

## RESEARCH PAPER



WILEY

# The Asian grass lizard (*Takydromus sexlineatus*) does not respond to the scent of a native mammalian predator

Charlotte Van Moorleghe  | Raoul Van Damme 

Laboratory for Functional Morphology,  
Department of Biology, University of  
Antwerp, Wilrijk, Belgium

## Correspondence

Charlotte Van Moorleghe, Laboratory  
for Functional Morphology, Department  
of Biology, University of Antwerp,  
Universiteitsplein 1, B-2610 Wilrijk, Belgium.  
Email: charlotte.vanmoorleghe@  
uantwerpen.be

## Funding information

This study was supported by funding from  
the University of Antwerp (30152).

## Abstract

Lacertid lizards use chemical cues emitted by saurophagous snakes to evade predation. Whether these lizards can detect and respond to the chemical cues of predatory mammals has not been studied. As many mammals carry distinct body odours and/or use chemical cues for intraspecific communication, lizards can be expected to use these chemicals as early warning cues. To test this idea, we observed the behaviour of Asian grass lizards (*Takydromus sexlineatus*) that had been transferred to an unfamiliar test arena containing one of four scent treatments. No particular scent was applied to the arena in the control situation. Diluted aftershave served as a pungency control. In the snake treatment, scent of the Oriental whip snake (*Ahaetulla prasina*) was applied. We included this treatment to learn how Asian grass lizards react to predator chemical cues. Finally, in the mongoose treatment, the lizards were confronted with scent cues of several small Indian mongooses (*Herpestes auropunctatus*). Snake scent elicited foot shakes, startles and tail vibrations. These are behaviours that in lacertid lizards are associated with stressful situations such as predatory encounters. Surprisingly, lizards confronted with mongoose scent exhibited none of these stress-indicating behaviours. In fact, their behaviour did not differ from that of lizards subjected to an odourless control treatment. These results raise concern. Mongooses are rapidly invading ecosystems worldwide. If lizards that have co-evolved with mongooses are unable to detect these predators' presence through chemical cues, it seems highly unlikely that evolutionary naïve lizards will develop this ability rapidly.

## KEYWORDS

chemodetection, lacertidae, mammalian predator, native predators, saurophagous snake, small Indian mongoose

## 1 | INTRODUCTION

Predation is considered a major selective force shaping the morphology, physiology, behaviour and life history of prey animals (reviewed in Kats & Dill, 1998 and Lima & Dill, 1990). Rapid detection and accurate identification of the predator are often key to surviving a predatory encounter (Banks & Dickman, 2007; Cox & Lima, 2006). Accordingly,

many prey species have evolved sense organs capable of detecting predatory cues (Derby & Sorensen, 2008; Kotrschal, Deacon, Magurran, & Kolm, 2017; Pereira & Moita, 2016; Takahashi, 2014).

Lacertid lizards are known to have keen chemical senses: (a) the olfactory system with the sensory epithelium situated in the nose and (b) the vomerolfactory system in which scent molecules are transported via the tongue to the Jacobson's organ in the roof of

the mouth (Cooper, 1996; Halpern, 1992; Halpern & Kubie, 1984; Schwenk, 1993). Studies on a variety of lacertid species have shown that these senses assist in the detection of saurophagous snakes (e.g. Amo, López, & Martín, 2004; Mencia, Ortega, & Pérez-Mellado, 2016; Thoen, Bauwens, & Verheyen, 1986). However, it is unclear whether lizards also use their chemoreceptive systems to detect and identify mammalian predators (Weldon, 1990). Many mammalian predators of lacertid lizards carry distinctive body odours (Gorman, 1976; May, Bowen, McGregor, & Timberlake, 2012), produce scented urine or excrements (Burnham, Bender, Eiceman, Pierce, & Prasad, 2008; Fendt, Endres, Lowry, Apfelbach, & McGregor, 2005; Greene, Wallen, Moresco, Goodwin, & Drea, 2016) and/or scent mark their territory (Gorman & Trowbridge, 1989). One could imagine lizards exploiting these scents as early warning cues. However, whether lizards can actually detect and recognise mammal scents has, to our knowledge, never been examined.

A handful of studies have been performed focussing on other lizard taxa. New Zealand skinks and geckos exhibited no response to the chemical cues of introduced ship rats (*Rattus rattus*). However, cues of a native reptile predator also failed to evoke a behavioural response, suggesting that the lizard species involved in that study had inadequate chemical senses to begin with (Monks, Nelson, Daugherty, Brunton, & Shine, 2019). In New Caledonia, endemic skinks (*Caledoniscincus austrocaledonicus*) avoid refuges scented with the odours of *Rattus* sp. and feral cats (*Felis catus*), while endemic geckos (*Bavayia septuiclavis*) only avoided the scent of *R. exulans*, the predator with which they have been coexisting longest (i.e. 3,000 years; Gérard, Jourdan, Cugnière, Millon, & Vidal, 2014; Gérard, Jourdan, Millon, & Vidal, 2016). These studies may also paint a partial picture because they consider responses to non-native mammalian predators that were only fairly recently introduced into the lizards' habitat. Perhaps these lizards have had insufficient time to evolve a proper identification-response system towards these mammals in particular. Webster et al. (2018) found that Boulenger's skinks (*Morethia boulengeri*) and southern marbled geckos (*Christinus marmoratus*) stopped foraging in response to the scents of native quolls (*Dasyurus maculatus*) and dingoes (*Canis lupus dingo*).

Here, we investigate the ability of a lacertid lizard (the Asian grass lizard, *Takydromus sexlineatus*) to detect chemical cues of a native mammalian predator, the small Indian mongoose (*Herpestes erpunctatus*). For comparison, we used scent of the native Oriental whip snake (*Ahaetulla prasina*) to evoke a baseline anti-predatory reaction in the lizards. Information on how a lizard responds to mongoose chemical cues is particularly relevant as the small Indian mongoose and the Javan mongoose (*H. javanicus*), which were formerly considered as being one species (Veron, Patou, Pothet, Simberloff, & Jennings, 2007), have been intentionally introduced into ecosystems worldwide to control rats and snakes. In many cases, they also preyed considerably on native mammals, birds and other reptiles, sometimes even leading to local extinctions (reviewed in Hays & Conant, 2007). For this reason, mongooses are considered one of the hundred most dangerous invasive species in the world (Lowe, Browne, Boudjelas, & De Poorter, 2000).

## 2 | MATERIALS AND METHODS

### 2.1 | Study species

The Asian grass lizard is a small lacertid lizard with well-developed chemical senses (Baeckens et al., 2017; Cooper, Paulissen, & Habegger, 2000) that lives in grassland habitats, agricultural sites and near human settlements (Pauwels, 2000) throughout its distributional range in Southeast Asia (from southern China to the Indonesian islands of Sumatra and Java and the island of Borneo; Zhao & Adler, 1993). Habitats occupied by this lizard are frequented by native generalist predators, including the small Indian mongoose (Chutipong, Duckworth, Timmins, Willcox, & Ario, 2016; Nellis, 1989) and the Oriental whip snake (Sharma, 2003). Both the small Indian mongoose and Oriental whip snake are highly opportunistic feeders with more or less overlapping diets. Mongooses eat reptiles, small rodents and birds, besides invertebrates and plant material (Hays & Conant, 2007; Lewis, van Veen, & Wilson, 2010; Nellis, 1989). The Oriental whip snake has also been observed in the wild feeding on various kinds of lizards, other snakes, (amphibious) fish, birds and small mammals (Dunbar & Dunbar, 2015; Pauwels, 2000; Vogrin, McCleary, & Benel, 2016). Therefore, mongooses and snakes are expected to be equally relevant predators of the Asian grass lizard.

### 2.2 | Lizard housing conditions

We obtained twenty adult male Asian grass lizards (average snout-vent length: 56.71 mm, range 52.69–63.45 mm; average body mass: 4.03 g, range 2.68–6.24 g) via the pet trade (Amfibia BVBA). The animals had been caught in the wild on Java, Indonesia. Individuals were housed in groups of three to five in terraria measuring 100 × 50 × 50 cm (length × width × height). The floors of the terraria were covered with paper towels, which were changed weekly. We added branches and stones as environmental enrichment. A 60 Watt incandescent lamp suspended at one side of the terrarium provided a temperature gradient of between 23 and 32°C, allowing the lizards to thermoregulate and maintain body temperatures to near-optimal levels (Zhang & Ji, 2004). Additionally, a UVB lamp was suspended inside the terrarium to prevent a vitamin D deficiency (Adkins et al., 2003). Lighting maintained a 12:12 hr light:dark circadian rhythm. Water was available ad libitum. Furthermore, we sprayed the terraria daily to guarantee an optimal humidity. Lizards were fed vitamin E-dusted crickets (*Acheta domesticus*) twice a week.

### 2.3 | Scent collection

Mongoose scent was collected from eight males, caught on Korčula island in Croatia and housed individually at the research facility of IDT Biologika GmbH in Dessau-Roßlau, Germany. Scent from the Oriental whip snake was obtained from one wild-caught Indonesian male obtained via the pet trade (La Ferme Tropical) and housed at

the laboratory in Antwerp. The use of only one individual as a donor of the treatment stimulus is not considered best practice and is discouraged by Kroodsmas, Byers, Goodale, Johnson, and Liu (2001) and Hurlbert (1984). However, our purpose was merely to use the snake's scent in generating a baseline anti-predatory response by grass lizards to compare mongoose-evoked behaviour with. We deemed this treatment appropriate as such. Paper towels were placed in the home cages of the predators for a period of 5 days. We used clean tweezers at all times while handling the paper towels. Human contact with the animals during scent collection was limited, and the paper towels were left untouched by carers. These precautions ensured that contamination with human scent was avoided. After the scent collection period, the paper towels were taken from the home cages, cut into 5 × 5 cm pieces with clean scissors and either placed into double plastic bags for storage in a freezer at -20°C or immediately used in focal observations. If stored, the paper towels were kept for maximum one month. Mongoose chemical samples were transported on dry ice to the laboratory in Antwerp. Freezing prevents the scent from ageing before use in focal observations (Bytheway, Carthey, & Banks, 2013). Preliminary experiments showed that the described storage and handling of the samples does not prevent a response by two other lacertid lizards (*Zootoca vivipara* and *Podarcis melisellensis*) to predator odours. Frozen scent samples reached room temperature within a minute after taking them out of the freezer (confirmed by an unpublished pilot study), after which a focal observation could start.

In addition to the predator scent, we also prepared an odourless control by clipping 5 × 5 cm pieces out of clean paper towels. A pungency control was prepared by administering one drop of diluted aftershave (one volume of Mennen Skin Bracer to 9 volumes of deionised water) onto a 5 × 5 cm piece of clean paper towel. This control represents scent that is not predator related (Mennen Skin Bracer contains only plant-based castor oil as opposed to animal-derived castoreum sometimes found in cosmetics) and is unknown to the lizards (Cooper, Perez-Mellado, Vitt, & Budzynski, 2003). Therefore, any reaction by the lizards towards this treatment should not be due to fear, but the consequence of general chemosensory and explorative behaviour.

## 2.4 | Focal observations

The procedure for the focal observations was adapted from Thoen et al. (1986) and is commonly used for testing predator cue recognition in lacertid lizards (Downes & Bauwens, 2002; Ortega, Mencia, & Pérez-Mellado, 2017; Van Damme & Quick, 2001). We observed the lizards in a closed test arena measuring 50 × 40 × 40 cm (l × w × h). One of the arena's walls was coated with a dark window film (Norauto), which allowed us to observe the lizard without disturbing it. A 60 Watt incandescent lamp, installed centrally in the roof of the arena, provided an optimal temperature for lizard activity. A few seconds before every behavioural test, the observer rubbed a paper towel piece comprising one of the four scent treatments across the

floor and thereafter placed it in a randomly chosen corner of the test arena. Three additional towel pieces, arbitrarily selected from among all towels treated with the same scent as the first one, were placed in the remaining corners of the arena. We chose not to subject every individual to all treatments, because previous studies found that lizards tend to become indolent after repeated testing (Gérard et al., 2014; Van Moorlegheem, Huyghe, & Van Damme, 2020). Instead, we assigned each lizard to one of two experiments. In Experiment A, eleven lizards were observed in the two control situations (odourless and pungency control) and in the *A. prasina* ("snake") treatment. In Experiment B, the remaining nine lizards were observed in the odourless control situation and in the *H. auropunctatus* ("mongoose") treatment. In both experiments, the different scent treatments were presented according to a balanced test design. A period of approximately 24 hr was left between consecutive trials for the same lizard individual.

During a time period of 10 min, which began shortly after the lizard was placed in the centre of the test arena, the following behaviours were scored: the time spent Walking, Not-moving, Basking, Nudging and Standing up-right against one of the test arena's walls, and the amount of Tongue flicks (indicative of chemical sampling; Graves & Halpern, 1990), Labial licks, Head rubs (the lizard rubs its head sideways over the substrate), Tail vibrations, Startles and Foot shakes. The latter three are considered to be indicative of stress or linked to predator-escape strategies in lizards (Font, Carazo, Pérez i de Lanuza, & Kramer, 2012; Mori, 1990; Van Damme & Quick, 2001). See Thoen et al. (1986) and Monks et al. (2019) for a detailed description of all aforementioned behaviours. After each observation, the lizard was placed back in its home terrarium. The test arena was cleaned with 70% ethanol and left to dry before the next observation could begin.

## 2.5 | Statistical analysis

Statistics were performed using R version 3.3.0 (R Core Team, 2016). We ran a Factor Analysis of Mixed Data (FAMD; Lê, Josse, & Husson, 2008) on the behavioural variables for each experiment. Data points for the behavioural variables were transformed to improve normality (Table 1) prior to FAMD analyses. Some of the behavioural variables exhibited highly skewed distributions with an excess of zeros. Because transformations did not help, we recoded these variables into binomial quantities (Table 1), with 0 indicating that the focal lizard did not perform the behaviour and 1 indicating that it did. We used linear mixed-effect models (LMM; lme4 package; Bates, Mächler, Bolker, & Walker, 2015) to test the effect of Treatment (either the odourless control, pungency control, snake or mongoose scent) on the scores of each observation on the main dimensions produced by the FAMD. Besides Treatment, Trial and Treatment × Trial were also entered as explanatory variables into these models. The variable Trial takes on a value equal to the number of times that the lizard had been observed in a behavioural test before the current

**TABLE 1** The main dimensions (i.e. with eigenvalues greater than 1) retrieved from the FAMD analyses of Asian grass lizard behaviour, with associated LMM results, as well as, contributions of the relevant behavioural variables for (a) Experiment A and (b) Experiment B

(A)

		Dimension 1			√Dimension 2		
	Eigenvalue	4.91			2.09		
	Variance (%)	44.65			19.02		
	Cumulative variance (%)	44.65			63.68		
Mixed-effect models	Explanatory variables	Treatment	Trial	Treatment × Trial	Treatment	Trial	Treatment × Trial
	Predictor weight	0.83	0.15	0	0.98 <sup>⊗</sup>	0.3	0
Behavioural variables	No-move <sup>†</sup>	<b>15.08<sup>‡</sup></b>			0.32		
	Walk <sup>†</sup>	<b>17.17<sup>‡</sup></b>			1.80		
	√Tongue flick	<b>14.96<sup>‡</sup></b>			0.00		
	√Labial lick	3.60			0.78		
	Foot shake <sup>bin</sup>	8.97			7.50		
	Startle <sup>bin</sup>	0.56			<b>32.15<sup>‡</sup></b>		
	Head rub <sup>bin</sup>	5.30			7.18		
	Bask <sup>bin</sup>	9.23			7.44		
	Nudge <sup>bin</sup>	12.31			0.06		
	Stand-up <sup>bin</sup>	12.65			8.32		
Tail vibration <sup>bin</sup>	0.16			<b>34.45<sup>‡</sup></b>			

(B)

		Dimension 1 <sup>2</sup>			Dimension 2		
	Eigenvalue	4.38			1.29		
	Variance (%)	54.75			16.09		
	Cumulative variance (%)	54.75			70.85		
Mixed-effect models	Explanatory variables	Treatment	Trial	Treatment × trial	Treatment	Trial	Treatment × Trial
	Predictor weight	0.25	0.15	0	0.14	0.4	0.02
Behavioural variables	No-move	0.02			0.36		
	√Walk	<b>0.21<sup>‡</sup></b>			0.00		
	3√Tongue flick	<b>0.20<sup>‡</sup></b>			0.00		
	Foot shake <sup>bin</sup>	0.12			0.00		
	Bask <sup>bin</sup>	0.00			<b>0.59<sup>‡</sup></b>		
	Nudge <sup>bin</sup>	<b>0.18<sup>‡</sup></b>			0.01		
	Stand-up <sup>bin</sup>	0.14			0.01		
Labial lick <sup>bin</sup>	<b>0.13<sup>‡</sup></b>			0.02			

Note: For the mixed-effect models, variables with predictor weights greater than 90 are indicated with a reference mark (⊗). As for the FAMD results, those contributions greater than or equal to 70% of the highest value for each dimension are marked with a diesis (‡).

√ square-root transformed; 3√ third-root transformed; <sup>†</sup> Box-Cox transformed; <sup>2</sup> squared; <sup>bin</sup> coded into a binomial quantity.

observation and therefore indexes possible habituation effects. Predictor weights (=the summarised Akaike weights of all candidate models in which an explanatory variable appears) were used to estimate the probability that a certain variable is a component of the best model (Symonds & Moussalli, 2011).

To study Treatment effects in more detail, we also ran mixed-effect models on individual behavioural variables. LMMs were used for normally distributed variables (Table S1). For the full models that included the amount of performed Tongue flicks as a dependent variable, we added the time the lizards spent Walking (transformed

to reach normality) as a covariate, as well as all two-way interactions with Treatment and Trial. This is necessary as it corrects for the positive correlation between Tongue-flicking and Walking (Schulterbrandt, Kubie, Von Gizycki, Zuri, & Halpern, 2008; Thoen et al., 1986; Van Damme, Bauwens, Thoen, Vanderstighelen, & Verheyen, 1995). The binomial variables describing whether lizards had been seen Basking, Nudging and Standing up-right were analysed using generalised linear mixed-effect models (GLMM; lme4 package) with a binomial fit and a logit link function. The effect of Treatment and Trial on the number of Foot shakes, Head rubs and Startles was also examined using GLMMs. Depending on which best fitted the data, a Poisson or negative binomial fit and a log link function were used (Table S1). The proportion of observations in which Tail vibrations were performed was analysed using a Fisher's exact test instead of mixed models, as this behaviour was completely absent for some scent treatments.

Lizard identity was entered into all LMMs and GLMMs as a random effect to account for the repeated use of the same lizard (Figure S1). Assumptions regarding normality of residuals (for LMMs), homoscedasticity and linearity were met and the data were checked for overdispersion (in the case of GLMMs). Models were compared using the second-order Akaike Information Criterion (AICc) as well as their Akaike weights ( $w_i$ ) (Symonds & Moussalli, 2011). The significance of pair-wise differences in behaviour over scent treatments was assessed using the Bonferroni correction for multiple testing in the lsmeans package in R (Lenth, 2016).

### 3 | RESULTS

#### 3.1 | Experiment A: snake recognition

The FAMD resulted in two new composite variables that jointly accounted for approximately 64% of the behavioural variation lizards exhibited in Experiment A (snake vs. controls; Table 1a). The first dimension represented a gradient in explorative behaviour, with high scores for lizards that exhibited long bouts of Walking (factor loading = +0.92) and elevated Tongue flick rates (+0.86) but little No-move behaviour (-0.86). We found little evidence that either Treatment, Trial or their interaction induced this variation (Table 1a). The second FAMD dimension correlated strongly with the incidence of Startle behaviour (+1.57) and Tail vibrations (+2.61) and can, therefore, be considered a stress-gradient. Lizards observed in the snake treatment scored significantly higher on this second dimension (with more likely instances of Startling and Tail vibrations) than lizards in both control situations ( $t_{24,2} = -3.31$ ,  $p = .0089$  and  $t_{24,2} = -3.78$ ,  $p = .0027$  when compared to the odourless and pungency control, respectively; Table 1a). Behaviour in both controls did not differ significantly from each other ( $t_{24,2} = 0.48$ ,  $p = 1.00$ ).

Post-hoc testing based on univariate mixed models (Table S1a) revealed that snake scent indeed evoked significantly more Startles ( $Z = -4.70$ ,  $p < .0001$ ) compared to the odourless control (Table 2

& Figure 1a). This was also the case for the number of foot shakes ( $Z = -1.73$ ,  $p = .022$ ; Table 2 & Figure 1b). Tail vibrations were exclusively observed when the snake scent was presented to the lizards ( $p = .012$ , Fisher's exact test; Table 2 & Figure 1c). When confronted with the diluted aftershave as a pungency control, lizards only performed significantly more Head rubs during the observation round compared to the odourless control situation ( $Z = -4.44$ ;  $p < .0001$ ; Table 2 & Figure 1d).

#### 3.2 | Experiment B: mongoose recognition

The first two dimensions of the FAMD explained approximately 71% of the total behavioural variance. As in Experiment A, the first FAMD dimension indicated the level of explorative behaviour, characterised by Walking (+0.95) and Tongue-flicking (+0.94), and now also Nudging behaviour (+2.08) and Labial licks (+1.12). Neither Treatment nor Trial, or a combination of both explained variation along this axis (Table 1b). The second dimension reflected variation in the duration of Basking behaviour primarily (-0.70). Again, neither scent treatment nor trial number influenced the scores on this axis (Table 1b). Additionally, not a single Tail vibration or Foot shake and only one Startle was seen across all behavioural trials in Experiment B (Table 2). None of the tests on individual behavioural variables revealed an effect of Treatment (Table S1b and Figure S1). It proved impossible to run a GLMM for the binomial variable Basking, because the random effect term (Lizard individual) caused the model to become overfit. A Fisher's exact test revealed no Treatment effect ( $p = 1.00$ ).

### 4 | DISCUSSION

Asian grass lizards in our experiments changed their behaviour when confronted with snake chemicals. Scent of the Oriental whip snake elicited Startles, Foot shakes and Tail vibrations, indicative of stress. This suggests that Asian grass lizards, like other lacertids previously studied (e.g. Amo et al., 2004; Mencia et al., 2016; Van Damme & Quick, 2001), can detect the odour of saurophagous snakes and relate it to increased predation risk, even in the absence of visual cues. Surprisingly, however, the scent of the mongoose did not evoke any notable changes in the lizards' behaviour. We discuss a number of non-mutually exclusive hypotheses to explain this discrepancy.

First, lizards may not react to mongoose odour simply because they have not evolved the necessary odorant receptors. We have no information on the nature of mongoose kairomones, nor on the kind of receptors available in the lizards' epithelia (Silva & Antunes, 2017), so we cannot test this explanation directly. Both Oriental whip snakes and mongooses are genuine predators of the Asian grass lizard, and they have both coexisted with it for a long time. As a small caveat, the lizards in our experiments originated from Java and have, therefore, coexisted with the Javan mongoose rather

**TABLE 2** Behaviours observed in Experiments A and B and their mean (range) values over Treatment

	Experiment A			Experiment B	
	Odourless control	Pungency control	<i>A. prasina</i>	Odourless control	<i>H. auropunctatus</i>
No-move	513.75 (357.77–600)	472.22 (366.32–600)	541.14 (385.04–600)	335.63 (0–600)	320.5 (2.05–600)
Walk	31.22 (0–78.2)	68.89 (0–178.73)	29.61 (0–85.07)	40.67 (0–145.74)	82.15 (0–253.17)
Tongue flick	109.55 (6–258)	197.55 (0–340)	94.27 (4–415)	64 (0–221)	222.89 (0–853)
Labial lick	66.82 (28–168)	76.36 (21–183)	46.91 (2–116)	6.44 (0–24)	9.89 (0–31)
Bask	45.92 (0–232.04)	35.9 (0–137.06)	20.98 (0–133.85)	123.19 (0–576.04)	155.06 (0–597.95)
Nudge	4.55 (0–26.65)	12.04 (0–93.1)	0.27 (0–1.78)	2.29 (0–11.73)	10.15 (0–41.61)
Stand-up	4.25 (0–21.69)	7.85 (0–32.18)	7.97 (0–42.5)	78.44 (0–600)	30.26 (0–112.34)
Foot shake	3.18 (0–15)	4.45 (0–26)	5.36 (0–23)	2.56 (0–13)	4.22 (0–26)
Startle	0.27 (0–2)	0.18 (0–2)	4.45 (0–22)	–	–
Head rub	1.09 (0–6)	4.55 (0–16)	1.18 (0–6)	–	–
Tail vibration	0 (0–0)	0 (0–0)	11.09 (0–52)	–	–

Note: The values of the timed variables No-move, Walk, Bask, Nudge and Stand-up are presented in seconds, whereas those for Tongue flick, Labial lick, Foot shake, Startle, Head rub and Tail vibration are shown as counts. A hyphen indicates combinations of behaviours and scent treatments for which data were insufficient to calculate means.

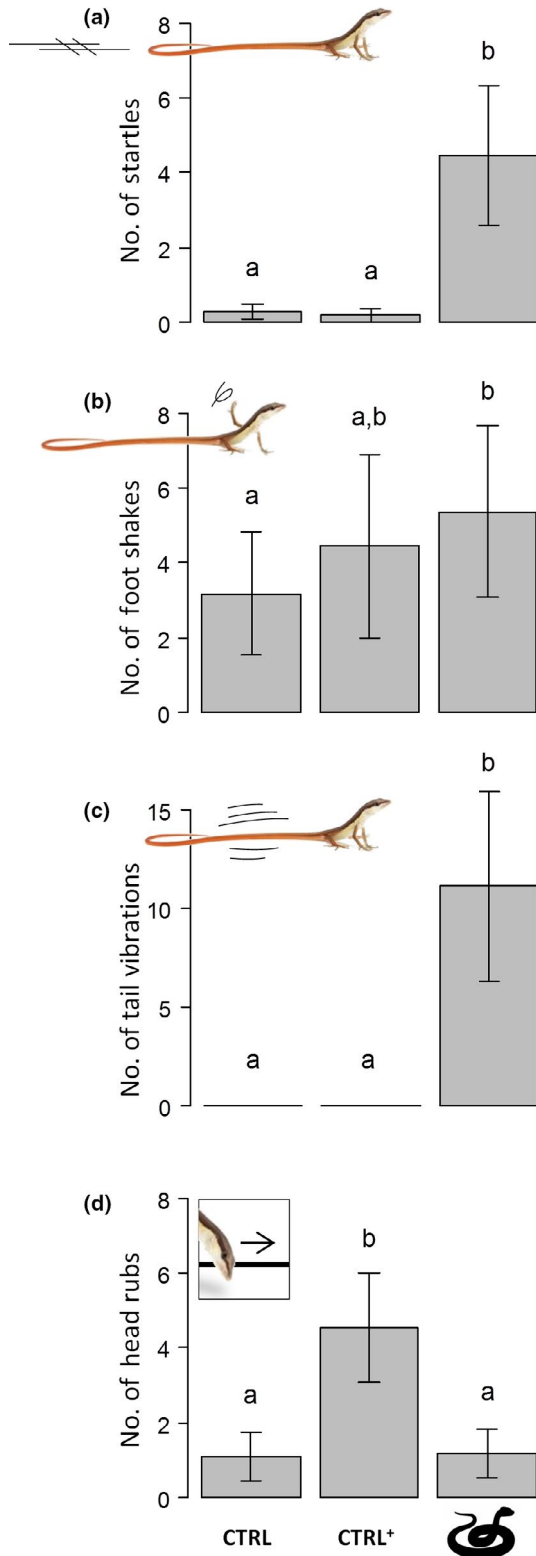
than with the Indian mongoose. However, it seems unlikely that this could explain the lizards' lack of response to mongoose scent. The two *Herpestes* species have diverged only recently (5 Mya) and are still interbreeding (Patou et al., 2009; Veron et al., 2007). Moreover, several studies have shown that scents of closely related mammals tend to be highly similar (Bininda-Emonds, Decker-Flum, & Gittleman, 2001; Carthey, Bucknall, Wierucka, & Banks, 2017).

Therefore, it is difficult to see why natural selection would bestow lizards with odorant receptors for snake but not mongoose scent. Evolutionary constraint could be one explanation—perhaps it is easier for lizards to evolve receptors for reptilian rather than for mammalian odours. For instance, lizards may have evolved chemoreceptors for the detection of conspecific cues in a social or reproductive context. Co-opting such receptors for predatory recognition may be more likely for phylogenetically related predators that perhaps emit more similar chemicals (snakes) than for distantly related ones (mammals). Alternatively, being able to detect mongoose scent may not be selected for. Kats and Dill (1998) have argued that the benefits of chemosensory recognition (i.e. early warning) must be traded-off with its costs regarding the energy and time spent by responding. Perhaps the scent of a snake in our experiments is more informative than that of mongooses. Asian vine snakes (*Ahaetulla*) are well-camouflaged ambush predators that pass much of their time waiting motionless for passing prey (Chowdhury, Maji, Chaudhuri, Dwari, & Mondal, 2017; Kartik, 2018). The scent of a vine snake is therefore a reliable (and, due to its concealment, possibly the only) cue for its proximity. In sharp contrast, mongooses are active hunters that forage over large distances and maintain wide home ranges (Pitt, Sugihara, & Berentsen, 2015). The scent of a mongoose may not be very informative about its whereabouts. Visual cues may be more reliable signs of mongoose menace (Brock, Bednekoff, Pafilis, & Foutopoulos, 2015).

A second possible reason for our lizards' failure to respond to mongoose scent is that the response is learned, and therefore,

requires prior exposure to the stimulus. We judge this explanation to be highly unlikely for three reasons. First, our animals were wild-caught in Java, Indonesia, shortly before the experiments. Both mongooses and whip snakes are abundant in the area (Chutipong et al., 2016; Thy et al., 2012), so our study animals may have been exposed to scents of the predators before experimentation. Also, chemosensory predator recognition in other lizard species is innate rather than learned (Martín, Ortega, & López, 2015; Van Damme et al., 1995), so lizards probably do not need prior exposure with the stimulus to mount an anti-predatory response. Finally, it is difficult to see why lizards would need prior exposure to mongoose scent, but not snake scent to mount an anti-predator response.

In the previously suggested explanations, the lack of response towards mongoose scent was thought to result from the lizard's inability to detect the chemical cues. A second possibility is that the lizards detect and recognise the scent, but "choose" not to exhibit Foot shakes, Tail vibrations and Startles. Font et al. (2012) have argued that these behaviours (seen in many lacertids) work as pursuit-deterrent signals—the prey notifying the predator that it has been detected and that any further attack will be pointless. Pursuit-deterrent signals are more likely to work with ambush predators than with active foragers. Oriental whip snakes rely on concealment and will launch fast, unexpected attacks on unwary prey, often within the vegetation over-heading the prey. However, as these snakes are rather slow when moving over ground (Sharma, 2019), it seems unlikely that they will engage in the pursuit of an alarmed lizard. Mongooses, on the other hand, are fast and agile hunters that will actively pursue lizards (Lewis et al., 2010). Foot shakes, Tail vibrations and short Startles are probably more likely to draw the attention of a mongoose than to discourage it from attacking (Conover, 2007). In addition, these behaviours require the lizard to stop moving, which could be the wrong strategy when threatened by a fast-moving predator. With this reasoning, the lizards' lack of (visible) response towards mongoose scent can be considered adaptive.



It should be noted that our experimental set-up might have precluded certain types of anti-predator behaviour. For instance, we did not provide lizards with hiding places or climbing structures that they might use to escape from predators, perhaps mammal predators in particular. It would be interesting to repeat the tests in more natural conditions. On the other hand, a lizard sensing a dangerous

**FIGURE 1** Behavioural responses of the Asian grass lizard to three different scent treatments. Group means for behaviours performed during the odourless control (CTRL), pungency control (CTRL<sup>+</sup>) and Oriental whip snake scent treatment (snake silhouette) are given, with the error bars being representative of the standard error. Letters above the bars indicate whether two group means are significantly different ( $p < .05$ ) from each other (indicated with a different letter) or not (indicated with the same letter). Post-hoc multiple comparisons with Bonferroni correction were used for comparison of means, with the exception of the data for Tail vibrations, in which the Fisher's exact test was used. Insets are a visual representation of each behaviour which is also noted along the y-axis. The original picture was taken by Mickael Leger

odour while in an unfamiliar, open environment can be expected to behave differently compared to a lizard in the same setting, but without dangerous cues at hand. This was not the case for animals in the mongoose treatment.

A third explanation of the lizards' apparent apathy towards mongoose chemical cues could be that the individuals used in Experiment B were, for some unknown reason, generally less responsive than the individuals in Experiment A. The fact that the control treatments of both experiments differ (Table 2) may hint in that direction. On the other hand, the difference in overall responsiveness between lizards in the control situation of Experiments A vs. B could be due to differential carry-over and/or habituation effects. Indeed, the effect of treatment history differed between Experiments A and B (Figure S2). In Experiment A, lizards that were first tested in a snake-scented environment exhibited a stronger response in the control environment than lizards that had no previous experience with snake scent either because they were tested for the first time, or had only been tested before in the pungency control environment. This suggests that the former lizards perceived the new environment as potentially dangerous on the basis of their previous experience. In Experiment B, lizards that were first tested in the mongoose-scented environment exhibited less stress responses in the control environment than lizards in the control treatment that were tested for the first time. This may reflect habituation to a new, but apparently safe, environment and reinforces the idea that mongoose scent is not detected or perceived as dangerous.

Studying anti-predator strategies that are efficient against the small Indian mongoose (i.e. those employed by prey in the mongoose's native range) is relevant in the light of the multiple introductions to ecosystems worldwide and the resulting predatory pressures on local prey (Hays & Conant, 2007). If other squamate species, like the Asian grass lizard, fail to mount an anti-predator response when smelling mongoose-derived cues, this may help explain why the introduction of these carnivorans can have such disastrous effects on the local herpetofauna.

#### ACKNOWLEDGEMENTS


All methods and experimental protocols as described above were in accordance with Directive 2010/63/EU of the European Parliament and the policies and requirements of the Ethical Committee for

Animal Experiments of the University of Antwerp (file-number: 2015-34). We would like to thank J. Brecko, J. Scholliers and S. Goossens for helping with the experimental design and set-up, and J. Mertens and G. Meulemans for assistance during animal caretaking. We are also grateful for the aid of A. Kretzschmar, A. Vos and S. Ortmann, who arranged the preparation and transportation of mongoose-scented towels from the facilities of IDT Biologika GmbH in Dessau-Roßlau, Germany, to our own laboratory in Antwerp, Belgium. We additionally want to thank J. Meaney for linguistic advice and three anonymous reviewers who significantly improved drafts of the manuscript. Financial support was given by the University of Antwerp in the context of C.V.M.'s doctoral thesis.

## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## ORCID

Charlotte Van Moorleghe  <https://orcid.org/0000-0003-2780-8563>

Raoul Van Damme  <https://orcid.org/0000-0002-4585-6940>

## REFERENCES

- Adkins, E., Driggers, T., Ferguson, G., Gehrmann, W., Gyimesi, Z., May, E., ... Klaphake, E. (2003). Ultraviolet light and reptiles, amphibians. *Journal of Herpetological Medicine and Surgery*, 13(4), 27–37. <https://doi.org/10.5818/1529-9651.13.4.27>
- Amo, L., López, P., & Martín, J. (2004). Chemosensory recognition and behavioral responses of wall lizards, *Podarcis muralis*, to scents of snakes that pose different risks of predation. *Copeia*, 2004(3), 691–696. <https://doi.org/10.1643/CE-03-220R1>
- Baeckens, S., Herrel, A., Broeckhoven, C., Vasilopoulou-Kampitsi, M., Huyghe, K., Goyens, J., & Van Damme, R. (2017). Evolutionary morphology of the lizard chemosensory system. *Scientific Reports*, 7, 10141. <https://doi.org/10.1038/s41598-017-09415-7>
- Banks, P. B., & Dickman, C. R. (2007). Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology and Evolution*, 22(5), 228–229. <https://doi.org/10.1016/j.tree.2007.02.003>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bininda-Emonds, O. R., Decker-Flum, D. M., & Gittleman, J. L. (2001). The utility of chemical signals as phylogenetic characters: An example from the Felidae. *Biological Journal of the Linnean Society*, 72(1), 1–15. <https://doi.org/10.1006/bjil.2000.0492>
- Brock, K. M., Bednekoff, P. A., Pafilis, P., & Foutopoulos, J. (2015). Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? *Evolution*, 69(1), 216–231. <https://doi.org/10.1111/evo.12555>
- Burnham, E., Bender, L. C., Eiceman, G. A., Pierce, K. M., & Prasad, S. (2008). Use of volatile organic components in scat to identify canid species. *Journal of Wildlife Management*, 72(3), 792–797. <https://doi.org/10.2193/2007-330>
- Bytheway, J. P., Carthey, A. J. R., & Banks, P. B. (2013). Risk vs. reward: How predators and prey respond to aging olfactory cues. *Behavioral Ecology and Sociobiology*, 67(5), 715–725. <https://doi.org/10.1007/s00265-013-1494-9>
- Carthey, A. J. R., Bucknall, M. P., Wierucka, K., & Banks, P. B. (2017). Novel predators emit novel cues: A mechanism for prey naivety towards alien predators. *Scientific Reports*, 7(1), 1–9. <https://doi.org/10.1038/s41598-017-16656-z>
- Chowdhury, S., Maji, J., Chaudhuri, A., Dwari, S., & Mondal, A. K. (2017). *Ahaetulla nasuta* (green vine snake). Diet. *Herpetological Review*, 48(2), 444.
- Chutipong, W., Duckworth, J. W., Timmins, R., Willcox, D. H. A., & Ario, A. (2016). *Herpestes javanicus*. *The IUCN Red List of Threatened Species 2016*: e.T70203940A45207619. Available at <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T70203940A45207619.en>
- Conover, M. R. (2007). *Predator-prey dynamics: The role of olfaction*. Boca Raton, FL: CRC Press/Taylor & Francis Group.
- Cooper, W. E. (1996). Preliminary reconstructions of nasal chemosensory evolution in Squamata. *Amphibia-Reptilia*, 17(4), 395–415. <https://doi.org/10.1163/156853896X00117>
- Cooper, W. E., Paulissen, M. A., & Habegger, J. J. (2000). Discrimination of prey, but not plant, chemicals by actively foraging, insectivorous lizards, the lacertid *Takydromus sexlineatus* and the teiid *Cnemidophorus gularis*. *Journal of Chemical Ecology*, 26(7), 1623–1634. <https://doi.org/10.1023/A:1005534828701>
- Cooper, W. E., Perez-Mellado, V., Vitt, L. J., & Budzynski, B. (2003). Cologne as a pungency control in tests of chemical discrimination: Effects of concentration, brand, and simultaneous and sequential presentation. *Journal of Ethology*, 21(2), 101–106. <https://doi.org/10.1007/s10164-002-0082-7>
- R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>
- Cox, J. G., & Lima, S. L. (2006). Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution*, 21(12), 674–680. <https://doi.org/10.1016/j.tree.2006.07.011>
- Derby, C. D., & Sorensen, P. W. (2008). Neural processing, perception, and behavioral responses to natural chemical stimuli by fish and crustaceans. *Journal of Chemical Ecology*, 34(7), 898–914. <https://doi.org/10.1007/s10886-008-9489-0>
- Downes, S., & Bauwens, D. (2002). Does reproductive state affect a lizard's behavior toward predator chemical cues? *Behavioral Ecology and Sociobiology*, 52(6), 444–450. <https://doi.org/10.1007/s00265-002-0538-3>
- Dunbar, J. P., & Dunbar, T. M. (2015). *Ahaetulla prasina* (Asian vinesnake). Diet and feeding behavior. *Herpetological Review*, 46(2), 264–265.
- Fendt, M., Endres, T., Lowry, C. A., Apfelbach, R., & McGregor, I. S. (2005). TMT-induced autonomic and behavioral changes and the neural basis of its processing. *Neuroscience and Biobehavioral Reviews*, 29(8), 1145–1156. <https://doi.org/10.1016/j.neubiorev.2005.04.018>
- Font, E., Carazo, P., Pérez de Lanuza, G., & Kramer, M. (2012). Predator-elicited foot shakes in wall lizards (*Podarcis muralis*): Evidence for a pursuit-deterrent function. *Journal of Comparative Psychology*, 126(1), 87–96. <https://doi.org/10.1037/a0025446>
- Gérard, A., Jourdan, H., Cugnière, C., Millon, A., & Vidal, E. (2014). Is naiveté forever? Alien predator and aggressor recognition by two endemic island reptiles. *Naturwissenschaften*, 101(11), 921–927. <https://doi.org/10.1007/s00114-014-1233-8>
- Gérard, A., Jourdan, H., Millon, A., & Vidal, E. (2016). Knocking on heaven's door: Are novel invaders necessarily facing naïve native species on islands? *PLoS ONE*, 11(3), 1–14. <https://doi.org/10.1371/journal.pone.0151545>
- Gorman, M. L. (1976). A mechanism for individual recognition by odour in *Herpestes auropunctatus* (Carnivora: Viverridae). *Animal Behaviour*, 24, 141–145. [https://doi.org/10.1016/S0003-3472\(76\)80107-8](https://doi.org/10.1016/S0003-3472(76)80107-8)
- Gorman, M. L., & Trowbridge, B. J. (1989). The role of odor in the social lives of Carnivores. In J. L. Gittleman (Ed.), *Carnivore Behavior, Ecology, and Evolution* (pp. 57–88). New York, NY: Cornell University Press.
- Graves, B. M., & Halpern, M. (1990). Roles of vomeronasal organ chemoreception in tongue flicking, exploratory and feeding behaviour of



- the lizard, *Chalcides ocellatus*. *Animal Behaviour*, 39, 692–698. [https://doi.org/10.1016/S0003-3472\(05\)80380-X](https://doi.org/10.1016/S0003-3472(05)80380-X)
- Greene, L. K., Wallen, T. W., Moresco, A., Goodwin, T. E., & Drea, C. M. (2016). Reproductive endocrine patterns and volatile urinary compounds of *Arctictis binturong*: Discovering why bearcats smell like popcorn. *Science of Nature*, 103(5–6), <https://doi.org/10.1007/s00114-016-1361-4>
- Halpern, M. (1992). Nasal chemical senses in reptiles: Structure and function. In C. Gans, & D. Crews (Eds.), *Biology of the Reptilia*, Vol. 18 (pp. 423–532). Chicago, IL: The University of Chicago Press.
- Halpern, M., & Kubie, J. L. (1984). The role of the ophidian vomeronasal system in species-typical behavior. *Trends in Neurosciences*, 7(12), 472–477. [https://doi.org/10.1016/S0166-2236\(84\)80258-1](https://doi.org/10.1016/S0166-2236(84)80258-1)
- Hays, W. S. T., & Conant, S. (2007). Biology and impacts of Pacific island invasive species. 1. A worldwide review of effects of the small Indian mongoose, *Herpestes javanicus* (Carnivora: Herpestidae). *Pacific Science*, 61(1), 3–16. <https://doi.org/10.1353/psc.2007.0006>
- Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, 54(2), 187–211. <https://doi.org/10.2307/1942661>
- Kartik, A. (2018). *Ahaetulla nasuta* (Indian vine snake) diet. *Herpetological Review*, 49(2), 333.
- Kats, L. B., & Dill, L. M. (1998). The scent of death: Chemosensory assessment of predation risk by prey animals. *Écoscience*, 5(3), 361–394. <https://doi.org/10.1080/11956860.1998.11682468>
- Kotrschal, A., Deacon, A. E., Magurran, A. E., & Kolm, N. (2017). Predation pressure shapes brain anatomy in the wild. *Evolutionary Ecology*, 31(5), 619–633. <https://doi.org/10.1007/s10682-017-9901-8>
- Kroodsma, D. E., Byers, B. E., Goodale, E., Johnson, S., & Liu, W.-C. (2001). Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour*, 61(5), 1029–1033. <https://doi.org/10.1006/anbe.2000.1676>
- Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software*, 25(1), 1–18. <https://doi.org/10.1016/j.envint.2008.06.007>
- Lenth, R. V. (2016). Least-Squares Means: The R package lsmeans. *Journal of Statistical Software*, 69(1), 1–33. <https://doi.org/10.18637/jss.v069.i01>
- Lewis, D. S., van Veen, R., & Wilson, B. S. (2010). Conservation implications of small Indian mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: The Hellshire Hills, Jamaica. *Biological Invasions*, 13, 25–33. <https://doi.org/10.1007/s10530-010-9781-0>
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640. <https://doi.org/10.1139/z90-092>
- Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). 100 of the world's worst invasive alien species: A selection from the Global Invasive Species Database. *Aliens*, 12, 1–12. Retrieved from [http://interface.creative.auckland.ac.nz/database/species/reference\\_files/100English.pdf](http://interface.creative.auckland.ac.nz/database/species/reference_files/100English.pdf)
- Martín, J., Ortega, J., & López, P. (2015). Experience may allow increasing accuracy of the innate chemosensory recognition of snake predators by Iberian wall lizards. *Behavioral Ecology and Sociobiology*, 69(9), 1565–1572. <https://doi.org/10.1007/s00265-015-1968-z>
- May, M. D., Bowen, M. T., McGregor, I. S., & Timberlake, W. (2012). Rubbings deposited by cats elicit defensive behavior in rats. *Physiology and Behavior*, 107(5), 711–718. <https://doi.org/10.1016/j.physbeh.2012.03.007>
- Mencia, A., Ortega, Z., & Pérez-Mellado, V. (2016). Chemical discrimination of sympatric snakes by the mountain lizard *Iberolacerta galani* (Squamata: Lacertidae). *Herpetological Journal*, 26(2), 149–155.
- Monks, J. M., Nelson, N. J., Daugherty, C. H., Brunton, D. H., & Shine, R. (2019). Does evolution in isolation from mammalian predators have behavioural and chemosensory consequences for New Zealand lizards? *New Zealand Journal of Ecology*, 43(1), 3359. <https://doi.org/10.20417/nzjcol.43.10>
- Mori, A. (1990). Tail vibrations of the Japanese grass lizard *Takydromus tachydromoides* as a tactic against a snake predator. *Journal of Ethology*, 8(2), 81–88. <https://doi.org/10.1007/BF02350278>
- Nellis, D. W. (1989). *Herpestes auropunctatus*. *Mammalian Species*, 342, 1–6. <https://doi.org/10.2307/3504091>
- Ortega, Z., Mencia, A., & Pérez-Mellado, V. (2017). Rapid acquisition of antipredatory responses to new predators by an insular lizard. *Behavioral Ecology and Sociobiology*, 71(1), 1. <https://doi.org/10.1007/s00265-016-2246-4>
- Patou, M.-L., Mclenachan, P. A., Morley, C. G., Couloux, A., Jennings, A. P., & Veron, G. (2009). Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian *Herpestes*. *Molecular Phylogenetics and Evolution*, 53(1), 69–80. <https://doi.org/10.1016/j.ympev.2009.05.038>
- Pauwels, O. S. G. (2000). Herpetological investigations in Phang-Nga Province, southern Peninsular Thailand, with a list of reptile species and notes on their biology. *Dumerilia*, 4(2), 123–154.
- Pereira, A. G., & Moita, M. A. (2016). Is there anybody out there? Neural circuits of threat detection in vertebrates. *Current Opinion in Neurobiology*, 41, 179–187. <https://doi.org/10.1016/j.conb.2016.09.011>
- Pitt, W. C., Sugihara, R. T., & Berentsen, A. R. (2015). Effect of travel distance, home range, and bait on the management of small Indian mongooses. *Herpestes auropunctatus*. *Biological Invasions*, 17(6), 1743–1759. <https://doi.org/10.1007/s10530-014-0831-x>
- Schulterbrandt, T. G., Kubie, J., Von Gizycki, H., Zuri, I., & Halpern, M. (2008). Patterns of tongue-flicking by garter snakes (*Thamnophis sirtalis*) during presentation of chemicals under varying conditions. In J. L. Hurst, R. J. Beynon, S. C. Roberts, & T. D. Wyatt (Eds.), *Chemical Signals in Vertebrates 11* (pp. 345–356). New York, NY: Springer Science+Business Media LLC.
- Schwenk, K. (1993). The evolution of chemoreception in squamate reptiles: A phylogenetic approach. *Brain, Behavior and Evolution*, 41(3–5), 124–137. <https://doi.org/10.1159/000113830>
- Sharma, R. C. (2003). *Handbook: Indian Snakes*. Kolkata, India: Zoological Survey of India.
- Sharma, V. (2019). *Ahaetulla prasina* (Boie, 1827) - behaviour. India Biodiversity Portal, Species Page: *Ahaetulla prasina*. Available at: <https://indiabiodiversity.org/biodiv/species/show/238768> [Accessed date Sep 25, 2019].
- Silva, L., & Antunes, A. (2017). Vomeronasal receptors in vertebrates and the evolution of pheromone detection. *Annual Review of Animal Biosciences*, 5, 353–370. <https://doi.org/10.1146/annurev-animal-022516-022801>
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Takahashi, L. K. (2014). Olfactory systems and neural circuits that modulate predator odor fear. *Frontiers in Behavioral Neuroscience*, 8, 72. <https://doi.org/10.3389/fnbeh.2014.00072>
- Thoen, C., Bauwens, D., & Verheyen, R. F. (1986). Chemosensitive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. *Animal Behaviour*, 34(6), 1805–1813. [https://doi.org/10.1016/S0003-3472\(86\)80266-4](https://doi.org/10.1016/S0003-3472(86)80266-4)
- Thy, N., Nguyen, T. Q., Golynsky, E., Demegillo, A., Diesmos, A. C., & Gonzalez, J. C. (2012). *Ahaetulla prasina*. *The IUCN Red List of Threatened Species 2012: e.T176329A1439072*. Available at <https://doi.org/10.2305/IUCN.UK.2012-1.RLTS.T176329A1439072.en>
- Van Damme, R., Bauwens, D., Thoen, C., Vanderstighelen, D., & Verheyen, R. F. (1995). Responses of naive lizards to predator chemical cues. *Journal of Herpetology*, 29(1), 38–43. <https://doi.org/10.2307/1565083>

- Van Damme, R., & Quick, K. (2001). Use of predator chemical cues by three species of lacertid lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, and *Podarcis sicula*). *Journal of Herpetology*, 35(1), 27–36. <https://doi.org/10.2307/1566019>
- Van Moorleghe, C., Huyghe, K., & Van Damme, R. (2020). Chemosensory deficiency may render island-dwelling lizards more vulnerable to invasive predators. *Biological Journal of the Linnean Society*, 129(1), 128–142. <https://doi.org/10.1093/biolinnean/blz142>
- Veron, G., Patou, M. L., Pothet, G., Simberloff, D., & Jennings, A. P. (2007). Systematic status and biogeography of the Javan and small Indian mongooses (Herpestidae, Carnivora). *Zoologica Scripta*, 36(1), 1–10. <https://doi.org/10.1111/j.1463-6409.2006.00261.x>
- Vogrin, P. N., McCleary, R. J. R., & Benel, T. Y. (2016). *Ahaetulla prasina* (Oriental whip snake). Diet. *Herpetological Review*, 47(3), 471–472.
- Webster, C., Massaro, M., Michael, D. R., Bambrick, D., Riley, J. L., & Nimmo, D. G. (2018). Native reptiles alter their foraging in the presence of the olfactory cues of invasive mammalian predators. *Royal Society Open Science*, 5(10), 180136. <https://doi.org/10.1098/rsos.180136>
- Weldon, P. J. (1990). Responses by vertebrates to chemicals from predators. In D. W. Macdonalds, D. Muller-Schwarze, & S. E. Natynczuk (Eds.), *Chemical signals in vertebrates 5* (pp. 500–521). Oxford, UK: Oxford University Press.
- Zhang, Y. P., & Ji, X. (2004). The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae). *Journal of Thermal Biology*, 29(1), 45–53. <https://doi.org/10.1016/j.jtherbio.2003.10.007>
- Zhao, E. M., & Adler, K. (1993). *Herpetology of China*. Oxford, UK: Society of the Study of Amphibians and Reptiles.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Van Moorleghe C, Van Damme R.

The Asian grass lizard (*Takydromus sexlineatus*) does not respond to the scent of a native mammalian predator.

*Ethology*. 2020;00:1–10. <https://doi.org/10.1111/eth.13002>