

Original Article

Partners' personality types and mate preferences: predation risk matters

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Mate choice is known as an important behavior allowing females to choose the best mate to increase their reproductive success. To estimate male quality, females can use multiple traits. Among those, recent studies have shown that male personality traits could play an important role in mate choice as they are often linked to major life-history traits and can be heritable. However, because the relationships between life-history traits and personality traits are context dependent, females are expected to choose male personality types according to the mating context. In this study on common lizards (*Zootoca vivipara*), we examined the role of personality traits in female mate choice and mating behavior after experimentally manipulating the predation risk experienced by females prior to mating. We showed that females not exposed to predator cues preferred males with high-activity level, a heritable behavior. When females are exposed to predator cues prior to mating, this preference was reversed. High-activity levels generally increase competitive abilities and survival but could be detrimental when predators are present. Our results suggest that female common lizards choose males based on their personality types and can modify their preferences according to their environmental context in order to produce offspring that are better adapted to their environment.

Key words: common lizards, mate choice, pace-of-life syndrome, predation.

INTRODUCTION

Mate choice is an important sexual behavior, which allows females to increase their reproductive success (Andersson and Simmons 2006). Because they produce fewer and more costly gametes than males, females must be selective when choosing their mating partner (Andersson and Simmons 2006). Through mate choice, females can gain direct and/or indirect benefits. Females can gain direct benefits by choosing better foragers for instance or males providing higher parental care (Møller and Jennions 2001). They may also gain indirect benefits by choosing males based on traits related to genetic quality, thus improving the survival or the attractiveness of offspring (Zahavi 1997). Among male traits, it has been recently advocated that personality traits are important in mate choice and mating behavior (Godin and Dugatkin 1996; Schuett et al. 2010; David and Cézilly 2011; Schuett, Godin, et al. 2011). Personality traits refer to behavioral differences between individuals (boldness, exploration, activity, aggressiveness, and sociability), consistent over

time and/or across situations (Sih et al. 2004; Reale et al. 2010). Personality traits are linked to various life-history traits (Wolf et al. 2007; Boon et al. 2008; Smith and Blumstein 2008; Cote et al. 2010, 2013) and physiological traits (Koolhaas et al. 1999; Careau et al. 2008). It has been recently hypothesized that these correlated traits create pace-of-life syndromes (Reale et al. 2010) varying from slow (shy, low-activity level, low aggressiveness, high sociability, low growth rate, delayed reproduction, and long life) to fast individuals (bold, high-activity level, high aggressiveness, low sociability, fast growth rate, precocious reproduction, and short life). This pace-of-life syndrome is potentially issued from genetic correlations among traits (Reale et al. 2010) and thus the personalities of parents may shape offspring life history and success in natal environments. During mate choice, females could, therefore, use male personality types to acquire information on male life-history strategies and choose suitable mates (Schuett et al. 2010). Although a few studies have shown personality-dependent mate choice (Schuett et al. 2010), it remains unclear whether preferences for male personality types should vary among females of a species or not. On one hand, females can all have the same preference if a given male personality type increases reproductive success similarly for all females

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(e.g., bold males bringing more resources to females). On the other hand, females can differ in their preferences for male personality types because of behavioral or genetic compatibilities (Schuett et al. 2010). The latter case can lead to assortative or disassortative mate choice according to personality types. Disassortative mating can be explained by a higher fitness for offspring of intermediate types (Dingemans et al. 2004), whereas assortative mating can be explained by an increased behavioral coordination between partners for instance (Royle et al. 2010; Schuett et al. 2010). This idea is supported by a number of studies, which have demonstrated a better reproductive success for pairs with similar behavioral profiles (Both et al. 2005; Sinn et al. 2006; Schuett, Dall, et al. 2011; Ariyomo and Watt 2013). Moreover, female personality type can also change their ability to assess male behavioral traits and therefore their selectivity (David and Cézilly 2011).

Last, one rarely addressed possibility is that personality-dependent mating patterns may vary according to ecological contexts (Schuett et al. 2010). Mate choice has been shown to vary over time and across contexts and is one of the least repeatable behaviors (Bell et al. 2009). One context known to affect mating success and female mate choice is predation risk (Jennions and Petrie 1997; Koga et al. 1998). For instance, females may favor conspicuous males in a safe environment and inconspicuous males when predation risk is high because conspicuous males may be more subject to predation (Pocklington and Dill 1995; Gong and Gibson 1996; Johnson and Basolo 2003; Pilakouta and Alonzo 2013). On the other hand, one could expect females to choose more conspicuous males when predation risk is high if only high-quality males are able to invest into highly conspicuous behavior. Similar effects could be expected for personality-dependent mating behavior. Specific personalities, with a long-term consistency, could benefit offspring in some environments and turn into a cost in other environments. For example, it could be costly for females to produce bold offspring in a risky environment (e.g., lower survival rate), whereas it would be advantageous in a safer environment (e.g., increased foraging rate, Stamps 2007; Smith and Blumstein 2008). However, studies examining the links between personality and life-history traits in multiple contexts are scarce, and no study, to our knowledge, has examined how personality-dependent mate choice varies with ecological contexts.

Here, we studied the role of male and female personality traits in mating behavior in common lizards by manipulating predation risk prior to mating. In this species, consistent interindividual differences have been observed in sociability, exploration, boldness, and general activity and are likely involved in a pace-of-life syndrome (Cote and Clobert 2007; Cote, Dreiss, et al. 2008; Le Galliard et al. 2013). Females are mostly polyandrous and, although forced copulations by males do occur, females display preferences according to male size and heterozygosity level (Fitze et al. 2005, 2010; Richard et al. 2005; Laloï et al. 2011). Because males provide neither parental care nor nuptial gifts, and their sperm have low nutrient content (Depeiges et al. 1987), female mate choice is likely to be driven only by indirect benefits linked to male phenotype and ecological contexts. Moreover, in common lizards as in other lizard species, predation risk can have strong effects on behavior such as activity and basking behavior (Thoen et al. 1986; van Damme et al. 1995; Punzo 2007). We first measured exploration, sociability, and activity profiles in females and males, before mating assays and checked the relationship between these profiles, body size, body mass, and ventral coloration, traits potentially involved in mate choice in reptiles (Fitze et al. 2010; Olsson et al. 2013). Thereafter, we housed females with or without predator cues from a saurophagous snake

before testing their mate preferences in a sequential design in order to avoid male–male competition. Furthermore, our experimental design and our analyses allowed us to focus only on female mate preferences, excluding male preferences and forced copulations (see below). We predicted that females not exposed to predation risk prior to mating would prefer exploratory and more-active males because these traits can increase offspring fitness (Le Galliard et al. 2013). We also expected this preference to be reversed or cancelled after an exposure to predator cues because it might be costly for offspring to be exploratory and more active in risky environments. We further expected females exposed to predation risk prior to mating to prefer more social males because social grouping is a widespread antipredator strategy (Krause and Ruxton 2002). After mate choice assays, females were maintained in outdoor tanks for their gestation. At birth, offspring behavior was examined and we assigned paternity with a genetic sample. It allowed us to test whether behavioral profiles are heritable and therefore whether female mate choice for behavioral types can translate into differences in offspring behavioral type. After mate choice assays, males were also maintained in outdoor tanks with or without cues in order to test for behavioral modifications under predation risk.

MATERIALS AND METHODS

Species

The common lizard (*Zootoca vivipara*; Jacquin 1787) is a small lacertid (adult snout–vent length: males, 40–60 mm; females, 45–75 mm) generally found in humid habitats throughout Eurasia. Lizards become active in late March–early April and start hibernation in late September–early October. Males emerge from hibernation approximately 2 weeks earlier than females and the mating period occurs soon after female emergence. In this species, females can mate with one or several partners (Fitze et al. 2005). During mating attempts, the male grips the female on the posterior abdomen with its mouth and then tries to twist its body around female's body in order to introduce its hemipenis into the female's cloaca. As a result of the male's grip, the female's belly shows a U-shaped scars after mating (Bauwens and Verheyen 1985). Female can refuse to mate with males by escaping prior to gripping, or by struggling and biting, after the gripping has been initiated (Fitze et al. 2005, 2010; Laloï et al. 2011).

Study site and housing conditions

The experiment was conducted at the Station of Experimental Ecology in Moulis (Ariège, France). The lizards were captured in late June 2011 from natural populations of the Cévennes. They were subsequently marked by toe clipping and released into semi-natural enclosures (100 m²), in our experimental system—the Metatron (Legrand et al. 2012), with natural lizard habitat (dense vegetation, hides, and rocks). Each enclosure is delimited by tarpaulins buried 30 cm into the ground, preventing escape and preventing avian and terrestrial predation (Legrand et al. 2012). Fifty males and 60 females were released in 2 separate enclosures, females and males being kept separated in order to keep females unmated until the following year. In mid-March 2012, just after emergence, the surviving individuals were caught, 22 males first, then 44 females 3 weeks later. All males and females were weighed and measured for their body size and ventral coloration. The ventral coloration of males ranges from yellow to red with dark spots, whereas female ventral coloration ranges from cream to orange. As

in previous studies (Cote, Le Galliard, et al. 2008; Fitze et al. 2009), the lizard's belly coloration was measured, over the visual spectrum (300–700 nm), using a miniature spectroradiometer and we derived estimates of hue, chroma, and brightness. We measured the coloration on 2 body parts (thorax and belly) and averaged the 2 values for each color parameters. Lizards were then housed in individual terraria containing 3 cm of soil, a shelter (a piece of eggs carton), a water dish, and a piece of absorbent paper to collect odors for sociability assays. In one corner of the terrarium, ultraviolet and incandescent 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 1 cricket (*Acheta domestica*).

Measuring personality traits

First, we measured 3 personality traits (sociability, exploration, and activity) on males and females before mating assays. Personality assays were done after maintaining lizards 1 week indoors. All assays were done in glass terraria (25 × 15.5 × 15 cm). Twenty-four individuals were tested each day. Exploratory behavior was tested in the morning and social tendency in the afternoon in the same terrarium. Activity was measured during these 2 assays (see below). Data were collected using “The Observer” software, which allows to measure the duration of different behaviors.

For the exploration assay, we offered lizards the opportunity to enter a novel environment with a resource after acclimatizing them to a “home compartment” (Réale et al. 2007). Here, the resource was the heat provided by a bulb. A polyvinyl chloride (PVC) opaque wall divided the terrarium into a small and a large compartment (1/3:2/3) with a shelter in each compartment, as far as possible from each other. The day before the assay, each individual was placed into the small compartment to acclimatize for at least 12 h (17:00–09:00) with a bulb providing 30 min of heat the morning before the assay started. 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 compartment (novel environment). Turning off the light in the home compartment allowed us to decrease interindividual variation in the motivation to bask. After 15 min, we removed the separation between compartments and measured for 10 min the latency to enter the novel compartment; the time spent in this compartment, and the time spent walking in each compartment. We used these variables to estimate exploratory tendency with a principal component analysis (PCA, see below). At the end of the assay, we divided terraria in 3 compartments with PVC walls and put individuals in the middle compartment. We provided a heat source above this compartment until the sociability assay.

We measured individual social tendency with the reaction to conspecific odor (Cote and Clobert 2007) using a choice assay between a shelter with the odor of conspecifics and a shelter without odor. We used odors of 2 individuals of the same sex as the focal individual to avoid reactions due to intersexual interactions and reactions to a specific individual. We used 8 pairs of odors that we randomly assigned to focal individuals. The paper with mixed odor was put under a shelter at one end of the experimental terrarium (divided in 3 compartments) and a piece of paper without odor was put in the shelter at the other end of the terrarium. The odor-free paper was collected from vacant terraria maintained under the same conditions than inhabited terraria. We started the assay by removing the walls separating compartments and let individuals to familiarize with shelters for 10 min. Then, we observed for 10 min the time spent in each compartment and the time spent under each

shelter to estimate social tendency with a PCA. A measure of general activity was also estimated from the time spent walking during the 2 previous assays with a PCA (see below).

Fourteen days after the first personality assays and 3 days after the last mating assay (see below), we performed personality assays again to estimate behavioral repeatability.

Predation risk treatment prior to mating

For the predation risk treatment, we alternatively collected the odor from 2 green whip snakes (*Hierophis viridiflavus*)—one captured and maintained in our laboratory in a room separated from the lizards' room (License 2012-10 DREAL) and the second snake, from a reptile zoo (<http://www.lafermedesreptiles.fr/>). Green whip snakes are generalist feeders, preying on small mammals, reptiles, and birds. Green whip snake neonates forage mainly on lizards, and although adult individuals feed mostly on rodents, reptiles account for nearly 20% of their diet (Lelievre et al. 2012). Green whip snakes occur in sympatry with common lizards in their southern distribution; however, they are allopatric to this particular population of the Cévennes mountains. Although allopatry could be viewed as a problem, previous studies on common lizards showed that lizards reacted to both the presence of sympatric and allopatric predator olfactory cues and showed little response to the nonpredator snake and civet control odor cues (Thoen et al. 1986). We choose the green whip snake because it was a common species around our station and because the absence in the Cévennes allowed us to control for lizards' previous encounter with this predator.

Snakes were maintained with little calcite slabs to collect snake odor. The experimenter collected slabs using gloves and rubbing the belly of snakes. Other slabs, kept in another room, were collected as control. After each assay, all slabs were cleaned with 70% ethanol, rinsed, and put back with snakes or in a control box.

After personality assays, we randomly divided the 44 females in 2 groups with different housing conditions: a control group without predator cues and an experimental group with predator cues. Females from the 2 groups were not significantly different in body size ($F_{1,42} = 0.002$, $P > 0.95$) and personality traits ($P > 0.30$ for all personality traits). We simulated predation risk by putting slabs with or without predator odor in females' terraria. Slabs were changed every 2 days. Females were maintained with slabs 4.6 ± 1.2 days before mating assays. Males were not exposed to predator odor and kept in another room. We simulated predation risk prior and not during mating assays to 1) test for mate choice integrating predation risk in the environment rather than for reaction to the presence of predators while mating and 2) prevent changes in males' behavior due to predation risk during mating.

Mate choice assays

We used enclosures containing mixed-sexed populations in the Metatron to check for cues of the beginning of mating period (mating scars on females and spring molting of males; Bauwens et al. 1989) in order to know when mating assays should start. Mating assays started 28 March 2012 and lasted for 12 days. Over 2 days, we presented to each female 2 different males, sequentially to avoid male–male competition. Males can fertilize up to 14 females and females give birth to offspring that may be fathered by up to 5 different males (Laloi et al. 2004; Fitze et al. 2005). We mated each female with 2 males to avoid rejection of males by females because of too many partners. In this species, males are on average smaller than females and males can force copulation if they are larger

than females. To minimize forced copulations, larger males were presented to larger females. Females were on average 7.2 ± 3.3 mm larger than males. There was no significant size difference between the 2 potential partners of a female ($t = -0.63$, $P = 0.53$), and male size did not change with mating order ($F_{1,82} = 0.26$, $P = 0.61$). Except for body size, we randomly chose males. We checked that male behavioral scores did not change with mating order (exploration: $F_{1,82} = 0.01$, $P = 0.91$; sociability: $F_{1,82} = 0.03$, $P = 0.85$; activity: $F_{1,82} = 0.14$, $P = 0.70$). Each of the 22 males performed 4 ± 1 standard deviation mating assays, which is much lower than the average number of mating in natural populations, and mating assays for the same male were always separated by 1 day. Males also did not differ in size ($F_{1,82} = 0.17$, $P = 0.68$), the number of previous mating assays ($F_{1,82} = 0.58$, $P = 0.45$), and their behavioral scores ($P > 0.18$) between the 2 predation risk treatments.

Mating assays were done in large terraria ($80 \times 30 \times 40$ cm) containing soil and lighted with a bulb (40 W) and an ultraviolet lamp. Terraria were divided by a 1-way glass in 2 compartments: a small (20×30 cm) and a large compartment (60×30 cm). Each mating assay was recorded by a video camera. Before the assay started, each female was placed in the small compartment for an acclimatization phase. After 10 min, a male was placed in the large compartment; the 2 compartments still being separated. Thanks to the 1-way glass, females could watch the male's activity without influencing its behavior. After 20 min, the glass was removed, allowing partners to mate. If no mating attempt occurred, the assays were stopped after 1 h. Otherwise, we waited for the end of mating. Individuals were then put back in their housing terraria. The next day, we presented another male to the females.

We recorded several mating parameters. First, from the videos and mating scars, we checked whether females accepted to mate or not and if they tried to resist males attempt to copulate (i.e., trying to escape or to bite the male). For mated females, we also measured 2 other parameters of female willingness to mate: 1) the latency between the male biting behavior and the actual mating (insertion of the hemipenis in the female cloacae), thereafter named "mating latency." This latency is negatively related to the probability of the male fathering an offspring (estimate [\pm standard error {SE}]: -0.45 ± 0.23 , $\chi^2 = 64.45$, $P < 0.001$, unpublished data); 2) the duration of mating, the time between the hemipenis insertion and the separation of partners, which is highly variable and positively related to the probability of the male fathering an offspring (estimate [\pm SE]: 0.02 ± 0.006 , $\chi^2 = 42.85$, $P < 0.001$, unpublished data).

Heritability

Females and males were maintained in the lab until the end of mating assays. On April 25th, we moved them in 1000-L cattle tanks, separating sexes; females were maintained in 4 tanks and males in 2 tanks (11 per tank) for another experiment (Bestion, Teyssier, Aubret, Clobert and Cote, in preparation). We collected a tail tip (genetic sample) from each male and female before moving them. Tanks contained 20 cm of soil litter, eleven 50-mL Falcon tube in the litter, 3 halved flower pots used as refuges, sod, and 2 small dishes for water. Each week we added 100 crickets and water in the dishes. These conditions were highly suitable for lizards. For the other experiment, the conditions during gestation were manipulated in 2 female tanks and 2 female tanks were kept as a control. Therefore, we only quantified the heritability on juveniles from females maintained in tanks where the conditions during gestation were not manipulated (control tanks, $n = 12$ females, 7 from

predation risk treatment and 5 from no predation risk treatment prior mating). Just before parturition, on May 26th, we caught all females and brought them to the lab. We kept them as described earlier. At birth, we collected the tail tip from the 59 juveniles born in the control tanks in order to assign paternity and, 2 days after birth, juveniles performed an activity assay as described earlier. We focused on activity levels because our results showed that females' mate preference (i.e., mating probability and mating latency) was based on male activity profile (see Results). Genomic DNA of females, males, and juveniles was extracted from tail tips using the QIAquick 96 Purification Kit (QIAGEN) according to the manufacturer's instructions after a digestion of tissue samples with proteinase K. Individuals were genotyped using 8 microsatellite markers routinely used (White et al. 2011; Richard et al. 2012). We checked for perfect match between juveniles and their mother and assessed paternities (no mismatch between male and juvenile) using CERVUS software, v.3.0 (Kalinowski et al. 2007). We could then assign each offspring to each male and also estimate the heritability of activity profiles. The paternity could not be assessed for offspring from 1 female. Only a subset of males fathered offspring. The 59 juveniles were fathered by 9 males.

Males' behavioral reaction to green whip snake cues

Finally, we verified whether cues from this snake species reduced lizard activity and basking levels, which are classical antipredator responses to various predatory snakes (Thoen et al. 1986; van Damme et al. 1990, 1995). After the mating sessions, we kept the 22 males in 2 cattle tanks (see above) of 2 treatments: with or without cues from green whip snakes (11 in each treatment). We collected predator cues (as described above) using 10 slabs per cattle tank. We kept males with or without predator cues for 1 month, until May 26th, changing slabs every 3 days. For each male, activity level was measured before and after this period. We measured activity level in glass terraria ($25 \times 15.5 \times 15$ cm) with a shelter and a bulb above the shelter. After 10 min of acclimation in a terrarium, we measured the time spent walking within 10 min.

Statistical analyses

Personality traits

To summarize the data collected during the behavioral assays (before and after mating assays separately), we performed PCA for each personality trait studied (exploration, sociability, and activity) with JMP v.7 software. The PCA for exploratory tendency included the latency to enter in the novel environment, the time spent in this compartment, and the time spent walking in the novel environment and in the home compartment. We added the time spent walking in home compartment to find the axis illustrating exploration and not activity (low component loading for the time spent walking in the home compartment relative to other components). For the social tendency, we performed a PCA using the time spent in each compartment with and without conspecific odor (excluding neutral compartment) and also the time spent under each shelter. The PCA for general activity included the time spent active in the 2 personality assays (exploration and sociability). The selected axes had an eigenvalue greater than 1 (Jackson 1993).

The behavioral consistency over time (before and after mating assays) was assessed by intraclass correlation coefficients (Nakagawa and Schielzeth 2010) computed with 1-way repeated Anovas with individual identity as a fixed factor. We obtained the repeatability

of traits' expression of individuals across time (within-individual variance) relative to the change of the study population. We did not control for the differences in mean behavioral scores between the first and second sessions of behavioral assays (i.e., adjusted repeatability). However, we performed PCAs for each session separately and therefore there was no difference in mean scores.

We also analyzed the relationship between our 3 behavioral scores (exploration, sociability, and activity) and body size and ventral coloration before mating assays. We performed linear models for each behavioral score on females and males separately. Fixed factors were body size, hue, chroma, and brightness (package `lme4`, R software; Bates et al. 2011; R Core Team 2013). The significance of each effect was assessed using *F*-ratio tests.

Female mating preference

We performed mixed models with repeated measures (2 mating assays per female) for the probability of mating, mating latency, and mating duration (package `lme4`, R software; Bates et al. 2011; R Core Team 2013). Fixed factors were the first PCA axis for activity and the first PCA axis for sociability for males and females, the predation risk treatment, and 2-way interactions between partners' behavioral profiles and between predation risk treatment and behavioral profiles. We did not include the exploratory score because this trait was not repeatable (see Results) and because models would have been overparameterized. We added male identity as a random intercept and females identity as a random intercept nested within predation risk treatments. Even if previous studies showed that mate choice behavior can vary with mating order (Fitze et al. 2010), we analyzed together the 2 mating assays per female because our sample size and the probability to reject males per mating assay were low. However, there was no difference in mating probability, latency, or duration between mating assays, and we checked that the effects were similar for the 2 assays. We excluded mating trials during which males showed no sexual interest in females ($n = 10$ on 84 assays) because it would have been confounded with female acceptance. However, we kept them in Figure 2 to better illustrate the effect of female choice. We analyzed the probability to mate with a male using a generalized mixed model with a binomial distribution and a logit link. However, as the model did not converge, we performed a model without female identity after checking there was no effect of female identity on mating probability. Furthermore, we analyzed the mating probability for each mating assay separately. We found similar patterns in the 2 mating assays and we therefore believe our results did not arise from pseudoreplication. Although we reduced forced copulations by matching partners according to size, some males might still have forced some females to mate. Therefore, we ran the previous analysis a second time after removing the females that actively but unsuccessfully resisted male copulation attempts (by biting back or trying to escape) (Fitze et al. 2010). This is a highly conservative method because females often resist males for a short while even when they accept to mate afterward.

We log transformed the mating latency to obtain a normal distribution. This variable and the mating duration were analyzed with general linear mixed model after checking that residuals met the assumptions (normality and homogeneity of variances). One mating duration (92 min) was an outlier (Grubb's test for outlier), but including it or not did not change the results. The best model was selected with a stepwise backward selection.

Finally, after selecting the best models for mating probability, latency, and duration, we ran a post hoc analysis to check whether

our results on personality traits were not explained by confounding effects of body size and coloration parameters. We included in best models sequentially each covariate (body size and color parameters) and its interaction with predation risk treatment and checked if observed patterns on personality-dependent mate choice remained similar.

Heritability

The heritability of activity profile was analyzed using restricted maximum likelihood animal model using WOMBAT (Meyer 2007; Wilson et al. 2010). Additive and residual variance (V_A and V_R) were calculated using univariate animal models based on the pedigree. The heritability was calculated with $V_A/(V_A + V_R)$ (Wilson et al. 2010). We also added the clutch size for each father/mother pair (i.e., the number of sibling for each offspring) as a fixed effect to control for differences in weight between larger and smaller clutches. As it only slightly increased, but not significantly, the heritability estimate, we removed this effect from the model. We also studied the correlations between personality profiles of the parents and offspring, with Spearman rank correlations between the mean activity score of all offspring of each mother/father pair and the activity level of the mother, the activity profiles of the father, and the mid-parent activity level (i.e., mean activity score for females and males). We also ran these correlations on mean activity score of all offspring of each mother (i.e., from any father) and on mean activity score of all offspring of each father (i.e., from any mother) and it gave the same results. Therefore, we only showed the first set of correlations.

For all mixed models, the significance of each effect was assessed with likelihood ratio tests comparing the model deviance to a model without the factor/covariate/interaction studied.

Behavioral reaction to snake cues

We studied the effect on male behavior of exposure to snake olfactory cues. We performed a repeated measures analysis with a general linear mixed model for the time spent active. Repeated measures were the 2 behavioral observations, before and after maintaining males in cattle tanks with or without predator cues. Fixed factors included the predator cue treatment and the time of observation, and the male identity was the random factor. We obtained the significance of predator odor using likelihood ratio tests comparing the model deviance to a model without the predator odor. The time spent basking was not normally distributed and no transformation could normalize the distribution, so we performed a nonparametric Wilcoxon test on the behavioral observation after treatments.

RESULTS

Personality axes

For exploratory tendency, the first PCA axis explained 66% of the variance and it was negatively correlated with the latency to enter in the novel environment (Supplementary material) and positively correlated with the time spent in the novel environment and the time spent walking in this compartment (Supplementary material), whereas the component loading for the time spent walking in a familiar environment was lower (Supplementary material). We interpret higher scores on this axis as higher exploratory behavior.

For the social tendency, the first axis explained 52% of the variance. It was positively correlated with the time spent in the compartment

and under the shelter without odor (Supplementary material) but negatively correlated with the time spent in the compartment and under the shelter with conspecific odor (Supplementary material). We interpret higher scores on this axis as lower sociability.

General activity included the time spent active in the 2 personality assays (exploration and sociability), the first axis explained 60% of the variance and was positively correlated with the time spent active in the 2 tests (Supplementary material). We interpret higher scores on this axis as higher activity.

PCAs on behaviors after mating assays provide axes with similar structures (Supplementary material). Repeatability measurements showed a high and moderate behavioral consistency for activity level and sociability, respectively, whereas exploratory tendency was not consistent (Table 1).

In females, social tendency and general activity were not significantly related to body size or color parameters ($P > 0.21$). Exploratory tendency was negatively related to body size (estimate [\pm SE] = -0.20 ± 0.09 , $F_{1,39} = 5.34$, $P = 0.03$). In males, exploratory tendency, social tendency, and general activity were not related to body size and color parameters ($P > 0.18$).

Female mating preference

Only 2 females rejected both males. On the 84 mating assays, 10 males did not try to mate (Figure 1, removed from further analyses) and females' rejection rate was 16%. The probability of mating depended on the predation risk treatment and male activity profile (Table 2). We, therefore, ran separate analyses for each predation risk treatment to explore this interaction. Females maintained without predator cues prior mating assays were more likely to mate with more-active males ($\chi^2 = 4.48$, $P = 0.03$). This effect was absent for females maintained with predator cues ($\chi^2 = 6e-04$, $P = 0.90$, Figure 1). Females and males sociability had no effect on the mating probability ($P > 0.10$). We then removed from this analysis females that actively but unsuccessfully resisted male copulation attempts. We found the same significant interaction (treatment \times male activity: estimate [\pm SE] = 2.01 ± 1.11 , $\chi^2 = 4.03$, $P = 0.04$).

For females accepting to mate, we analyzed mating latency. Mating latency depended on the predation risk treatment of females and partners' activity profiles (Table 3). For females exposed to predator cues prior to mating assays, the latency increased with male activity level ($\chi^2 = 5.05$, $P = 0.02$) and this effect was absent for females maintained without predator cues ($\chi^2 = 0.001$, $P = 0.90$, Figure 2). The activity profiles of the 2 partners also had an effect on the mating latency that increased when both partners were highly active (Table 3). Sociability had no effect on this latency ($P > 0.10$).

Mating duration was not influenced by predation risk treatments ($\chi^2 = 0.19$, $P = 0.66$). However, there was a significant interaction

between activity profiles of females and males (estimate [\pm SE]: -5.16 ± 1.53 , $\chi^2 = 12.19$, $P < 0.001$). For low-activity females, mating duration was increased with more-active males, but this effect did not exist for more-active females (Figure 3). Sociability had no effect on mating duration ($P > 0.10$).

Mating probability, latency, and duration were not related to body size and coloration ($P > 0.16$ for simple effects and interactions with predation risk treatment) and including these variables in models did not change the effects of partners' activity profiles and predation risk treatments.

Heritability

We could measure the activity of offspring from 12 females only (see Materials and Methods, 7 from predation risk and 5 from no predation risk prior mating, $n = 59$ juveniles). It prevented us from testing the effects of mother's predation treatment, but it allowed us to quantify the heritability of activity level. The activity profile showed a significant heritability ($h^2 = 0.41 \pm 0.26$, $\chi^2 = 7.49$, $P < 0.01$). Mid-offspring activity profile was strongly related to father's activity profile ($n = 13$, Spearman $\rho = 0.78$, $P = 0.002$, Figure 4) but not related to mother's activity profile ($n = 13$, Spearman $\rho = -0.34$, $P = 0.25$). It resulted in a nearly significant correlation between mid-offspring and mid-parent activity profiles ($n = 13$, Spearman $\rho = 0.53$, $P = 0.06$).

Behavioral reaction to predator cues

The time males spent active was significantly changed by the exposure to green whip snake odor for 1 month (estimate [with odor]: -112.30 ± 51.78 , $\chi^2 = 4.62$, $P = 0.03$, Figure 5). The time spent active was on average higher during the second activity assay, but the change in activity was significantly lower for lizards maintained with predator cues than for lizards maintained without predator cues. However, there was no effect of predator odor on the time spent basking ($\chi^2 = 0.01$, $P = 0.97$).

DISCUSSION

Here, we studied the role of female and male personality traits on mating behavior and mate choice after manipulating female predation risk prior mating or not. Personality traits are interindividual differences partly stable over time and across contexts (Sih et al. 2004) and often related to several life-history traits (Reale et al. 2010). Females could therefore use male personality types to choose suitable mates in order to increase their reproductive success (Schuett et al. 2010). We found that sociability and activity levels, but not exploratory tendency, were consistent over the mating period. Moreover, we could estimate the heritability of activity levels and found a heritability around 0.41, which is similar to the broad-sense heritability of 0.32 estimated in Le Galliard et al. (2013). We should interpret this estimate very carefully because of our low sample size and our highly simple pedigree, but correlations between activity profiles of offspring and parents suggested that this heritability is largely due to the father's activity profile. In common lizards, females could therefore choose males to produce more- or less-active offspring. We thereafter discuss the role of personality in female mate choice using 3 metrics of female willingness to mate (probability of mating, mating latency, and mating duration).

Activity profile and mate preference

Females mated more often with more-active males when they were not exposed to predator cues prior to mating. As direct benefits of

Table 1

Repeatability for the 3 personality traits measured before and after mating assays

	Repeatability ICC [95% CI]
Exploration	0.13 [-0.10, 0.36], $P = 0.13$
Sociability	0.25 [0.01, 0.46], $P = 0.01$
Activity	0.56 [0.37, 0.70], $P < 0.0001$

Intraclass correlation coefficients (ICCs) have been calculated with an identity effects (see Materials and Methods). 95% confidence interval (CI) coefficients are shown in brackets.

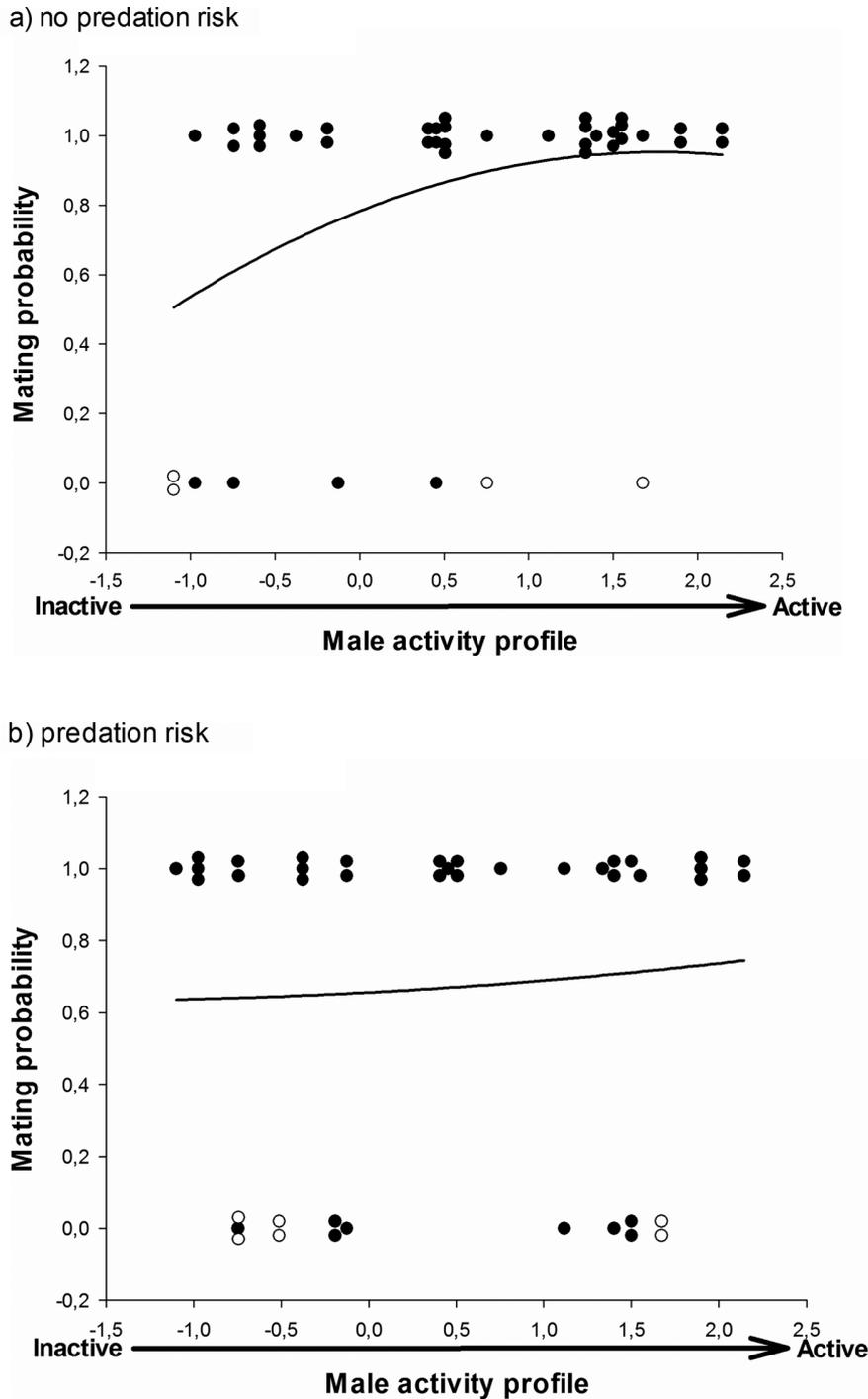


Figure 1

Mating probability according to predation risk treatments (a: no predation risk treatment, b: predation risk treatment) and males’ activity profiles. Open circles are trials where males showed no interest in the female tested and closed circles are trials where males tried to mate with the female. We show predicted lines from the model.

mate choice are unlikely in common lizards, females likely choose males in order to maximize their reproductive success and their offspring fitness (i.e., indirect benefits). Along with our heritability estimate, these results suggest that females could influence offspring behavior by choosing their mates based on their activity profile. High-activity levels can provide several benefits such as dominance in intraspecific interactions (David et al. 2011) and higher efficiency in finding food (Beauchamp 2000). Parental activity profiles can thus

have an effect on their reproductive success and offspring success (Budaev et al. 1999). Activity profile thus seems to be a good criterion for mate choice, as offspring could inherit male activity profile. Mating with males of different personality types can also change maternal physiological conditions and as a consequence offspring behavior and life-history traits. Furthermore, in our study, male activity profile also affected mating duration. More-active males mated longer with less-active females. Mating duration is associated with better fertilization.

Table 2
Effects of male and female activity profiles and of predation risk treatments on the mating probability

	Estimates \pm SE	Likelihood ratio test (degrees of freedom [df] = 1)
Intercept	1.46 \pm 0.51	—
Treatment (np)	0.61 \pm 0.83	$\chi^2 = 1.69, P = 0.19$
Female activity	-0.05 \pm 0.5	$\chi^2 = 1.00, P = 0.31$
Male activity	-0.05 \pm 0.46	$\chi^2 = 1.14, P = 0.28$
Treatment (np) \times	1.79 \pm 1.09	$\chi^2 = 3.79, P = 0.05$
Male activity		
Female activity \times	-0.31 \pm 0.41	$\chi^2 = 0.58, P = 0.44$
Male activity		

Generalized mixed model with male identity as random effects, binomial distribution, and a logit link. The significance is assessed with likelihood ratio tests. Estimates are given for the no predation risk treatment (np).

Table 3
Effects of male and female activity profiles and of predation risk treatments on the mating latency

	Estimates \pm SE	Likelihood ratio test (df = 1)
Intercept	1.60 \pm 0.09	—
Treatment (np)	-0.10 \pm 0.13	$\chi^2 = 8.9, P = 0.002$
Female activity	-0.03 \pm 0.07	$\chi^2 = 4.02, P = 0.04$
Male activity	0.24 \pm 0.06	$\chi^2 = 4.01, P = 0.04$
Treatment (np) \times	-0.19 \pm 0.09	$\chi^2 = 4.55, P = 0.03$
Male activity		
Female activity \times	0.15 \pm 0.04	$\chi^2 = 10.79, P = 0.001$
Male activity		

General linear mixed model with male identities as random effects and the mating latency log transformed. The significance is assessed with likelihood ratio tests. Estimates are given for the no predation risk treatment (np).

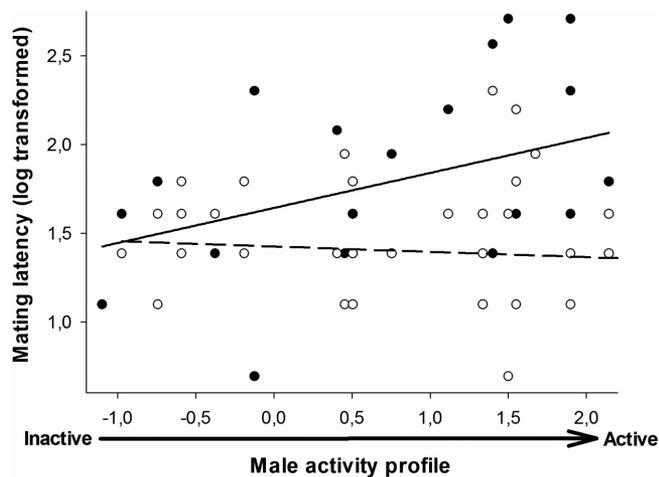


Figure 2
Log-transformed mating latency (min) according to the female predation risk treatments (closed circles and solid line: predation risk treatment, open circles and dashed line: no predation risk treatment) and male activity profile. One duration (92 min) was an outlier (Grubb's test for outlier) and is therefore not shown.

Less-active females may mate longer with more-active males to produce high-activity offspring although this need may be relaxed for highly active females. Further studies should perform a full crossed mate choice design with 2 distinct activity types for both partners and

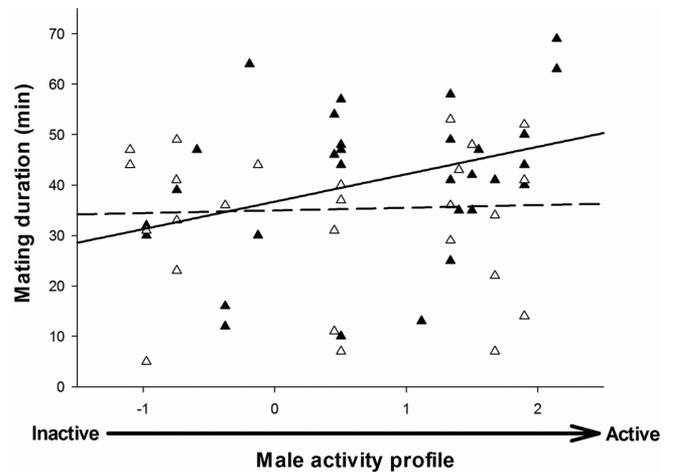


Figure 3
Mating duration (min) dependence on activity profiles of males and females. Females were divided into low- and high-activity classes based on mean activity score for females as a cutoff point (closed triangles and solid line: female of lower activity level, open triangles and dashed line: female of higher activity level).

study the consequences on offspring behavior. Regardless of these

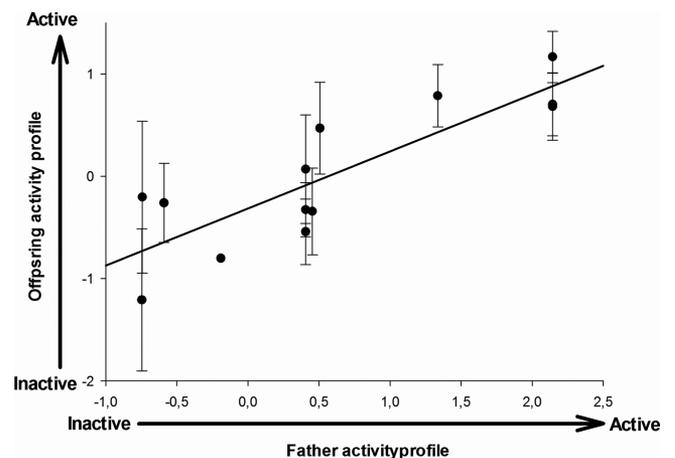


Figure 4
Correlation between offspring and their fathers' activity profiles. Each point is the mean activity score (\pm SE) for offspring from each father/mother pair.

considerations, our results suggest a female preference for more-active males in a context free of predator. This pattern is different compared with females that had been exposed to predators.

Context-dependent mate preference

When females were maintained with predator cues prior to mating, the probability of mating was not related to male activity, as it was in a context free of predator, and the mating latency was longer with more-active males. These results can have several explanations. First, the search for mates and the assessment of male quality as well as the mating duration are costly for females when predation risk is high (Jennions and Petrie 1997). Females should display no mate preference in such a situation as is shown in other species (Godin and Briggs 1996; Gong and Gibson 1996). Our results on mating latency suggest that females might even have a lower preference for more-active males. Females exposed

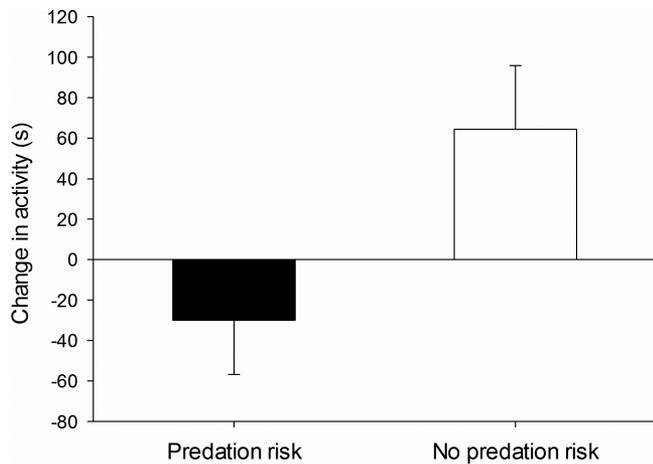


Figure 5

Change in time spent active (seconds \pm SE) after an exposition to cues from green whip snakes or not (black: predator cues and white: no predator cues).

to predator cues prior to mating had higher mating latencies when mated with more-active males. This means that the time between male bite and the introduction of hemipenis, when partners are mostly immobile, is longer when females experienced predator cues prior to mating. This contradicts the cost of mate choice explanation because partners are mostly immobile during this latency and vulnerable to predation. It suggests that females resisted more to more-active males. Because mating latency is negatively related to the probability of fathering offspring, we could predict a lower fertilization by more-active males when females experienced predator cues. However, it remains unclear whether female resistance (i.e., mating latency) directly decreases male investment in the mating (e.g., decreased ejaculate), or whether mating latency only shows female willingness to mate with a given male but does not directly decrease male investment and therefore females control the male that fertilize eggs by other means. Higher activity levels could be costly in environments of high predation risk, explaining the decrease in activity level with predator cues in this species (Thoen et al. 1986; van Damme et al. 1990, 1995; this study) and others (Moses and Sih 1998; Punzo 2007). Indeed, it has been shown in other species that decreasing activity in response to predation risk increases survival (Downes 2002) and this should be particularly true in common lizards, a species living in dense vegetation (van Damme et al. 1990). Females that experienced predator cues could be less willing to mate with more-active males in order to produce offspring of lower activity level and increase offspring survival in an environment with predation risk. Our estimate of heritability and the correlation between father and offspring activity profiles corroborate this explanation. However, an exposure to predation risk can strongly modify maternal and egg physiology, which can modify offspring phenotype (Sheriff et al. 2009; Storm and Lima 2010; Giesing et al. 2011). Maternal effects might therefore interact with mate choice to shape offspring phenotype in order to minimize offspring predation risk. Finally, we expected females to choose more sociable males in a context of predation risk, as social grouping decreases the probability of being predated through a dilution/confusion effect or a socially mediated antipredator strategy (Krause and Ruxton 2002). However, mating behavior was not dependent on the mates' social tendencies, both in nonpredatory and predatory contexts. Likely explanations are that our experimental design,

presenting only 1 male at a time, did not allow the female to assess male social behavior or that social grouping is not an anti-predator strategy in this species.

Female preference versus forced copulation

To assess the influence of personality traits and predation context on female willingness, we used the probability of accepting a male and 2 other metrics when females did mate. This species displays male and female mate choice and forced copulations. The 3 forces all act together to produce mating patterns in natural populations and could potentially change our interpretation. First, more-active males can be more willing to mate because the activity type can be linked to life-history strategies. For example, a higher activity level can be part of a fast pace of life syndrome where individuals grow faster and reproduce earlier at the expense of life expectancy (Reale et al. 2010). Moreover, males can vary in their preferences for females as shown in a previous study (Fitze et al. 2008). Even if male willingness to mate and mate choice can somehow explain mating patterns, its influence is probably low because the number of male gametes is less limited and male common lizards can mate with multiple females (up to 12 females). In our analysis, we discarded the influence of male mate choice by removing trials where the male showed no interest in the presented females (i.e., no biting/mating attempt). Large males can also sometimes force copulations when females are not interested in mating (Fitze et al. 2008). Females were always larger than males in our study, but we cannot rule out the possibility of forced copulations. Therefore, we also analyzed the mating probability after removing trials where the female unsuccessfully resisted male copulation attempts. These mating events were not always the consequences of forced copulations because females may fight for a short while to assess male strength. It is, however, certain that females that mated without resistance are not forced to mate. The analyses with or without such cases showed the same results suggesting that female preferences likely explain the observed patterns. Moreover, we studied mating latency and mating duration. The variation in mating latency is mostly explained by females trying to escape from males and can therefore be related to female willingness to mate. The mating duration is also highly variable and, in almost all assays, females ended the copulation (i.e., females moved away from the male). However, variation in mating duration has probably additional causes such as male investment level in the mating. Because these metrics are linked to the probability for a male to father offspring (see Methods), females may have other ways to control paternity.

CONCLUSION

Recent studies have shown that male personality traits could play an important role in mate choice as they are often linked to major life-history traits and can be heritable. Our study showed, on common lizards, that female mate choice varied with male activity levels, a partly consistent and heritable behavior. Females mated more often with more-active males. This preference for more-active males was however reversed when females were exposed to predation risk prior to mating. One explanation is that females could then produce offspring with a lower activity level and a higher life expectancy when predators are present. Although future studies need to experimentally tease apart the effect of personality traits from other phenotypic traits (Godin and Dugatkin 1996; Schuett, Godin, et al. 2011), our results suggest differential patterns of selection on activity profiles according to predation risk in living habitats.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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