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Chemical discrimination of sympatric snakes by the mountain lizard Iberolacerta galani (Squamata: Lacertidae)

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We conducted an experiment on chemical discrimination of two saurophagous snakes (the smooth snake, *Coronella austriaca* and the Seoane's viper, *Vipera seoanei*) as well as the aquatic *Natrix maura*, by the mountain lizard *Iberolacerta galani.* Using terraria, 24 lizards were exposed to scents by the three snakes as well as an odourless control. We quantified fourteen behavioural variables, twelve of which significantly differed among treatments. Lizards are able to recognise the scents of both predatory snakes, and react to them with intense antipredatory responses. The antipredatory behaviour found in *I. galani* was similar for the scents of the two different predatory snakes, despite differences in their foraging behaviour. The behaviour displayed by lizards confronted with chemical cues suggests an adaptation to minimise the likelihood of being attacked.

Key words: antipredatory behaviour, chemoreception, *Iberolacerta galani*, Lacertidae, Reptiles, Squamata

INTRODUCTION

The hunting efficiency of predators goes hand in hand with the efficiency of antipredatory behaviours of prey (Vermeij, 1994). Recognising predators through chemoreception is common in vertebrates (fish: Helfman, 1989; Hirvonen et al., 2000; amphibians: Semlitsch & Gavasso, 1992; birds: Roth et al., 2008; mammals: Apfelbach et al., 2005; reptiles: Cooper, 1990; Dial & Schwenk, 1996; Downs & Shine, 1998; Van Damme & Quick, 2001; Labra & Niemeyer, 2004; see also Kats & Dill, 1998 for a review), and the responsiveness of prey is linked to the relationship with the predator (threat-sensitivity hypothesis: Helfman, 1989).

Reptiles have highly developed mechanisms of chemical communication, and offer a unique opportunity to study antipredatory behaviour based on chemical stimuli (Schwenk, 1995). Lizards use chemoreception to locate food (Cooper, 1994), in social interactions (Verbeek, 1972), and to identify potential predators (Thoen et al., 1986; Dial et al., 1989; Cooper, 1990; Webb et al., 2009). Many reptiles show specific antipredatory behaviours in response to chemical cues that prevent potential attacks (Kats & Dill, 1998; Mason & Parker, 2010).

It is well-established that lizards behave distinctly when presented with odours of potential predators (Thoen et al., 1986; Van Damme et al., 1990, 1995; Van Damme & Castilla, 1996; Van Damme & Quick, 2001). In the case of the genus *Iberolacerta*, *I. cyreni* is able to assess the risk of predation and to balance the costs

and benefits of reacting to different visually detectable attacks (Martín et al., 2009a). Moreover, *I. cyreni* is able to flexibly respond to attacks from terrestrial predators that differ in intensity, suggesting that it can adjust its behaviour according to the costs associated with the perceived risk of predation (Martín et al., 2009b).

In this study, we used the León rock lizard, *I. galani* from isolated high mountain habitats as a model organism. The population under study co-occurs with two terrestrial predators: the smooth snake (*Coronella austriaca*) and the Seoane´s viper (*Vipera seoanei*), as well as the aquatic snake *Natrix maura*. *Coronella austriaca* is a saurophagous species which uses mixed strategies of ambush behaviour and active foraging (Goddard, 1984; Galán, 1998), while *V. seoanei* is mainly an ambush predator and a generalist forager that includes lizards in its diet (Saint-Girons, 1983; Braña, 1998a). *Coronella austriaca* is a non-venomous constrictor species, while *V. seoanei* is venomous. *Natrix maura* uses mixed foraging strategies and mainly feeds on invertebrates, amphibian larvae and fish (Hailey & Davies, 1986; Braña, 1998b). We establish whether *I. galani* is able to identify chemical cues from snake predators, describe the response of lizards to chemical cues from predators, and describe differences in antipredatory responses. Our hypothesis is that *I. galani* is able to recognise the scent of its predators and react to them with antipredatory responses (Thoen et al., 1986). The expected antipredatory response would include a decrease of lizard movement, combined with a high rate of tongue-flicks, tail waving and other jerking movements.

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MATERIALS AND METHODS

Study species

The León rock lizard, *I. galani*, is a recently described lacertid lizard endemic to North-Western Spain (Arribas et al., 2006). It inhabits rocky substrates above the tree line (>1400 m), and is an insectivorous species (unpublished data). The ecology of *I. galani* is mainly unknown.

Maintenance and experimental procedures

On 31 May 2012, 24 adult lizards were collected by noosing (*X*±SE, SVL=65.0±1.69 mm) at the Natural Monument "Lago de La Baña" (León province, Spain). For transport to the laboratory, lizards were kept in individual cloth bags placed inside individual terraria. To obtain the scents of snakes, adult individuals of *C. austriaca, V. seoanei* and *N. maura* were captured in the same area and on the same day. Snakes were transported in a different vehicle than lizards in order to avoid any odour mixture. The experiments were performed during the first week of June 2012. Lizards were kept in individual terraria (40 x 25 x 30 cm) with a substrate of artificial grass, and fed daily with crickets and *Tenebrio molitor* larvae; water was provided *ad libitum*. Snakes were housed in separate terraria (50 x 30 x 30 cm) with a substrate of artificial grass and water *ad libitum*. To avoid odour mixture, snake terraria were placed in different rooms.

Our experimental protocol was similar to those previously employed with geckos (Dial & Schwenk, 1996; Downes & Shine, 1998; Webb et al., 2009) and lacertid lizards (Thoen et al., 1986; Van Damme et al., 1995; Van Damme & Quick, 2001). We used an empty odourless terrarium as a control, and three terraria for treatments: one with the odour from *N. maura*, and two terraria with odour cues from *C. austriaca* and *V. seoanei.* In all four experimental terraria (60 x 40 x 40 cm) we placed absorbent paper on the floor to retain the odour of each treatment. The control terrarium had the floor covered with clean absorbent paper. In the three experimental terraria, a snake was introduced 24 hours before trials. The terraria were closed with transparent plastic covers. The snakes were removed from their terraria two minutes before a trial and re-introduced after the trial. Each lizard was subjected once to each treatment following a random order of permutations (4!=24 permutations), resulting in 96 trials (24 lizards x 4 treatments). Each lizard was tested once a day within the normal activity period (0900 to 1700 hours).

The test room was dark and only the terrarium was illuminated by a 75 W bulb 50 cm above it. A temperature of 30°C was maintained in the terrarium, which is within the set-point range of preferred body temperatures of *I. galani* (unpublished data). To avoid a potential decrease in the scent concentration, we closed the terrarium with a transparent cover when the lizard was placed inside it, and recorded its behaviour over 15 minutes. All terraria were marked in six sectors of equal surface in order to count the number of times the lizard moved from one sector to another. Two observers were placed two metres from the terrarium opposite eachother. One observer recorded with binoculars the number of tongue flicks and antipredatory variables. The second observer recorded the number of movements and changes among sectors. At the conclusion of the study (6 days), animals were released at their capture sites.

Behavioural observations

We started to record a lizard's behaviour five seconds after placing it in the centre of the experimental terrarium. The duration of each trial was 15 minutes. Fourteen behavioural variables were recorded: (i) Walk: the lizard walks normally, (ii) Change among sectors: the

Table 1. Mean±SE of each behaviour and results from Friedman's Test (Chi-squared values and *p*-values; *n*=24, df=3) for the 4 experimental treatments (Control, *Natrix*, *Coronella* and *Vipera*). [1] Significant differences are marked with *.

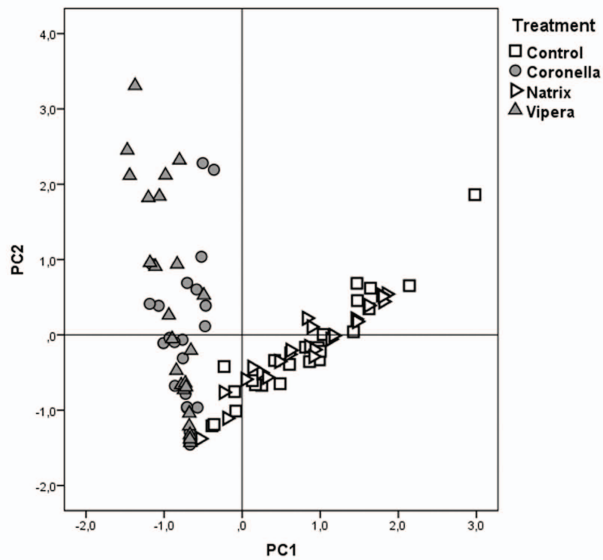|	Mean±SE (*n*=24)					
Behaviours	Control	*Natrix*	*Coronella*	*Vipera*	Friedman's Chi-squared	Friedman's *p*-value[1]
(i) Walk	74.5±9.72	75.29±7.76	1.91±0.63	0.12±0.12	62.16	<0.0001*
(ii) Ch. among s.	20.88±2.73	21.92±2.57	5.79 ±1.59	3.46±0.61	48.71	<0.0001*
(ii) Slow	0	0	12.42±2.18	14.79±2.23	64.82	<0.0001*
(iv) Tongue-Flick	194.6±18.93	212.10±13.34	155.4±21.61	189.20±24.7	5.18	0.159
(v) Snout	29.83±4.69	27.88±3.28	4.12±1.22	3.25±0.84	53.08	<0.0001*
(vi) Rubbing	70.08±10.43	68.04±8.92	4.58±1.51	2.87±1.17	61.06	<0.0001*
(vii) Stand and s.	5.12±1.5	6.71±1.28	0.67±0.32	0.25±0.18	39.71	<0.0001*
(viii) Head bob	0.17±0.13	0.12±0.69	6.54±1.42	8.87±1.82	46.94	<0.0001*
(ix) Foot shake	2.46±1.42	2.15±0.77	9.67±2.45	14.96±4.76	17.98	0.0004*
(x) Head raise	5.79±1.03	5.83±1.09	1.46±0.51	0.96±0.39	32.67	<0.0001*
(xi) Tail waving	0	0.04±0.04	7.41±3.15	14.71±4.07	41.89	<0.0001*
(xii) Walk time	231.50±32.43	227.7±22.65	5.12±1.76	0.12±0.12	62.71	<0.0001*
(xiii) Slow time	0	0	161.4±31.45	221.7±31.95	65.39	<0.0001*
(xiv) No move	662.2±32.64	668.2±23.32	738.9±31.54	678.6±31.94	7	0.072

Fig. 1. Scatterplot of PCA values clustered by treatment. PC1 describes the type of behaviour exhibited by *Iberolacerta galani*, and PC2 is correlated with the number of times lizards moved through sectors of terraria.

lizard moves from one to another of the six predefined sectors of the terrarium, (iii) Slow: the lizard walks slowly and with stalking or scattered movements (see for example, Thoen et al., 1986), (iv) Tongue-flick (TF): the lizard extrudes its tongue and quickly retracts it into the mouth, (v) Snout: the lizard taps the wall of the terrarium with the snout, (vi) Rubbing: the lizard rubs its head with the walls of the terrarium, (vii) Stand and scratching: the lizard stands up against the wall of the terrarium and scratches it with the forelegs, trying to escape, (viii) Head raise: the lizard raises the head with its forelimbs straighten, (ix) Tail waving: the lizard waves the tail in a horizontal plane, (x) Foot shake: the lizard moves the forelimbs rapidly up and down, (xi) Head bob: the lizard

moves its head up and down, (xii) Walk time: total time the lizard moves normally, (xiii) Slow time: total time the lizard moves in slow motion, and (xiv) No move: total time the lizard stays immobile. For the first 11 variables, we counted the number of times the lizard performed each behavioural pattern. We quantified the last three variables as the length of the behavioural pattern in seconds.

Data analysis
We performed all statistical analyses in an R environment (v.2.12.1, R Development Core Team, 2013). Because neither the original nor log-transformed data met the requirements of parametric statistics for any of the treatments, we analysed the data with non-parametric tests. We used the repeated measures Friedman's test to assess differences among treatments and control. We then performed post-hoc multiple comparisons for Friedman's test (Giraudoux, 2012). We also performed a Principal Components Analysis (PCA) of the 14 variables in order to summarise behavioural patterns and visualize differences. We conducted PCA using the prcomp function (Crawley, 2007). Since values of individuals for PCA axes met the assumptions of parametric statistics, we finally performed a repeated measures ANOVA from values of PCA axes to assess for differences in behavioural responses.

RESULTS

We observed two distinct behavioural patterns which can be interpreted as normal or antipredatory behaviour. Normal behaviour, observed during trials with the control and *Natrix* scent, consisted of walking and exploratory movements, head raising, head rubbing or wall scratching (the typical behaviour of a lizard trying to escape from a terrarium). These behaviours were virtually absent during trials with scents from predatory

Table 2. Post-hoc paired comparisons of Friedman's Test of the 12 variables in which differences between treatments were detected. Observed values of Friedman's post-hoc comparisons. Abbreviations of experimental treatments are: CON (Control), NAT (*Natrix*), COR (*Coronella*) and VIP (*Vipera*). * denotes a significant difference. [1] Critical values of Friedman's post-hoc comparisons are 28.12 for α=0.01 and 23.60 for α= 0.05.

Behavioural variable	Significance levels (α)[1]	Paired Comparisons[2]					
		CON-NAT	CON-COR	CON-VIP	NAT-VIP	NAT-COR	COR-VIP
(i) Walk	0.01	4	45*	55*	51*	41*	10
(ii) Ch. among s.	0.01	2	37.5*	46.5*	48.5*	39.5*	9
(iii) Slow	0.01	0	46*	50*	50*	46*	4
(v) Snout	0.01	1	42.5*	48.5*	47.5*	41.5*	6
(vi) Rubbing	0.01	2	43.5*	50.5*	52.5*	45.5*	7
(vii) Stand and s.	0.01	6	30*	34*	40*	36*	4
(viii) Head bob	0.01	1.5	38*	40.5*	39*	36.5*	2.5
(ix) Foot shake	0.05	6	30.5*	21.5	15.5	24.5*	9
(x) Head raise	0.01	2	30*	36*	38*	32*	6
(xi) Tail waving	0.05	1	23.5	37.5*	36.5*	22.5	14
(xii) Walk time	0.01	4	41*	51*	55*	45*	10
(xiii) Slow time	0.01	0	43*	53*	53*	43*	10

snakes where we observed lizards in slow motion, doing jerky movements such as head bob, tail waving and foot shakes described as typical antipredatory behaviours (see for example Thoen et al., 1986; Webb et al., 2009). We found significant differences between treatments in 12 of the 14 variables: Walk, Change among sectors, Slow, Snout, Rubbing, Stand and scratching, Head bob, Foot shake, Head raise, Tail waving, Walk time and Slow time ($p<0.001$ in all cases, Table 1). We did not find significant differences in two variables: Tongue-flick ($\chi^2=5.18$, $p=0.159$, see Table 1) and No move ($\chi^2=7.00$, $p=0.072$, see Table 1).

In post-hoc comparisons, we did not find significant differences between Control and *Natrix* for any of the 12 variables, and between treatments with *Vipera* and *Coronella* (Table 2). However, we found significant differences between Control and *Coronella* and *Natrix* and *Coronella* in 11 variables (all except Tail waving). We also found significant differences between Control and *Vipera* and *Natrix* and *Vipera* in 11 variables (all of them except for Foot shake, see Table 2).

For the PCA, Bartlett's test of sphericity was significant ($\chi^2=1573.47$, df=91, $p<0.0001$), indicating that the correlation among variables were different from zero. Thus, the 14 studied variables were suitable for dimensionality reduction with PCA. The first two Principal Components (PCs) explained 72.57% of the variation. The first principal component (PC1) explained 46.76% of the observed variation, and was positively correlated with Walk time, Walk, Snout, Rubbing, Change among sector, Head raise and Stand and scratching, as well as negatively correlated with Slow time, Slow, Head bob, Tail waving, Foot shake and No move (Table 3). Therefore, this axis describes two different kinds of behaviour: normal behaviour (positive values) and antipredatory behaviour (negative values). The second component (PC2) explained 25.81% of the variation in the data. It was positively related with TF, Slow time, Slow, Foot

Table 3. Correlation between each of the 14 behavioural variables measured in *Iberolacerta galani* and the first (PC1) and second principal component axes (PC2) of PCA.

Variables	PC1	PC2
Walk Time	0.951	0.122
Walk	0.946	0.102
Snout	0.899	0.272
Rubbing	0.896	0.164
Change among sector	0.856	0.283
Head raise	0.645	0.190
Stand and scratching	0.621	0.098
Head bob	-0.565	0.526
No move	-0.403	-0.847
Tongue-Flick	0.302	0.813
Slow time	-0.582	0.739
Slow	-0.575	0.648
Foot shake	-0.417	0.629
Tail waving	-0.430	0.589

shake, Tail waving, Head bob and Change among sector, and negatively related with No move (Table 3). Thus, this axis discriminated between individuals who remained motionless for a long period (negative values of PC2) and those that displayed high levels of activity, probably associated with antipredatory behaviour (Fig. 1). There are significant differences between the values of PC1 of Control and *Natrix* treatments from one side and the values of PC1 of *Coronella* and *Vipera* treatments from the other side (repeated measures ANOVA, $F_{1, 47}=224.76$, $p<0.0001$) highlighting the differences between normal and antipredatory behaviours.

DISCUSSION

This study showed that *I. galani* is able to recognise chemical cues from the predatory snakes *C. austriaca* and *V. seoanei*. Lizards react to these chemical cues by displaying a highly consistent antipredatory behaviour. No differences in behaviour were found between lizards subjected to the odourless control and those subjected to the scent of *N. maura*. Hence, *N. maura* is not recognised as a predator by *I. galani,* despite the strong scent of viperine snakes (Braña, 1998b). The fact that lizards do not recognise *N. maura* as a predator is congruent with its aquatic lifestyle and diet. Even if rare consumption of terrestrial lizards is described in the south of the Iberian Peninsula (Pleguezuelos & Moreno, 1989), the viperine snake does not feed on lizards (Hailey & Davies, 1986; Galán, 1988; Santos & Llorente, 1998, Santos et al., 2006).

The antipredatory behaviour observed during trials with scents from *C. austriaca* and *V. seoanei* was similar to behavioural patterns observed in other lacertid lizards (Thoen et al., 1986; Van Damme et al., 1995; Van Damme & Quick, 2001). We found significant differences between the two types of behavioural responses (Control and *Natrix* vs. *Coronella* and *Vipera*) in 12 of our 14 variables under study and, consequently, in overall behaviour when variables are combined in a PCA. This demonstrate that normal and antipredatory behaviour show quantitatively different behavioural patterns. In addition, the PCA revealed that the differences are more evident when lizards moved more during the trials.

The reaction of *I. galani* to chemical stimuli was similar for *C. austriaca* and *V. seoanei*. The observed intensity in the response was consistent with the fact that both species are important predators of lizards (Galán, 1998; Braña, 1998a). Nonetheless, we predicted that lizards exhibit different behavioural reactions due to adaptations to avoid predation from ambush versus active snakes (e.g., as shown for other species in Sherbrooke, 2008). Our findings may denote that both potential terrestrial predators represent an equivalent threat. However, it is also possible that the scents of both snakes elicit similar behavioural reactions, while visual displays of *C. austriaca* and *V. seoanei* would trigger different antipredatory responses. Similar antipredatory behaviours of geckos to chemical cues of predatory snakes with different foraging strategies have been observed previously (Webb et al., 2009).

Antipredatory behaviour of *I. galani* includes slow motion accompanied by jerky movements, tail waving and foot shakes. Slow motion might be a behavioural adaptation to decrease the chances of being detected (Labra & Niemeyer, 2004). Avoiding detection by predators can also save the energy costs of fleeing (Lima & Dill, 1990; Martín et al., 2009a). The remaining visual displays described in the antipredatory behaviour of *I. galani* have previously been reported in other species (see for example Thoen et al., 1986; Van Damme & Quick, 2001). Tail waving and foot shakes would not be advantageous for lizards trying to go undetected by snake predators. Nevertheless, tail waving is a well-known antipredatory mechanism related to the caudal autotomy capacity of lacertid lizards (Arnold, 1984, 1988). For *I. galani*, the advantage would be evident when facing a venomous snake such as *V. seoanei*.

The number of times the lizard changes among sectors of the terrarium provides a reliable indication of the extent of movements. Lizards moved significantly less when they detected chemical cues of predators. It is likely that less movement entails a lower probability of being detected by a predator (Lima & Dill, 1990). Moreover, lizards do not stand and scratch when they detect chemicals from predators, which could be another behavioural adaptation for crypsis.

We did not find significant differences between the four chemical stimuli in the number of TFs performed by lizards, while other studies reported an increase when lizards face the scents of predatory snakes (Thoen et al., 1986; Cooper, 1990; Van Damme et al., 1995; Van Damme & Quick, 2001; Webb et al., 2009, but see also Labra & Niemeyer, 2004). Nonetheless, lizards under high predation pressures from a specific predator might need to perform less TFs to identify chemical cues (Mori & Hasegawa, 1999). Another advantage to reduce the number of TFs when lizards recognise predator scents could be to divert the predator's attention from the head (Weldon, 1990; Cooper, 1994). Lizards can also perform other antipredatory behaviours before any tongue flick (Dial & Schwenk, 1996). Labra and Niemeyer (2004) suggested that behavioural studies on chemical discrimination of predators should focus on other behavioural variables, because it is difficult to interpret TFs due to their broad use. Furthermore, TFs do not necessary imply that lizards are recognising a predator, since some species respond to chemical cues by olfaction before performing any TFs (Cooper, 1998). The number of TFs may also be related to their own foraging strategy (Cooper & van Wyk, 1994; Cooper, 2000).

This study confirms that *I. galani* can recognise their snake predators by chemical detection and react with a set of well-defined behavioural patterns that probably minimise the chance of being detected by snakes. Such cryptic behaviour may be adaptive under the conditions prevailing at high mountain habitats, where lizards show reduced daily and annual activity periods. Thus, lizards would maximise the chances of survival and avoid the costs of fleeing. It is interesting that *I. galani* is able to discriminate predators from other similar organisms by chemical cues, thereby avoiding the potential costs

of fleeing from a snake that does not pose a threat. Antipredatory behavioural patterns of *I. galani* lizards are similar to the chemical cues of both snakes, and *I. galani* may have acquired a single mechanism to identify and avoid terrestrial predators regardless of their foraging strategy.

ACKNOWLEDGEMENTS

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