lizards (*Zootoca vivipara*) adjust the use of conspecific cues about predation risk depending on whether the information is maternally or personally acquired. We experimentally manipulated the presence of predator scent in gestating mothers and their offspring in a full-crossed design. We then tested the consequences for social information use by monitoring offspring social response to conspecifics previously exposed to predator cues or not. Lizards were more attracted to the scent of conspecifics having experienced predation cues when they had themselves no personal information about predation risk. In contrast, they were more repulsed by conspecific scent when they had personally obtained information about predation risk. However, the addition of maternal information about predation risk canceled out this interactive effect between personal and social information: lizards were slightly more attracted to conspecific scent when these two sources of information about predation risk were in agreement. A chemical analysis of lizard scent revealed that exposure to predator cues modified the chemical composition of lizard scents, a change that might underlie lizards' use of social information. Our results highlight the importance of considering multiple sources of information while studying antipredator defenses.

**Key words:** antipredator behavior, conspecific attraction, disturbance cues, inadvertent social information, maternal stress, private information, transgenerational plasticity

## INTRODUCTION

Prey frequently respond to the risk of predation via plastic physiological, morphological, and/or behavioral changes, with strong implications for individual fitness (Lima 2002; Benard 2004). The most common antipredator behaviors include active escape, reduction of activity, shelter use, or grouping behavior (Krause et al. 2002; Lima 2002; Winandy et al. 2015). Although these behavioral defenses are expected to enhance survival, they may also be costly (Lind and Cresswell 2005). For example, reducing activity or increasing the time spent in refuge alleviates the risk of being detected by a predator but also decreases foraging and mating opportunities. Consequently, individuals should experience energy

allocation trade-offs between predator avoidance and other essential activities (Lima 1998). Organisms should, therefore, benefit from obtaining information about predation risk to maximize their benefit–cost ratio of antipredator behaviors.

Prey may rely on a variety of cues from different sources to assess predation risk. Throughout their life, individuals gain information by personal experience, which implies observation, detection, and/or direct nonlethal encounter with predators. Individuals can also gain information from parental cues carried over to the next generation (i.e., transgenerational effects). In particular, if mothers have reliable information about the risk of predation that their offspring are likely to encounter in the future, they can shape their offspring's phenotype to be better defended against predators (Sheriff and Love 2013; Sheriff et al. 2017). For example, offspring produced by mother exposed to predation risk can exhibit morphological defense (e.g., the helmet morph in *Daphnia*; Agrawal et al. 1999; the

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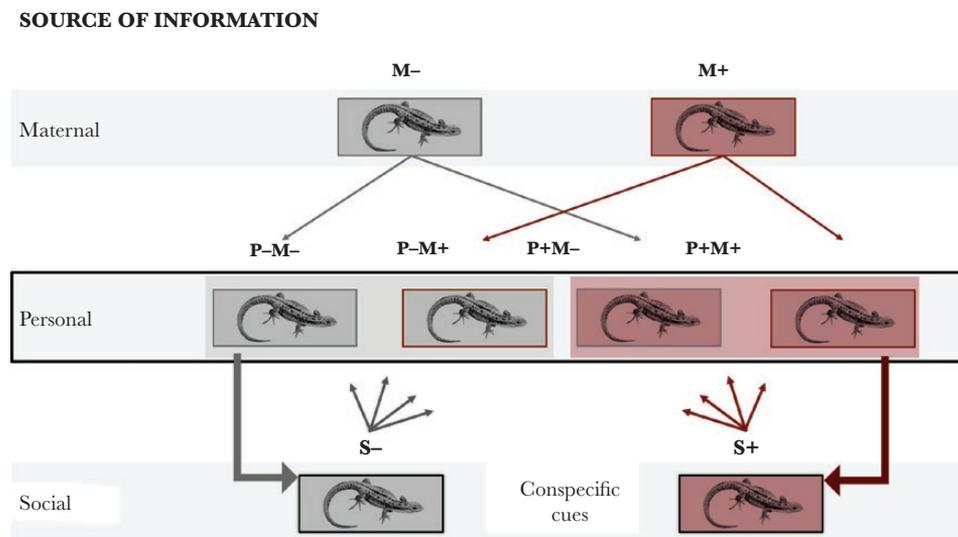


snakes between the two treatments (populations with snakes: 16 females and their 44 juveniles in the predation risk treatment and 16 females and 42 juveniles in the control treatment; populations without snakes: 10 females and 24 juveniles in the predation risk treatment and 12 females and 27 juveniles in the control treatment). We maintained females in 24 outdoor tanks (1100 L; diameter: 1.70 m, two females in each tank, except one tank of each treatment with three females) containing 20 cm of soil litter, dense vegetation, one dish for water, and a weekly addition of crickets, *Acheta domestica*. We provided refuges by adding several 5-cL falcon tube in the litter, three half flower pots, and two perforated bricks. A basking area was available in the center of the tanks using a few rocks and three logs. These housing conditions were highly suitable for lizards as shown in previous experiments (Bestion et al. 2014; Teyssier et al. 2014). Gestation usually lasts 2–3 months depending on air temperature. During the last month of gestation, we manipulated maternal information by exposing the females to predator or control scent (see below for the detail description of the procedure). Before the first parturition, females were brought to the lab in 35- × 18- × 22-cm individual terraria filled with 5-cm substrate, providing two shelters (on and under the ground) and a water bowl. A light bulb (25 W) and an UV lamp provided, respectively, a heat source and light from 9 AM to noon and from 2 PM to 5 PM. In addition, each terraria were water sprayed three times a day. Food was provided daily with two crickets per lizard. Since the lizard populations used in this study are viviparous, we separated all newborns from their mother just after parturition. In total, we raised 137 juveniles that we marked by toe clipping (approved by the ethical committee and the French government: APAFIS#15897-2018070615164391 v3) and sexed by counting the number of ventral scales (Massot et al. 1992). Each clutch, whose mother was either exposed or unexposed to predator scents, was equally split between the two treatments for personal information.

Using this full-crossed design (Figure 1), we exposed two generations of lizards to predator cues: offspring unexposed from mother unexposed (P–M–,  $n = 39$ ; P for personal information and M for maternal information), offspring unexposed from mother exposed (P+M–,  $n = 30$ ), and offspring exposed from mother unexposed (P–M+,  $n = 36$ ), and offspring exposed from mother exposed (P+M+,  $n = 32$ ). Offspring were raised in 24 outdoor tanks (in the same maintenance conditions as described before). We randomly distributed the juveniles into 12 tanks of a control treatment and 12 tanks of a predation treatment (five to seven individuals in each tank), checking there were no difference in body size or body mass between treatments (body size:  $t = -1.127$ ,  $P = 0.261$ ; body mass:  $t = -0.344$ ,  $P = 0.731$ ). The density and sex ratio were similar between treatments (generalized linear model with a Poisson distribution and a log link, number of lizards:  $P- = 6.00 \pm 0.21$ ,  $P+ = 5.92 \pm 0.19$ ,  $P = 0.93$ ; number of females (with number of lizards as a covariate):  $P- = 0.55 \pm 0.02$ ,  $P+ = 0.52 \pm 0.02$ ,  $P = 0.78$ ). Offspring personal exposure was manipulated twice: just after birth at the juvenile stage (in summer 2014) and 1 year later at the subadult stage (in summer 2015).

### Predation risk treatments

We used the cues of a natural predator, the green whip snake, *Hierophis viridiflavus*. Common lizards have an innate recognition of snakes as a threat and their highly developed tongue-vomer nasal system allows them to detect chemicals that are left on the substrate by the snake predator. Lizard responses to snake scents strongly decreases the chance of capture (Downes 2002). Common lizards live in dense vegetation and their population density is much higher than that of snakes. Direct encounters with snakes are, therefore, rare but highly lethal. This innate aversion of lizard to predatory scents is thus subjected to minor ontogenetic changes and is stable



**Figure 1**

Sources of information about predation risk. The predation treatment (light gray and dark red for, respectively, unexposed and exposed to predation cues) was manipulated in each of the three source of information following a full-crossed experimental design. Half of the gravid mothers were exposed to predation risk (i.e., maternal information). After hatching, each clutch was divided in halves and raised with or without predation risk (i.e., personal information) in order to have all combination of treatment between mothers and offspring: offspring unexposed from mother unexposed (P–M–,  $n = 39$ ; P for personal information and M for maternal information), offspring unexposed from mother exposed (P–M+,  $n = 36$ ), offspring exposed from mother unexposed (P+M–,  $n = 30$ ), and offspring exposed from mother exposed (P+M+,  $n = 32$ ). The social information was provided by cues from conspecific (using feces) that were either previously exposed (S+) or unexposed (S–) to predation risk.

over long periods of time without an encounter with a snake (Van Damme et al. 1995; Bestion et al. 2014).

We kept the green whip snake in a terrarium providing a water bowl, a shelter, and a light bulb for basking. To collect snake odors, we placed calcite tiles ( $3 \times 3 \times 0.6$  cm) in the snake cage for 3 days and gently rubbed, using rubber gloves, on the snake body before use. We used identical tiles (i.e., blank tiles), kept in a separate room, for the control treatment without snake scent. We placed five tiles in each outdoor home tank, blank tiles for the control tanks, and tiles with cues for the predation tanks. Every 3 days for 4 weeks, we exchanged old tiles of both treatments for new ones before olfactory cues could vanish in the outdoor tanks. This same predator exposure protocol was used for all sources of information: the maternal exposure in Mai 2014, the offspring exposure in August 2014 at juvenile stage, and in August 2015 at subadult stage. While we did not use any physical encounters to maintain the potential antipredatory response, 1 month of exposure to predatory cues is not enough to trigger habituation (Downes 2001, 2002). Moreover, we did not use the scent of the same snake for exposure at the juvenile and subadult stages. This scent novelty should maintain lizard responsiveness and avoid habituation process. Previous studies show that both within- and between-generation responses are induced by predator olfactory cues manipulated over a month (Shine and Downes 1999; Bestion et al. 2014), which makes this procedure, along with ethical considerations, the most suitable option.

### Social information and attraction to conspecific cues

Social information about predation was provided after the second exposure to predation cues at the subadult stage (in late summer 2015). We assessed individual social response to the cues of conspecifics that were previously exposed to predator cues (S+) or not (S-). Following the full-crossed-design experiment (Figure 1), half of the lizards from each treatment (i.e., P-M-, P-M+, P+M-, and P+M+) were exposed to S+ and the other half were exposed to S-. To do so, we collected pooled scents from the lizards maintained in each of the 24 tanks just after the predation treatment at the subadult stage (August 2015). These 24 groups (12 from the control treatment and 12 from the predation treatment) were housed separately in large terraria ( $35 \times 18 \times 22$  cm) covered by paper towel during 1 week. Twenty-four pieces of paper containing the feces of each group were then used during the social attraction test. Each tested lizard was exposed to 1 of the 24 different scents, always avoiding the scent of their own group to exclude the possibility that lizards were exposed to their own feces or to feces from a conspecific that they already knew. Lizards were cleaned using an antiparasite solution (©frontline) before being released in the terraria and could, therefore, not bear predator cues from tiles on them. We collected the papers devoid of conspecific scent from vacant terraria maintained in the same conditions as our inhabited terraria.

We tested social attraction with a choice assay between two compartments with or without scents of conspecifics. This type of assay is commonly used in common lizards and other lizard species to quantify individuals' social strategies (Cote and Clobert 2007; Cote et al. 2008; Rodríguez-Prieto et al. 2011; Teyssier et al. 2014; Le Galliard et al. 2015; Mell et al. 2016). In reptiles, lizards' scents convey various types of information about the donor (Martín and Lopez 2010, 2014). Therefore, the assay allowed us to measure attraction to conspecific cues depending on donors' characteristics

(i.e., social information; Léna et al. 1998, 2000; Aragón et al. 2006). We used glass terraria ( $34 \times 17 \times 25$  cm) divided into three compartments: a shelter without conspecific scents was put at one end of the terrarium and a shelter with conspecific scents was put at the other end of the terrarium. We placed each lizard in the central compartment (devoid of shelter and scent) for 4 h and we started the assay by removing the walls separating the compartments. After 10 min of acclimation to the two shelters, we recorded for another 10 min the time spent in each compartment and on/under each shelter to estimate social tendency. Video were analyzed using "The Observer" software, allowing the exact measurement of the time in each location. The observer was blind to the treatment of individuals.

### Analysis of scent chemical composition

We analyzed the chemical composition of scent samples collected in the 24 terraria in the same manner as those used for the social attraction test (12 from the control treatment and 12 from the predation treatment). This means that, for each group, the sample was made of several pieces of paper towel with feces and was composed of a mix of individual scents. We collected feces instead of femoral secretions because feces are also commonly used in lacertid lizard to simulate olfactory responses (López et al. 1998; Aragón et al. 2000; Moreira et al. 2008) and chemical communication based on femoral secretions is relatively less important in this species (Gabirot et al. 2008). Samples were collected using surgical pliers cleaned with alcohol and rinsed with sterile water between each population. Samples of paper towel and soil from vacant terraria were also collected as controls. Samples were disposed in glass vials and kept at  $-80$  °C until analyses.

Chemical compounds were analyzed using solid-phase microextraction with a Stableflex fiber (50/30 $\mu$ m DVB/CAR/PDMS, Supelco, Sigma-Aldrich, Bellefonte, PA). Samples were placed at 50 °C for 20 min, and the fiber was then exposed to the headspace of the glass vials (without touching the towel) for 20 min. Absorbed chemicals were then analyzed on a mass spectrometer quadrupole detector (ISQ QD) coupled to a Trace 1300 gas chromatography (Thermo Fisher Scientific Inc) with a capillary column (Restek RTX-5MS 30 m  $\times$  0.25 mm, 0.25  $\mu$ m film thickness, 5% diphenyl, and 95% dimethylpolysiloxane) and a splitless injector (300 °C). Ionization was performed by electron impact (70 eV, source temperature 250 °C). Helium was the carrier gas (1.2 mL/min). The oven temperature was initiated at 40 °C for 1 min, and then programmed to increase 10 °C/min to 300 °C and held at 300°C for 5 min. The scan range of the mass spectrometer was 60–500 m/z. Blanks were regularly interspersed throughout the sample analyses. After removing the compounds found in paper towel and soil (i.e., control sample without feces), we obtained 62 different peaks (i.e., compounds). The relative abundance of compound refers to the relative areas of the selected peaks that were restandardized to 100%. Tentative compound identification was performed based on mass spectral fragmentation patterns and comparison with the NIST mass spectral library using Xcalibur software.

### Statistical analysis

To summarize the data collected during the social attraction test, we performed a principal component analysis (PCA) using the time spent in each compartment (i.e., with or without conspecific scents, excluding the central compartment) and the time spent on

and under each shelter. These data were scaled to unit variance before the analysis. The PC1 axis explained 39% of the variance and had an eigenvalue of 2.32. It was positively correlated to behaviors in the compartment without scent (PC loadings: 0.94 for the total time spent in the compartment without scent and 0.6 for the time spent under the shelter) and negatively correlated to behaviors in the compartment with conspecific scent (PC loadings:  $-0.92$  for the total time spent in the compartment with scent and  $-0.44$  for the time spent under the shelter). To make interpretation easier, we multiplied scores by  $-1$ . Higher scores on the PC1 axis then corresponded to higher attraction to conspecific scent (i.e., higher sociability).

Afterward, we used linear mixed models to assess the effect of maternal, personal, and social information about predation (single effects and interactions between these three factors) on social attraction. We added sex and body size (snout-vent length) as covariates as they can influence sociability (Michelangeli et al. 2016), and mother identity and tank group as random intercepts. Sex and body size did not affect the use of conspecific cues ( $P > 0.11$  for simple effects and interactions with the three sources of information) and were, therefore, removed from the model. We then used likelihood ratio tests to estimate the significance of factors and interactions in the model and provided the summary of parameter estimates and confidence interval (95%). To test the additive effects of information sources about predation risk on social attraction, we ran a linear regression by scoring the number of sources as follows: 0 when there were neither personal nor conspecific cues about risk, 1 when there were either a personal information or conspecific cue about risk, and 2 when there were both personal information or conspecific cue about risk. Compliance with the requirement of the fitted linear model were checked using Shapiro–Wilk normality test on the model residuals assessing social attraction ( $W = 0.988$ ,  $P = 0.29$ ).

We assessed the effect of predation risk on lizard chemical profile. We first analyzed the number of compounds present in each of the 24 chemical profiles (each tank) using a generalized linear model assuming a Poisson error distribution and a log link. We then perform analysis on the occurrences (presence/absence) of chemical compounds that convey threshold information. We identified differences in the occurrence of compounds between treatments using a linear discriminant analysis (LDA) effect size on the 62 initial compounds using the Galaxy platform (<http://huttenhower.sph.harvard.edu/galaxy/>) with a 0.05  $P$ -value threshold and a LDA score  $>2$  (Supplementary Table 1). As a cross-validation, we also ran a similarity percentage analysis on the occurrence of the 62 compounds (Supplementary Table 2) and considered the compounds identified as different in both LDA and similarity

analysis as important. We then summarized the occurrence of the 62 compounds using a LDA and a multiple correspondence analysis (MCA). The two methods are complementary as the LDA summarizes differences in chemical profiles between treatments in a single variable and the MCA summarizes chemical profiles regardless of the treatments. The contribution of each compound to the first axis of an LDA was examined using linear models with LDA axis as a dependent variable and the occurrence of the compound as an explanatory variable (Supplementary Table 3). For the MCA, we kept the first two axes (i.e., MC1 and MC2) as they explained, respectively, 12.62% and 10.80% of the variance and had an eigenvalue of 0.12 and 0.11, respectively. The contribution (in percentage) of each compound to the first two axis of the MCA is in Supplementary Table 4.

We used the occurrences above rather than the relative abundances because a high proportion of relative abundances were equal to 0, which complicated the transformation needed for the PCA and LDA. However, the analysis using relative abundances largely supported the results based on the occurrence data (see Supplementary Material). The LDA analysis using galaxy identified the same compounds (Supplementary Table 5) and the LDA axis on abundances was highly correlated to the LDA axis on occurrences (estimate: 0.99, standard error [SE] = 0.04,  $R^2 = 0.96$ ,  $P < 0.0001$ ). The contribution of each compound to the first axis of an LDA was examined using Spearman rank correlations (Supplementary Table 6). For the PCA, we kept the first two axes (i.e., PC1 and PC2) as they explained, respectively, 13.97% and 11.36% of the variance and had an eigenvalue of 8.66 and 7.04, respectively. The component loadings of the relative abundance of chemical compounds can be found in Supplementary Table 7.

A final post hoc analysis investigated whether the identified differences in chemical profiles between exposed and unexposed donors are responsible for the effect of predation risk on the use of conspecific cues. We compared effects sizes of the predation risk treatment of cue donors (i.e., the social information as reported in Table 1) and of the chemical profiles on social attraction. Similar or higher effect sizes would suggest that the descriptor may convey the social information about predation risk, while lower effect sizes would suggest additional unidentified information carriers. To do so, we ran the same linear model with maternal, personal, and social treatments on lizard sociability (as in Table 1), but replacing the social information treatment by the descriptors of the cues used for the social information assay (Supplementary Table 8). The descriptors were the number of compounds, the two MCA axes, the LDA axis, and the occurrence of compounds that differed between predation and control treatment. We extracted effect sizes (standardized

**Table 1**  
Summary results of LMM model relating the effect of the different sources of information (i.e., maternal, personal, and social) and their interaction on lizard attraction to conspecific cues

Parameters: source of information	Estimates	SE	$X^2_1$	95% CI	$P$ value
Maternal	0.472	0.479	2.001	−0.447, 1.391	0.157
Personal	1.297	0.515	1.795	0.303, 2.286	0.180
Social	0.868	0.463	0.420	−0.022, 1.758	0.517
Maternal × Personal	−0.791	0.702	0.379	−2.128, 0.587	0.538
Maternal × Social	−0.500	0.674	0.947	−1.792, 0.797	0.330
Personal × Social	−2.192	0.708	4.709	−3.544, −0.821	<b>0.030</b>
Maternal × Personal × Social	2.255	1.020	4.886	0.225, 4.214	<b>0.027</b>

Significant effects are highlighted in bold.

beta coefficients) and compared it to the effect for the predation risk treatments of cue donors in interaction with maternal and personal treatments. Note that caution about conclusion should be exercised, as only an experimental manipulation of chemical profiles would permit us to test directly the role of chemical profile. Finally, we performed the same post hoc analysis using the descriptors of compound abundance: the LDA axis of the abundance, the two PCA axis, and the abundance of compounds that differed between predation and control treatment (Supplementary Table 9). We provided *P* values in Supplementary Tables 8 and 9 for information purposes. Only the effects sizes should be interpreted as they are not influenced by the post hoc multiple testing. Analyses were performed in R 3.5.1 ([www.r-project.org](http://www.r-project.org)) using FactoMinR (Lê et al. 2008), ggplot2 (Wickham et al. 2016), lme4 (Bates et al. 2007), sjstats (Lüdtke 2019), MASS (Ripley et al. 2013), and vegan (Oksanen et al. 2007) packages.

## RESULTS

### Effect of sources of information on sociability

Personal and maternal information interacted to shape the use of social information about predation risk (Table 1). We found a significant interaction between personal and social information on lizards' sociability, but only when mothers were not exposed

to predator cues (Table 2; Figure 2a). In this case, lizards with personal information about predation risk were repulsed by the scent of conspecifics exposed to predator cues ( $\chi^2_1 = 50.579$ ,  $P < 0.001$ ), while naïve lizards tended to be attracted by these conspecifics scents ( $\chi^2_1 = 3.147$ ,  $P = 0.076$ ). Maternal exposure to predation risk canceled out this interaction between personal and social information (Table 2): sociability tended to increase with the number of sources of information about risk (estimates = 0.442, SE = 0.237,  $\chi^2_1 = 3.478$ ,  $P = 0.062$ ; Table 2; Figure 2b).

### Effect of predation risk on conspecific scent

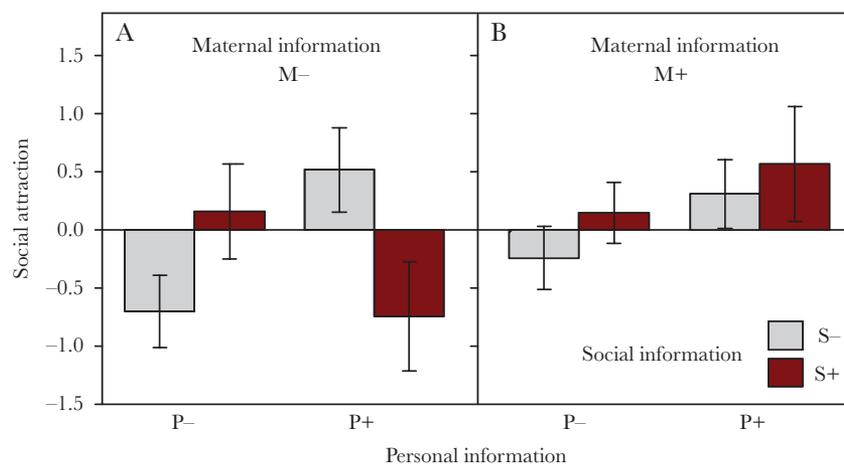
The exposure of individuals to predator cues significantly decreased the number of chemical compounds forming lizard scents ( $\chi^2_1 = 7.394$ ,  $P = 0.007$ , mean  $\pm$  SE, S+: 16.8  $\pm$  1.2 and S-: 12.6  $\pm$  1.1). The LDA effect size analysis showed that two compounds substantially differed between the profiles of exposed and unexposed lizards (Supplementary Table 1), which is also confirmed by the similarity percentage analysis (Supplementary Table 2). Other compounds were also identified from the correlations with the LDA axis (Supplementary Table 3) and the similarity percentage analysis (Supplementary Table 2), but it is likely that they had a weaker role in the chemical differentiation. The predation treatments had a significant effect on the LDA axis ( $F_{1,22} = 106.1$ ,  $P < 0.001$ , mean  $\pm$

**Table 2**

**Summary results of LMM models relating the effect of personal and social information about predation risk on lizard sociability in the presence (M+) and absence (M-) of maternal information about predation**

Maternal information	Parameters: source of information	Estimates	SE	$\chi^2_1$	95% CI	<i>P</i> value
M-	Personal	1.217	0.546	0.222	0.164, 2.269	0.637
	Social	0.859	0.515	0.025	-0.138, 1.853	0.875
	Personal $\times$ Social	-2.121	0.782	7.357	-3.630, -0.613	<b>0.007</b>
M+	Personal	0.528	0.463	2.383	-0.367, 1.428	0.123
	Social	0.365	0.445	1.269	-0.491, 1.251	0.260
	Personal $\times$ Social	-0.000	0.657	0.000	-1.389, 1.308	0.999

Significant effects are highlighted in bold.



**Figure 2**

Interactive effect of multiple sources of information about predation risk on lizard social attraction. The variation of social attraction (mean  $\pm$  SE) according to the interaction between personal and social information depended on the maternal information about predation: (a) in the absence of maternal information about predation risk (M-), there is a significant interaction between personal information (P- vs. P+) and social information (S-, light gray bars; S+, dark red bars); (b) in the presence of maternal information about predation risk (M+), there is a slight increase of sociability when the number of sources of information about the actual risk of predation increased. See Results for statistics.

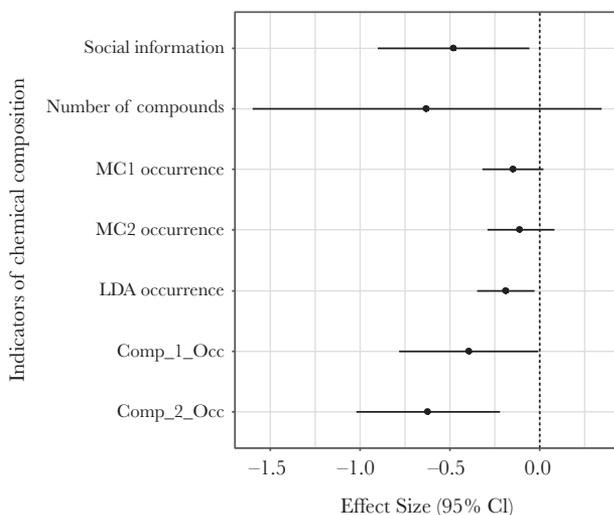
SE,  $P+$ :  $-1.251 \pm 0.857$  and  $P-$ :  $1.751 \pm 0.386$ ) but had no effects on the two MCA axes (MC1:  $F_{1,22} = 1.276$ ,  $P = 0.271$  and MC2:  $F_{1,22} = 0.902$ ,  $P = 0.353$ ). The tentative identification of chemical compounds indicated that the two main compounds, Compound\_1 (i.e., X154) and Compound\_2 (i.e., X167), may be respectively a derivative of naphthalenol and an unsaturated alcohol.

We then investigated whether the descriptors of donors' cues could explain the effect of predation risk of conspecific donors by comparing effect sizes. The effect size of the interaction between personal, maternal, and social information is similar to the effect size of the interaction using the LDA first axis and more particularly using the occurrence of Compound\_1 and Compound\_2 instead of the social information treatment (Supplementary Table 8; Figure 3).

Overall, the various analyses of the relative abundance of the chemical compounds showed very similar results to the analysis based on their occurrence. Indeed the LDA effect size analysis highlighted the same two compounds (Supplementary Tables 5 and 6). The post hoc analyses comparing effect sizes showed that the effect size of the interaction between personal, maternal, and social information is similar or slightly lower than the effect size of the interaction using the PC2 and the abundance of Comp\_1 and Comp\_2 instead of the social information treatment (Supplementary Table 9, Supplementary figure 1).

## DISCUSSION

We assessed how personally and maternally acquired information altered lizards' responses to conspecific cues. We found that personal and maternal information interacted to shape lizard responses to conspecific cues about predation risk. The scent of conspecifics exposed to predation risk attracted more focal lizards when they had no personal information about the risk, while it repulsed them when they also had personal knowledge about the risk.



**Figure 3** Interactive effects of the occurrence of chemical composition on lizard sociability. Comparison of effect size (95% CI) of the triple interaction between maternal information, personal information, and social information (S- vs. S+) and the triple interaction between maternal information, personal information, and the different indicators of chemical composition on lizard sociability. The indicators of chemical composition are the number of compounds, the two axes of the MCA on the occurrence (i.e., MC1 and MC2), the LDA first axis of the occurrence, and the occurrence of two compounds: Comp\_1\_Occ and Comp\_2\_Occ.

Furthermore, we found that maternal information about predation risk canceled out this interactive effect between personal and social information, with individuals tending to be more social when sources of information about risk added up.

Prey are known to assess the risk of predation when making decisions about how to behave (Lima 2002). Decision-making often results in a trade-off between risk and other rewarding activities (e.g., foraging and mating; Kats and Dill 1998). An accurate risk assessment requires reliable information about predation at a given time and location. Such information can be acquired via multimodal sensory cues, including sight, tactile, and chemical signals made by conspecifics. In our study, we manipulated the exposure to predation risk using scents of a snake predator because it is known to elicit antipredator behavior in common lizards through maternal and personal exposure, even 1 month after exposure (Bestion et al. 2014; Teyssier et al. 2014). Such permanent strong defense behavior without any actual encounter with predators can be explained by the low encounter rate between lizards and snakes in the wild because of the dense vegetation and the comparatively lower density of predators. It can further be explained by the high probability that a snake is successful in catching a lizard when an actual attack occurs. We further showed that common lizards can use olfactory cues from conspecifics to assess predation risk, while it was already known that they can perceive different donors' characteristics through scents (i.e., relatedness; Léna et al. 1998; past experiences of competition; Aragón et al. 2006; Aragón et al. 2006). Chemical cues released by a conspecific may signal individual stress levels (Douglas III et al. 2018), body condition (Martín and Lopez 2010), or health status (Martín et al. 2007), and lizard species are particularly prone to use such signals to assess mating partners or competitors (reviewed in Mason and Parker 2010). Predation risk usually requires chemicals from injured conspecifics (i.e., alarm cues) to elicit behavioral defense in other conspecifics (Crane and Ferrari 2013). However, prey can also release a chemical signal when detecting a predator (i.e., disturbance cues; Chivers and Smith 1998; Griffin 2004) or have a modified scent after experiencing predation risk as found in another lacertid lizard species (Aragón et al. 2008).

Individuals may rely on cues intentionally or inadvertently produced by conspecifics (defined as social information: Danchin et al. 2004; Dall et al. 2005; Blanchet et al. 2010) to cope with limited personal information about challenging environmental conditions. In the context of predation risk, acquiring social cues may be less costly and, therefore, more adaptive than acquiring the information personally through a direct encounter with a predator (Blanchet et al. 2010). Moreover, no personal information about predation risk can be unreliable because predators circulate in the environments, and their actual presence can be highly variable in space and time. A prey may then overestimate the degree of risk (Johnson et al. 2013), and a response to predator cues could be observed even if they came from only a single source (Nesse 2005; Blanchet et al. 2010). However, when an individual eventually encounters a predator, social cues may become less relevant and additional cues about risk may even signal an acute increase in predation risk. In the absence of maternal cues, we found that social and personal information about risk increase the attraction toward conspecific scents when these information sources are uncoupled, supposedly because grouping may decrease predation risk (Lima and Dill 1990; Krause et al. 2002). Indeed, an increase in sociability is a common antipredator strategy in lizard that allows for collective vigilance (i.e., increased detection of predators; Downes and

Hoefer 2004; Lanham and Bull 2004) and a risk-dilution effect (i.e., a lower probability for a single individual to be captured; Ioannou 2017). However, in the absence of maternal cues, lizard personally informed about predators avoided the scents of social partners that were also exposed to predator scents. The accumulation of information sources about predator presence, through personal and social information, may indicate a temporally or spatially acute risk of predation. Lizards may, therefore, avoid the scent of predator-exposed conspecifics because it signals immediate danger, while the scent of unexposed conspecifics is attractive because it might signal safe conditions. The safest strategy could then be to avoid a particular social partner who has recently encountered a predator.

Transgenerational information can strongly influence prior expectations about individuals' risk and, in turn, the use of social information. We found that the exposure of mothers to predation risk during gestation canceled out the observed interaction between personal and social information and was replaced by a weak but significant additive effect of information sources affecting lizard social responses. The attraction toward conspecific scents increased gradually with the number of sources of information about predation risk from lizards with only maternal information to lizards personally, socially, and maternally informed. Additional cues might increase an individual's confidence in the state of the environment, causing a multiplicative effect on their sociality. A higher level of sociability could indeed be an efficient antipredator strategy in a risky environment. While additivity is less expected in discrete traits, such as a defensive morphology (McCollum and Van Buskirk 1996; Buoro et al. 2012), it is more likely to occur in gradual behavioral traits. Maternal information signals environmental conditions on a larger temporal scale than does personal information. When maternal and offspring information matches, it signals a persistent risk across generations (Sheriff et al. 2017), which can explain the additive effect of information sources. The environmental/maternal-matching hypothesis states that maternal stress can be adaptive if the maternal and offspring environmental conditions match (Sheriff et al. 2017). In our study, when personal and maternal information about risk matched (P+M+), social information was less valuable. Indeed, individuals showed high attraction to conspecific cues whether or not this conspecific was exposed to predation risk as, in a persistent risk of predation, being more sociable could be beneficial. On the contrary, social information had stronger effect when there was no personal and maternal information about risk (P-M-). In this case, individuals were only attracted by social cues of conspecifics that had been exposed to predation risk, which mirrors cases where acquiring personal information is costly (Webster and Laland 2008). If social cues were misleading, it would only result in reduced foraging or mating opportunities, while not responding to a relevant danger cue could result in higher mortality risk by predation. Prey might thus benefit from erring on the side of caution (Johnson et al. 2013).

Finally, we also attempted an assessment of the molecular mechanisms responsible for social information by collecting feces samples from groups of lizards exposed and unexposed to predation risk to identify potential changes in their chemical scent profiles. In our study, predators never injured lizards as we never exposed lizards to actual predators, so there were no compounds released upon injury (i.e., damage-release chemical alarm signals; Chivers et al. 1996). Despite no physical encounter with predators, as in natural populations, the exposure to predator cues changed the chemical composition of lizard scents collected from feces. We found fewer chemical compounds in the scent of lizards exposed

to predation risk compared to unexposed lizards. Our conservative analysis revealed that two compounds were differently expressed between treatments. The tentative identification of the chemical compounds matches expectations since Lacertid lizards usually have alcohols in their secretions, and alcohols can be detected by conspecifics (Martín and López 2014). This modification of scent profile may have provided chemical cues for risks and triggered the observed behavioral response to conspecific scents. We also ran post hoc analyses replacing the predation risk treatment of donors' scents by a few descriptors summarizing chemical profiles and compared effect sizes. We expected similar or larger effect sizes if chemical profiles were indeed the mechanisms behind social responses to conspecific scents, and this is what we observed for the two compounds differently expressed between treatments. However, caution should be exercised in interpreting this preliminary investigation of chemical profiles and their influences. In-depth chemical analysis and manipulative experiments are required to provide a more precise identification of chemical cues and to ascertain their influences on lizard's behavior.

## CONCLUSION

Prey generally have incomplete information about their environment and have to rely on other source of information to assess the risk of predation. In our study, the scents of conspecifics exposed to predation risk acted as social information shaping behavioral responses. However, when personal and social information conflicted, which is mostly the rule in stochastic environments, decision-making can be hampered. Transgenerational information seemed to alleviate the uncertainty about risk when personal and social information mismatched. Transgenerational cues can provide information on a larger temporal scale and influence the prior expectations of individuals about their environment. Moreover, ancestors' experience is the first possible source of information an individual can get and, therefore, may have large effects on phenotypic outcomes (Dufty Jr et al. 2002; Fawcett and Frankenhuis 2015; English et al. 2016; Donelan and Trussell 2018a). Maternal exposures to predation cues may adaptively prepare the phenotype of offspring for more stressful environmental conditions (Uller 2008; Sheriff and Love 2013; Sheriff et al. 2017) but also induce changes in the developmental trajectory of offspring, leading to direct or delayed effects on individuals from the embryonic stage to adulthood (Love and Williams 2008; Nettle and Bateson 2015). Here, we found that maternal stress affected how offspring used the cues from conspecifics later in life. While our study raises interesting perspectives on how animals integrate information from a wide variety of sources to make decisions, we believe additional studies on this and other taxa are required to replicate our results and test the generality of our conclusions. Understanding the complex mechanisms involved in the integration of multiple information sources within and among several generation deserves further attention (Sheriff et al. 2017).

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

**Supplementary Table 1** Linear discriminant analysis on the occurrence of chemical compounds in samples from lizards exposed (P+) and unexposed to predation (P-) using the LefSe platform (<http://huttenhower.sph.harvard.edu/galaxy/>). These compounds were selected using linear discriminant scores (LDA > 2.0) and Mann-Whitney test ( $p_{MW} = p\text{-value}$ ,  $p < 0.05$ ).

**Supplementary Table 2** Similarity percentage analysis on the occurrence of chemical compounds in samples from lizards exposed (P+) and unexposed to predation (P-). The contribution of the compound to between-treatments dissimilarity and its standard deviation (SD) are provided. P-values are obtained from a permutation test with 1000 permutations. The compounds with a contribution larger than 0.01 are shown.

**Supplementary Table 3** The part of each compound on the LDA axis was analyzed with a linear model with LDA axis as a dependent variable and the occurrence of the compounds as an explanatory variable. Significant ones are highlighted in bold.

**Supplementary Table 4** Contributions (in %) of the chemical compound to the first two axis of the MCA (MC1 and MC2).

**Supplementary Table 5** Linear discriminant analysis on the abundance of chemical compounds in samples from lizards exposed (P+) and unexposed to predation (P-) using the LEfSe platform (<http://huttenhower.sph.harvard.edu/galaxy/>). These compounds were selected using linear discriminant scores (LDA > 2.0) and Mann-Whitney test ( $p_{MW} = p\text{-value}$ ,  $p < 0.05$ ).

**Supplementary Table 6** Spearman coefficient and p-value for the correlations between the first axis of the LDA and the abundance of each compound. Significant ones are highlighted in bold.

**Supplementary Table 7** Component loadings of the relative abundance of chemical compound observed from principal components analyses: Correlations between the 62 different compounds identified in the samples compound and the first two axis of the PCA (PC1 and PC2).

**Supplementary table 8** Effect of the indicators of chemical composition on lizard sociability: the number of compounds, the two axis of the MCA on the abundance (*i.e.*, MC1 and MC2) and the LDA first axis of the occurrence. We analyzed the triple interaction with maternal and personal information to extract effects sizes and compare it to the effect size of the treatment. Significance is only reported for information and should not be used to compare the strength of effects.

**Supplementary table 9** Effect of the indicators of chemical composition on lizard sociability: the number of compounds, the two axis of the PCA on the abundance (*i.e.*, PC1 and PC2) and the LDA first axis of the abundance. We analyzed the triple interaction with maternal and personal information to extract effects sizes and compare it to the effect size of the treatment. Significance is only reported for information and should not be used to compare the strength of effects.

### Supplementary Figure 1 Interactive effects of the abundance of chemical composition on lizard sociability

Comparison of effect size (95% CI) of the triple interaction between maternal information, personal information and social information (S- versus S+) and the triple interaction between maternal information, personal information and the different indicators of chemical composition on lizard sociability. The indicators of chemical composition are the number of compounds, the two axis of the PCA on the abundance (*i.e.*, PC1 and PC2), the LDA first axis of the abundance and the abundance of two compounds: Comp\_1\_Ab and Comp\_2\_Ab.

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