

Use of Predator Chemical Cues by Three Species of Lacertid Lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, and *Podarcis sicula*)

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ABSTRACT.—Three species of lacertid lizards (*Lacerta bedriagae*, *Podarcis tiliguerta*, and *Podarcis sicula*) are able to detect the former presence of the saurophagous snake *Coluber viridiflavus* by tongue flicking. Lizards tongue flicked more in cages previously inhabited by the predatory snake than in clean cages or in cages treated with eau-de-cologne. They also exhibited behavioral acts typically associated with stressful situations (foot shakes, tail vibrations, starts) more frequently when predator chemicals are present. Individuals from the two *Podarcis* species that came from populations syntopic with *C. viridiflavus* were also able to distinguish between chemical cues from this saurophagous predator and a nonsaurophagous snake (*Natrix maura*). In these lizards, the former presence of *N. maura* did not elicit higher tongue-flick rates or stress-indicating behaviors. In contrast, individuals of *Lacerta bedriagae* collected from a snake-free area increased tongue-flick rate and frequency of stress-related behavior in response to chemicals of both snakes, suggesting that prior contact is not required for chemosensory recognition of snakes in this species but may facilitate the distinction between different species of snakes. The presence of predator (*C. viridiflavus*) chemical cues induces a shift in the microhabitat use of the lizard species studied. In a large terrarium containing various substrates, lizards chose different types of microhabitats when chemical cues of *C. viridiflavus* were present than when absent and avoided the side of the terrarium labeled with the chemicals.

Although chemoreception is known to mediate many important behaviors in reptiles (for reviews, see Burghardt, 1970; Halpern, 1992; Mason, 1992), most studies on squamate chemoreception have concentrated on foraging behavior. Comparative analyses across lizard taxa revealed a strong association between foraging mode (widely foraging vs sit-and-wait predators) and the development of the vomeronasal apparatus (Schwenk, 1993, 1995; Cooper, 1994, 1995, 1997), suggesting that chemoreception evolved primarily to aid prey location and recognition. Much less is known about interspecific differences in the importance of chemoreception for other functions.

In this study, we assess the significance of chemoreception in the antipredator behavior of three lacertid lizard species. We want to know whether the lizards are able to detect and recognize chemical cues of a predatory snake, as has been demonstrated in other lacertids (Thoen et al., 1986; Van Damme and Castilla, 1996). In addition, we investigate whether the lizards use information on the presence of a predator when selecting microhabitats. We have chosen three species from the Mediterranean island of Corsica (France) for our experiments. The distributions of two of the species, *Podarcis tiliguerta* and *P. sicula*, coincide to a large degree with that of the predatory snake, *Coluber viridiflavus* (Delaugerre and Cheylan, 1992), and the individuals

used in our experiments come from populations that are most probably syntopic with the snake. *Lacerta bedriagae* is mostly restricted to high altitudes on Corsica and shows little or no overlap with that of *C. viridiflavus* (Delaugerre and Cheylan, 1992). We sampled a population that lives in a snake-free area. The three species also differ in microhabitat use (Lanza, 1955; Castilla et al., 1989; Van Damme et al., 1989, 1990b; Delaugerre and Cheylan, 1992). In the field, *P. tiliguerta* is the most catholic species; occurring almost anywhere on the island, although it is most often found near stone walls or rocks, which are used as basking sites. *Podarcis sicula* typically occupies densely vegetated areas. It is a ground-dwelling lizard that, when chased, dashes rapidly from one bush to another. *Lacerta bedriagae* is mostly found in open mountain areas, with little vegetation and large rocky outcrops. Using these species allows us to assess the significance of two potential sources of interspecific variation in the ability to recognize predators: (1) prior exposure to the predator; and (2) habitat structure. If previous exposure to the predator is important, we expect that *P. sicula* and *P. tiliguerta* will react more strongly to the chemicals than *L. bedriagae*. We may also expect that *L. bedriagae* and (to a lesser extent) *P. tiliguerta*, which live in open areas, rely more on visual cues and less on chemical information, whereas *P. sicula*, which lives in a habitat with limited visibility, will rely more on chemoreception.

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MATERIALS AND METHODS

Animals and Their Maintenance—Ten adult males of each species were captured by noose in the département Haut-Corse, France. *Podarcis sicula* were sampled from a population in the valley of the Fango, near Galéria. Individuals of *P. tiliguerta* were caught in the vicinity of the village of Pizio, and those of *L. bedriagae* close to the former skiing center of Haut-Asco. Lizards were transported to our laboratory in Kalmthout, Belgium, and housed in 100 × 50 × 50 cm terraria, each containing a layer of sand and some vegetation and flat stones. A 100-Watt bulb suspended above one side of the terrarium provided sufficient heat and light for 12 h/day. Water and food (crickets, dusted with vitamins and calcium) were provided ad libitum. Each terrarium contained five individuals of one species.

A single male *C. viridiflavus* (SVL 97 cm), caught in the vicinity of Chizé (Département Deux-Sèvres, France), was used to deposit chemicals into the experimental cages. Lizards are an important prey item for this species (Bruno, 1970, 1975; Bruno et al., 1973; Delaugerre and Cheylan, 1992). The snake was housed in a 70 × 50 × 50 cm terrarium in our laboratory but in a different room than the lizards. It was fed young mice.

A single female *Natrix maura* (SVL 45 cm), caught near Florac (Département Lozère, France), was used to put chemicals in the snake-control cages. The animal was kept in the laboratory in a terrarium similar as the one described above but equipped with a water basin. This snake was fed small fish weekly. *Natrix maura* is a largely aquatic snake that feeds mainly on fish, amphibians and invertebrates. It does not eat lizards (Hailey and Davies, 1986). This species inhabits the Iberian peninsula, the south of France and Switzerland, and northwest Africa (Gruber, 1989) and is absent from Corsica. The closely related *N. natrix* does occur on Corsica (Delaugerre and Cheylan, 1992), and does not normally eat lizards (Filippi et al., 1996).

Experiment 1: Chemical Cue Recognition—In our first series of experiments, we investigated whether individuals of the three species are able to perceive and recognize chemical cues left behind by the predatory snake *C. viridiflavus*. We observed the behavior of individual lizards in four types of experimental cages. The first type ("clean control") consisted of a 50 × 50 × 50 cm terrarium, containing a thin layer of sand covered with moss. The terrarium was unfamiliar to the lizards but contained no specific chemical information. The second type of cage ("cologne") was identical to the first, but some eau-de-cologne (Savane, frais-épicé) was sprin-

kled on the moss shortly before the lizard was introduced into the cage. This situation was used as a "pungency test," to observe responses to unknown chemical cues. Finally, lizards were tested in two types of cages that contained snake chemicals. The "Coluber" cage was a terrarium that had previously been inhabited by the *C. viridiflavus* snake; the "Natrix" cage had been inhabited by the *N. maura*. Both types of cages were otherwise identical to the control cages. The snakes spent a night in the experimental terraria and were removed shortly before the introduction of each lizard. A 100-W bulb was suspended 20 cm above the substrate of the terraria, providing enough heat to allow the lizards to attain body temperatures within their preference zone (32–36°C, Van Damme et al., 1990b). Each individual lizard (10 per species) was tested once in each situation. The order in which they were subjected to the four situations was assigned randomly. An individual was tested maximally once per day.

A 15-min observation session started immediately after the introduction of an individual lizard into the test terrarium. We recorded the behavior of the animal continuously by means of a specially designed computer program running on a PC (for details, see Van Damme and Castilla, 1996). The animal was observed from behind a one-way mirror placed against one side of the test-box. The other three sides were covered with paper.

We distinguished the following behaviors: (1) tongue flick—the lizard extrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate or is "waved" in the air; (2) walk—continuous, relatively fast forward movement; (3) slow motion—very slow movement accompanied by jerky or waving movements with the forelegs; (4) stand up—the lizard stands in an upright position against the glass wall of the terrarium and performs scratching movements with the forelegs; (5) no move—the lizard stands still, its abdomen resting on the substrate; this pattern can be accompanied by movements of the head, tail, or forelimbs; (6) bask—the lizard rests under the light bulb, with the ribs spread laterally; one or more feet are often tilted upward; (7) dig—the lizard digs with its forelimbs into the substrate; (8) start—sudden jump, most often followed by a quick, short run; (9) foot shake—the raised forelimbs are alternately and rapidly moved up and down; (10) tail vibration—the entire tail, or its posterior portion, is moved rapidly from side to side. At the end of the 15-min observation period, the computer program provides a list with the total duration (in sec) of behavioral acts 2–7 and counts of acts 1, 8, 9, and 10.

After experimentation, the lizard was re-

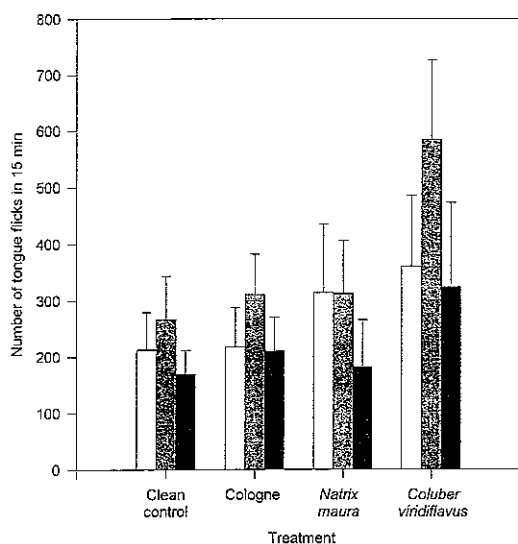


FIG. 1 Tongue-flick rates (number/15 min) of three lacertid lizards in the four experimental cages. Values are means (\pm SD) for 10 individuals per species. White bars: *Lucerta bedriagae*; grey bars: *Podarcis sicula*; black bars: *Podarcis tiliguerta*.

moved from the test cage and put back in its home terrarium. Sand and moss were removed from the cage, and the cage was thoroughly washed with soap and rinsed with water. New sand and moss were used for each observation session. We used four identical terraria, one for each situation.

We used repeated measures analysis of variance to assess effects of chemical treatment (within subjects factor) and variation among species (between subjects factor) on the mean duration or frequency of behavioral acts. The effect of treatment was then tested for each lizard species separately. All data were log₁₀-transformed to fulfill the requirements of normality and homogeneity of variances. We checked the symmetry conditions required for applying the multivariate approach to significance testing and adjusted degrees of freedom by multiplying them with the Greenhouse-Geisser ϵ , if necessary (Norusis, 1988). When the results of the repeated measures ANOVA indicated an effect of treatment, we used contrast analysis to test the significance of the following predicted specific differences: cologne control versus clean control (to test for effects of unfamiliar odors); *Coluber* versus clean control (to test the effects of chemicals of predatory snakes); *Coluber* versus cologne control (to test for differences between the effects of odors of predatory snakes and unfamiliar odors); *Natrix* versus *Coluber* (to test for differences between the effects of predatory and nonpredatory snake odors); and *Natrix* versus

clean control (to test for the effects of nonpredatory snake odors).

Experiment 2: Effects of Chemical Cues on Microhabitat Choice—The second experiment investigated whether chemical information associated with the (former) presence of a predatory snake is used in making decisions concerning the use of space. We observed lizards in a large (200 × 200 × 75 cm) terrarium that contained patches of seven types: bare sand (0.48 m²), moss (0.48 m²), low grass (*Poa annua*, approximately 7 cm high, 0.80 m²), tall grass (*Molinia caerulea*, approximately 40 cm high, 0.80 m²), bushes (*Lonicera* spp., approximately 30 cm high, 0.48 m²), tree trunks (*Pinus nigra*, approximately 25 cm high, 0.16 m²), and stone walls, consisting of loosely piled rocks (0.80 m²). A 150-W light bulb was suspended above each microhabitat patch. The distance between the bulb and the substrate was adjusted so that lizards would heat up equally fast in each patch. This was checked before experimentation, by measuring the body temperature of a dead lizard placed beneath the bulb in each patch. The terrarium was situated in an isolated room, and the animals were observed from behind a one-way mirror to minimize disturbance.

At the start of an experiment, five lizards of a given species were introduced into the terrarium and allowed to habituate to the new environment for 6 h. Subsequently, the microhabitat use of the lizards was recorded at 30-min intervals for a total of two days. We noted the substrate on which the animal rested or walked and the side of the terrarium in which it was located (see below). The animals were provided with food (crickets) and water (sprayed over all microhabitats) during the course of the experiments. After completion of the observations, the lizards were returned to their home terraria.

Lizards were first tested in a clean terrarium. After their removal, a wooden partition was placed in the middle of the terrarium, and the *C. viridiflavus* was introduced into one side (side S) of the box. It was allowed to crawl freely throughout one side of the terrarium for 24 h and was then removed. The wooden board was also taken away, and the five lizards were put back in the terrarium. Their use of space was recorded as in the control situation. The terrarium was organized in such a way that the lizards had all seven types of habitat patches available at both sides (labeled and unlabeled side). After the completion of each set of observations, the entire terrarium was cleaned and the vegetation replaced. Because all lizards were first tested in a blank cage, and then in a snake-labeled cage, the effect of snake presence on microhabitat use is confounded with order of testing in this experiment. Given the length of the

TABLE 1 Mean (\pm SD, $N = 10$) duration (in s) or number of the behavioral acts observed in the four experimental cages.

	<i>Lacerta bedriagae</i>				<i>Podarcis sicula</i>	
	Clean	Cologne	Natrix	Coluber	Clean	Cologne
Walk	179.0 \pm 104.9	287.5 \pm 97.4	264.2 \pm 139.4	270.3 \pm 81.7	476.7 \pm 165.9	497.6 \pm 142.4
Slow motion	0.0 \pm 0.0	0.1 \pm 0.3	8.7 \pm 18.4	17.9 \pm 25.2	1.6 \pm 4.1	23.7 \pm 64.8
Stand up	57.4 \pm 34.7	32.9 \pm 38.7	29.2 \pm 22.7	48.4 \pm 49.7	9.9 \pm 13.6	10.3 \pm 23.8
No move	471.7 \pm 109.2	408.3 \pm 98.8	407.5 \pm 150.4	413.9 \pm 93.7	200.7 \pm 230.7	202.8 \pm 159.1
Bask	182.2 \pm 84.5	163.2 \pm 71.1	180.4 \pm 149.4	149.4 \pm 113.4	180.1 \pm 102.0	137.8 \pm 97.9
Dig	9.7 \pm 14.7	8.0 \pm 9.2	9.9 \pm 15.4	0.1 \pm 0.3	30.9 \pm 39.5	27.8 \pm 21.8
Start	0.2 \pm 0.6	0.0 \pm 0.0	5.2 \pm 13.23	6.5 \pm 13.5	0.0 \pm 0.0	0.3 \pm 0.5
Foot shake	0.3 \pm 0.7	0.5 \pm 1.0	8.3 \pm 12.3	18.9 \pm 14.3	0.2 \pm 0.6	0.1 \pm 0.3
Tail vibration	0.3 \pm 0.3	0.4 \pm 0.3	5.4 \pm 6.2	16.7 \pm 10.2	0.9 \pm 1.0	0.7 \pm 0.6

habituation interval and the period of observation, we do not think that this confounding effect constitutes a serious problem, but it should be kept in mind when interpreting the results.

To test whether lizards avoided the half of the terrarium that had been labeled by the snake (side S), we determined the proportion of observations in either side for each individual and compared these values between the control and Coluber situation using repeated measures ANOVA. To test whether lizards changed their use of microhabitat in response to snake chemicals, we determined the proportion of observations on each microhabitat for each individual and compared these values between the control and Coluber situation using repeated measures ANOVA. Only observations in side S were counted in this analysis.

RESULTS

Experiment 1: Chemical Cue Recognition.—The former presence of the predatory snake *C. viridiflavus* elicited increased tongue-flick rates in all three species of lizards ($F_{3,81} = 41.70$, $P < 0.001$, Fig. 1). However, analysis of variance revealed a significant species \times treatment interaction effect ($F_{6,81} = 3.30$, $P = 0.01$) on the mean number of tongue flicks observed, indicating interspecific variation in the reaction to the four situations.

Contrast analysis revealed no differences in the mean number of tongue flicks observed in the clean control and the cologne situation in any of the three lizard species (all $P > 0.10$). In all three species, tongue-flick rates were higher in the Coluber-situation than in the clean control (all $P < 0.0004$) or the cologne situation (all $P < 0.02$). *Lacerta bedriagae* tongue flicked more in the Natrix situation than in the clean control ($F_{1,9} = 11.72$, $P = 0.008$). Tongue-flick rates in the Natrix and Coluber situations were equally high for this species ($F = 1.11$, $P = 0.32$). For the other two species, the differences in tongue-flick rates between the Natrix situation and the clean

control were not significant (both $P > 0.05$); both species tongue flicked more in the Coluber situation than in the Natrix situation (both $P < 0.003$). These results suggest that, although *P. sicula* and *P. tiliguerta* responded to chemicals of the predatory snake only, *L. bedriagae* responds with increased tongue flick rates to chemicals from both types of snakes.

Lizard behavior in the experimental cages differed in various aspects among species and among treatments (see Table 1). The duration of the walk behavior was similar in all four situations ($F_{3,81} = 2.17$, $P = 0.1$) but differed among species ($F_{2,27} = 4.45$, $P = 0.02$). *Lacerta bedriagae* moved less than the two *Podarcis* species. The species \times treatment interaction was not significant ($F_{6,81} = 0.97$, $P = 0.45$).

The mean duration of slow motion varied among species ($F_{2,27} = 6.73$, $P = 0.004$) and situations ($F_{2,3,63.2} = 13.23$, $P < 0.001$). The species \times treatment interaction effect was not significant ($F_{4,7,63.2} = 0.82$, $P = 0.53$). Slow motion was seen more often in *P. sicula* than in the other species. Contrast analysis revealed no differences in the mean duration of slow motion between the clean control and cologne situation in any of the three species (all three $P > 0.3$) or between the Natrix situation and the clean control (all three $P > 0.08$). The slow-motion behavior was seen more often in the Coluber situation than in the clean control (all three $P < 0.05$).

The mean duration of stand up also varied among species ($F_{2,27} = 12.42$, $P = 0.0001$) and situations ($F_{3,81} = 4.54$, $P = 0.005$). The interaction effect was not significant ($F_{6,81} = 1.57$, $P = 0.17$). *Podarcis sicula* performed this behavior much less often than the other two species. Mean duration of stand up did not differ between the clean control and the cologne situation in any of the three species (all $P > 0.10$), nor did it differ between the two snake situations (all $P > 0.16$). In *L. bedriagae* and *P. tiliguerta*, stand up was significantly less seen in both snake situations than in the control situa-

TABLE 1. Extended

<i>Podarcis sicula</i>		<i>Podarcis tiliguerta</i>			
Natrix	Coluber	Clean	Cologne	Natrix	Coluber
446.7 ± 201.1	552.9 ± 106.0	417.9 ± 94.9	391.8 ± 111.2	367.6 ± 184.5	413.0 ± 142.9
10.1 ± 13.1	47.2 ± 44.3	2.6 ± 8.2	0.0 ± 0.0	0.0 ± 0.0	18.8 ± 21.7
1.9 ± 3.03	5.9 ± 14.5	45.8 ± 39.9	57.2 ± 38.5	22.9 ± 29.9	26.1 ± 32.8
283.6 ± 257.2	195.1 ± 127.8	284.6 ± 133.9	292.4 ± 105.0	399.6 ± 228.3	246.7 ± 164.3
123.6 ± 81.8	94.4 ± 60.2	132.4 ± 60.7	145.8 ± 69.7	90.1 ± 56.3	189.8 ± 135.8
35.0 ± 35.3	7.8 ± 8.7	17.2 ± 25.4	12.7 ± 17.2	19.7 ± 41.2	5.8 ± 12.6
0.5 ± 0.7	2.5 ± 2.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 1.8
0.2 ± 0.6	1.3 ± 2.5	0.0 ± 0.0	0.9 ± 2.8	0.6 ± 0.8	17.1 ± 10.1
0.5 ± 0.4	1.1 ± 0.9	0.2 ± 0.2	0.2 ± 0.2	0.9 ± 0.8	5.6 ± 6.3

tions (all $P < 0.05$); in *P. sicula*, the difference was not statistically significant ($P = 0.1$).

The species \times treatment effect for the no move behavior was not significant ($F_{4,5,60.7} = 1.26$, $P = 0.29$). The mean duration of no move differed among species ($F_{2,27} = 5.12$, $P = 0.013$); *L. bedriagae* showed more of this behavior than the two *Podarcis* species. In the two *Podarcis* species, mean durations did not differ between the clean control and the cologne treatment (both $P > 0.75$). *Lacerta bedriagae* performed the no move behavior more often in the clean control than in the cologne treatment ($P = 0.007$). In all three species, no move was more frequently observed in the Natrix situation than in the clean control (all $P < 0.05$). The difference in mean duration between the Coluber situation and the clean control was significant in *L. bedriagae* ($P = 0.03$) but not in the other two species (both $P > 0.51$).

Chemical treatments had a different effect on the basking behavior of the three species (species \times treatment interaction: $F_{4,7,63.2} = 2.81$, $P = 0.025$). *Lacerta bedriagae* and *P. tiliguerta* basked equally long in all four situations (all planned comparisons $P > 0.2$), but *P. sicula* seemed to curtail its basking activity in the presence of *Coluber* chemicals (with respect to clean control: $P = 0.05$). It also basked less in the Natrix situation, but here the difference with the clean control was not significant ($P = 0.07$).

The mean duration of the digging behavior varied among situations ($F_{2,3,63.2} = 13.48$, $P < 0.0001$) and species ($F_{2,27} = 4.82$, $P = 0.016$). The interaction effect was not significant ($F_{4,7,63.2} = 0.32$, $P = 0.89$). *Podarcis sicula* dug more than the two other species. Mean duration of digging did not differ between the clean control and the cologne situation (all three $P > 0.2$). Lizards dug less in the Coluber situation than in the clean control, although the difference was not significant for *P. sicula*. There was no difference in the mean duration of digging between the Natrix situation and the clean control (all three $P > 0.78$).

The number of starts differed among treatments ($F_{1,8,48.6} = 13.79$, $P < 0.001$) but not between species ($F_{2,27} = 1.33$, $P = 0.28$). Starts were most frequently observed in the Coluber situation. Probably because of the high interindividual variability in this behavior, the repeated measures ANOVA does not reveal a species \times treatment effect ($F_{3,6,48.6} = 0.94$, $P = 0.45$). However, the data in Table 1 seem to suggest that, in contrast to both *Podarcis* species, *L. bedriagae* shows relatively high frequencies of starts in the Natrix situation.

The effect of treatment on the number of foot shakes varied among species (interaction effect: $F_{4,1,55.1} = 8.80$, $P < 0.001$). The average number of foot shakes did not differ between the clean control and the cologne situation in any of the three species (all $P > 0.7$). *Lacerta bedriagae* displayed more foot shakes in the Natrix situation ($F_{1,9} = 5.55$, $P = 0.042$) and in the Coluber situations ($F_{1,9} = 17.5$, $P = 0.002$) than in the clean control. The difference between both snake situations was not significant ($F_{1,9} = 3.54$, $P = 0.09$) in this species. *Podarcis sicula* exhibited equally few foot shakes in all situations (all planned contrasts, $P > 0.16$). *Podarcis tiliguerta* displayed foot shakes in the Coluber situation only (difference with clean control: $F_{1,9} = 28.4$, $P = 0.0005$). The number of foot shakes exhibited by this species in the Natrix situation was not different from that in the clean control ($F_{1,9} = 4.06$, $P = 0.075$). The difference between both snake situations was significant ($F_{1,9} = 23.96$, $P = 0.0009$).

The number of tail vibrations also showed an interaction between treatment and species ($F_{4,4,59.1} = 4.59$, $P = 0.002$). Again, differences between the clean control and the cologne treatment were not significant in any of the three species (all $P > 0.7$). Compared to the clean control, *L. bedriagae* vibrated its tail more often in the Coluber situation ($F_{1,9} = 10.00$, $P = 0.011$) and in the Natrix situation ($F_{1,9} = 4.89$, $P = 0.054$). The difference between both snake situ-

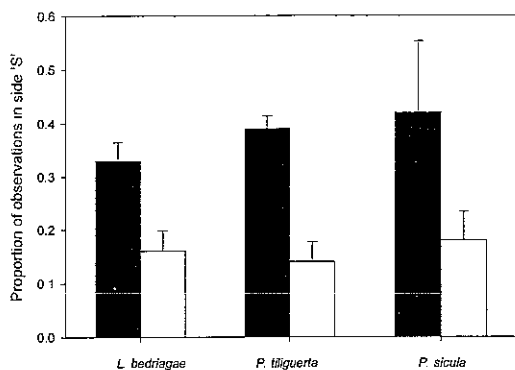


FIG. 2. Mean (\pm SE) proportion of time that individual lizards were seen in side S in the control (black bars) and Coluber situation (white bars). In the Coluber situation, side S contained snake chemicals.

ations was also significant ($F_{1,9} = 3.54$, $P = 0.02$). For *P. tiliguerta*, only the difference between the Coluber situation and the clean control was significant ($F_{1,9} = 5.02$, $P = 0.05$). *Podarcis sicula* exhibited this behavior rarely. In this species, none of the planned comparisons returned significant results.

Experiment 2: Effects of Chemical Cues on Microhabitat Choice.—All three species used side S less in the Coluber situation than in the control situation ($F_{1,26} = 44.70$, $P < 0.0001$, Fig. 2). There was no difference in the frequency of occurrence in side S among species ($F_{2,26} = 0.82$, $P = 0.45$) and the treatment \times species effect was not significant either ($F_{2,26} = 0.62$, $P = 0.54$).

In the control situation, *L. bedriagae* and *P. tiliguerta* were most often seen on the tree trunks and on the stone walls (Fig. 3). *Podarcis sicula* also made intensive use of the trunks but was seen far less on the walls. Instead, they spent relatively more time in the vegetation (tall grass, bushes) and on the moss.

A repeated measures MANOVA on the proportions of observations in the respective microhabitats revealed a strong interaction between treatment and species (Rao's $R_{12,26} = 5.47$, $P = 0.0001$), indicating that the change in microhabitat use in response to the snake chemicals differs among species. (The proportions for the microhabitat low grass were left out of this analysis to avoid the constant sum problem, i.e., the fact that the sum of all proportions must equal 1.) Univariate tests for each microhabitat revealed significant species \times treatment interaction effects for the proportions of lizards seen in bushes ($F_{2,18} = 28.71$, $P < 0.001$) and on moss ($F_{2,18} = 10.32$, $P = 0.001$). Although *L. bedriagae* and *P. tiliguerta* were seen less often in the bushes when snake chemicals were present, *P. sicula* strongly increased the use of this microhabitat

in that situation. The presence of snake chemicals inhibited the use of moss in *L. bedriagae* and *P. sicula* but stimulated it in *P. tiliguerta*. All three species were seen more on the wall ($F_{1,18} = 8.19$, $P = 0.01$) and less on the tree trunks ($F_{1,18} = 24.34$, $P = 0.0001$) in the Coluber situation than in the control situation. For the other microhabitats, effects of species and treatment were not significant.

DISCUSSION

Chemosensory Predator Recognition.—The data from our first experiment suggest that all three lizard species can perceive the presence of chemicals left behind by *C. viridiflavus*. This follows from the increased tongue-flick rates in a cage formerly inhabited by this snake. Tongue-flick rates in all three species are higher than in the clean control and in the cologne situation, indicating more persistent chemosensory investigation is stimulated by the snake chemicals than by a merely novel environment or by an unknown odor. Our results confirm those of Thoen et al. (1986) and Van Damme et al. (1990a) for *Lacerta vivipara* and those of Van Damme and Castilla (1996) for *Podarcis hispanica*; lacertid lizards seem to be able to detect the chemical cues of predatory snakes. This ability is apparently not restricted to a particular taxon of saurophagous snakes: there is now evidence that lacertids are able to recognize four species of potentially dangerous snakes, belonging to two families [Colubridae: *Coronella austriaca* (Thoen et al., 1986; Van Damme et al., 1990a), *Coluber viridiflavus* (this study); Viperidae: *Vipera berus* (Thoen et al., 1986; Van Damme et al., 1990a), *V. latastei* (Van Damme and Castilla, 1996)]. Geckos, skinks, and varanids have also been shown to be capable of identifying predatory snake chemicals (Dial et al., 1989; Cooper, 1990; Phillips and Alberts, 1992; Dial and Schwenck, 1996; Downes and Shine, 1998).

The behavioral changes in the Coluber situation suggest that the snake chemicals are recognized as cues for a potentially dangerous situation. This follows from the increase in the number of starts, foot shakes, and tail vibrations exhibited by the lizards and possibly from shifts in relative duration of the other behavioral acts. Some of these behavioral modifications may render the lizard less conspicuous (e.g., increase of slow motion, decrease of stand up), or increase its powers of observation (e.g., decrease of digging). In two of the species studied, the presence of *C. viridiflavus* chemicals also caused changes in the duration of the bask behavior. Previous work on *Lacerta vivipara* has demonstrated a complex interaction between antipredatory and thermoregulatory behaviors (Van Damme et al., 1990a). Precise thermoregulation

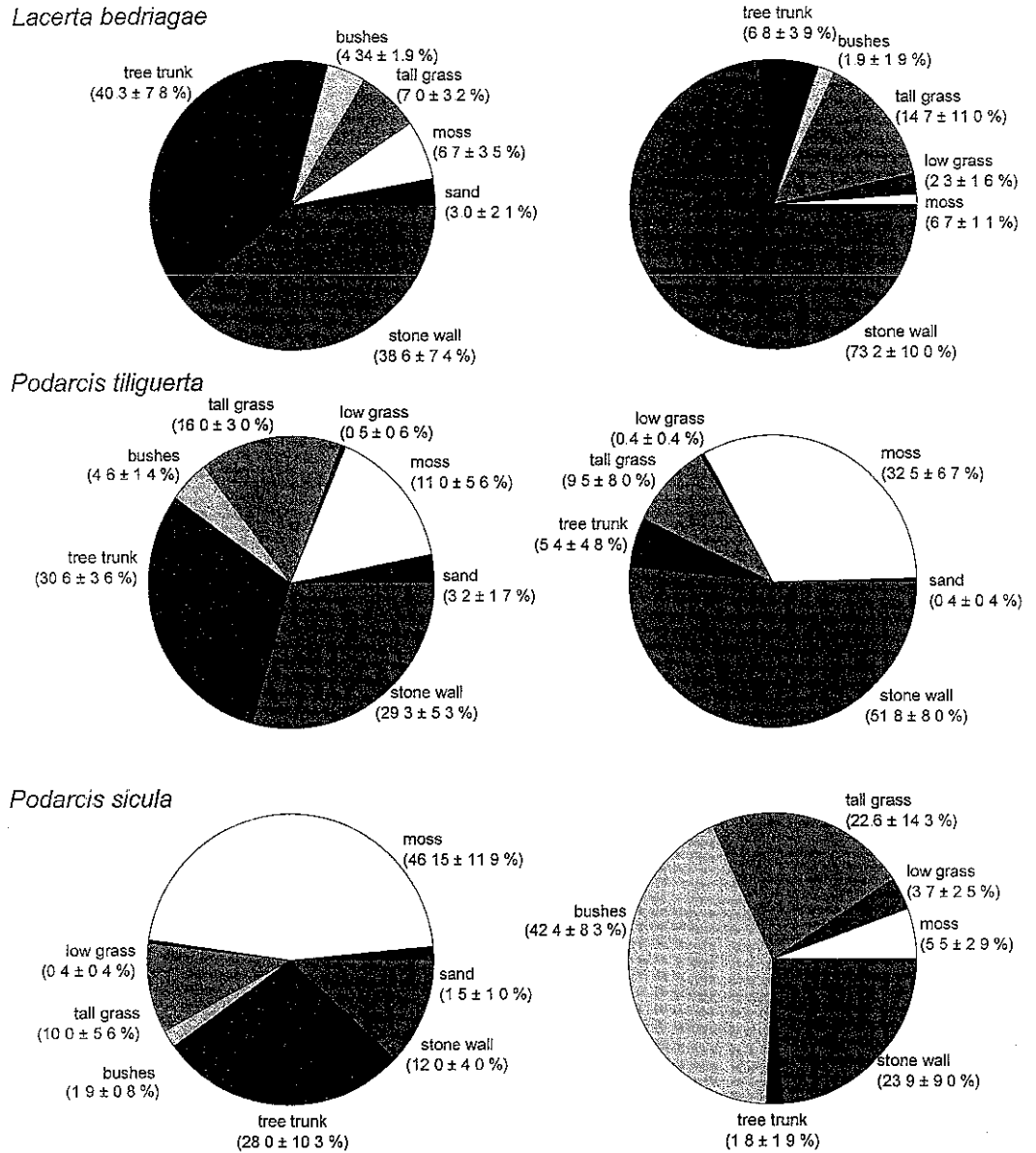


FIG. 3 Mean (\pm SE) proportion of time that individual lizards were seen in each microhabitat in the control (left) and the Coluber situation (right). Only observations on side S were counted

may enhance sprint speed and escape probability, but it may also increase exposure to predators. Our results suggest that the outcome of this conflict may vary among species.

High frequencies of starts, tail vibrations, and foot shakes seem typical for lacertid lizards that have detected predators or cues to their presence (see also Ihoen et al., 1986; Van Damme et al., 1990a, 1995; Van Damme and Castilla, 1996). The sudden, unpredictable starts may make the

lizard more difficult to catch. By waving their tails, lizards in threat of immediate predation may aim to deflect the attack of a detected predator toward the least viable part of their body (Cooper, 1998a, b). When observed in the absence of predators, the behavior has been explained as an anticipatory deflective display (Cooper, 1998a, b) or as a means to monitor predators that stalk lizards in a start-stop pattern (Magnusson, 1996). The latter hypothesis

may also provide a functional explanation for the increase in foot shakes observed in the snake situations (Magnusson, 1996).

It should be noted, however, that the foregoing functional interpretations could represent a case of adaptive story telling (Gould and Lewontin, 1979). Our first experiment does not allow to test the survival value of the observed behavioral responses. The changes may be mere signs of stress, without further adaptive significance. Moreover, by performing the experiments in a confined and structurally oversimplified environment, we deprived the lizard of the opportunity to exhibit several of its antipredatory strategies. For instance, it could not run away or hide itself. Testing the adaptiveness of the observed behavioral changes will require a more realistic setting (see also below, experiment 2).

Chemoreception seems to play an equally important role in all the species of lacertids studied. Lizards from different habitats, whether highly vegetated and structurally complex (heathland: *Lacerta vivipara*; mediterranean shrublands: *Podarcis sicula*) or more open (walls: *P. hispanica*, *P. tiliguerta*; montane meadows with boulders: *L. bedriagae*) seem capable of recognizing the former presence of snakes. Previous experience with the snakes does not seem prerequisite for being able to recognize their chemicals (see also Phillips and Alberts, 1992; Van Damme et al., 1995; Van Damme and Castilla, 1996; but see Downes and Shine, 1998).

We did find some indication that previous contact (within an individual lifetime, or genetic) may be of some significance. The two species that, in nature, are in contact with and are regularly preyed upon by snakes (i.e., *P. sicula* and *P. tiliguerta*) seem to be able to discriminate between dangerous snakes (*C. viridiflavus*) and harmless snakes (*N. maura*). In contrast, lizards from the snake-free location (*L. bedriagae*) do not discriminate between the two snakes. One may argue that both *Podarcis* species do not react to the chemicals of *N. maura* because this snake does not occur on Corsica. However, this would not explain the positive reaction of *L. bedriagae*. Moreover, the closely related (and equally non-saurophagous) *N. natrix* does occur on Corsica and is syntopic with the sampled *Podarcis* populations. Our results, therefore, suggest that *L. bedriagae* reacted to a more general snake odor, whereas *P. sicula* and *P. tiliguerta* have developed the ability to recognize hazardous snakes from harmless snakes. The latter ability seems adaptive in species that are regularly in contact with both types of snakes.

Predator-Induced Shifts in the Use of Space—In our second experiment, the three species differed markedly in their relative use of micro-

habitats. Habitat use in the terrarium is in remarkably close agreement with that in the field (see above, Lambert, 1967; Delaugerre and Cheylan, 1992; Van Damme et al., 1990b), suggesting that conditions provided in the experiment closely mimic those in a lizard's natural environment.

The preference of *L. bedriagae* and *P. tiliguerta* for the highest vertical elements in the terrarium increased in the presence of *C. viridiflavus* chemicals. *Podarcis sicula* reacted differently, shifting its use of space from open toward more heavily vegetated patches. We can think of two hypotheses to explain why lizards would change their habitat use in response to predatory chemicals. First, lizards may avoid microhabitats in which there is a great risk of encountering the predator. In this case, the habitat use of the lizards should be the inverse of that of the snake. This possibility seems unlikely for two reasons. First, we regularly observed the snake while it was labeling the experimental terrarium, and it seemed to make equal use of all microhabitats present. The snake was so big that it usually occupied several patches at the same time. In natural conditions too, *C. viridiflavus* uses a wide spectrum of microhabitats; it can be seen in dense vegetation but also climbs walls often (Delaugerre and Cheylan, 1992). Second, in this hypothesis, it is difficult to explain the different responses of the three lizard species. In addition, the lizards may select microhabitats where the risk of being caught is minimal. The observed differences among species would then reflect variation in escape tactics. Testing this hypothesis would require measuring locomotor performance on different substrates in the three species and observing the behavior during actual encounters.

Lizards of the three species avoided using the labeled half of the terrarium in the Coluber situation. The few times that lizards were seen on this side, they moved slower, adopted the low-profile slow-motion type of locomotion, tongue flicked more frequently and exhibited foot shakes. That is, their behavior was similar to that seen in the Coluber cages of experiment 1. Even during the control observations, lizards (especially *L. bedriagae* and *P. tiliguerta*) showed some preference for the side in question. This may be the result of the experimental set-up: the one-way mirror from behind which the animals were observed was located at that side. The increased use of the unlabeled side during the Coluber observations, however, can only be explained as an active avoidance of patches containing predator scents. These results show that lizards are not only able to recognize the chemicals of saurophagous snakes but that they also use this information to guide their use of space.

In nature, lizards may thus avoid potentially hazardous parts of their home range or refrain from entering dangerous unknown areas during dispersal.

It should be noted that, because of time constraints, we did not observe microhabitat use in the presence of nonpredatory chemical cues (cf cologne and *N. maura* treatments in experiment 1). Therefore, we cannot exclude the possibility that the shifts in space use observed in experiment 2 merely reflect the avoidance of novel scents. However, given the results of experiment 1, we are inclined to believe that the changes in microhabitat choice constitute a true antipredatory response.

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LITERATURE CITED

- BRUNO, S. 1970. Anfibi e rettili di Sicilia. Atti. Acca. Gio. Sc. Nat. Catania 7:1-144.
- . 1975. Note riassuntive sull'erpetofauna dell'isola di Montecristo (Archipelago Toscano, Mare Tirreno). Lav. Soc. Ital. Biogeogr., N.S. 5:1-98.
- BRUNO, S., S. DOLCE, G. SAULLI, AND M. VEBER. 1973. Introduzione ad uno studio sugli anfibi e rettili del Carso Triestino. Atti. Mus. Civ. Stor. Nat. Trieste 28:485-576.
- BURGHARDT, G. M. 1970. Chemical perception in reptiles. In D. G. Moulton and A. Turk (eds.), Advances in Chemoreception. I. Communication by Chemical Signals, pp. 241-308. Appleton-Century-Crofts, New York.
- CASTILLA, A. M., D. BAUWENS, R. VAN DAMME, AND R. F. VERHEYEN. 1989. Notes on the biology of the high altitude lizard *Lacerta bedriagae*. Herpetol. J. 1: 400-403.
- COOPER JR., W. E. 1990. Chemical detection of predators by a lizard, the broad-headed skink (*Eumeces laticeps*). J. Exp. Zool. 256:162-167.
- . 1994. Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetical relationships. J. Chem. Ecol. 20:439-487.
- . 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. Anim. Behav. 50: 973-985.
- . 1997. Correlated evolution of prey chemical discrimination with foraging, lingual morphology and vomeronasal chemoreceptor abundance in lizards. Behav. Ecol. Sociobiol. 41:257-265.
- . 1998a. Conditions favoring anticipatory and reactive displays deflecting predatory attack. Behav. Ecol. 9:598-604.
- . 1998b. Reactive and anticipatory display to deflect predatory attack to an autotomous lizard tail. Can. J. Zool. 76:1507-1510.
- DELAUGERRE, M., AND M. CHEYLAN. 1992. Atlas de repartition des batraciens et reptiles de Corse. Parc Natural Regional de Corse. Ecole Pratique des Hautes Etudes. L'Oikéma, Pampelune, Spain.
- DIAL, B. E., AND K. SCHWENCK. 1996. Olfaction and predator detection in *Coleonyx brevis* (Squamata: Eublepharidae), with comments on the functional significance of buccal pulsing in geckos. J. Exp. Zool. 276:415-424.
- DIAL, B. E., P. J. WELDON, AND B. CURTIS. 1989. Chemosensory identification of snake predators (*Phyllorhynchus decurtatus*) by banded geckos (*Coleonyx variegatus*). J. Herpetol. 23:224-229.
- DOWNES, S., AND R. SHINE. 1998. Sedentary snakes and gullible geckos: predator-prey coevolution in nocturnal rock-dwelling reptiles. Anim. Behav. 55: 1373-1385.
- FILIPPI, E., M. CAPULA, L. LUISELLI, AND U. AGRIMI. 1996. The prey spectrum of *Natrix natrix* (Linnaeus, 1758) and *Natrix tessellata* (Laurenti, 1768) in sympatric populations. Herpetozoa 8:155-164.
- GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. Lond. B Biol. Sci. 205:581-598.
- GRUBER, U. 1989. Die Schlangen Europas und rund ums Mittelmeer. Franckh'sche Verlagshandlung, W. Keller and Co., Stuttgart, Germany.
- HAILEY, A., AND P. M. C. DAVIES. 1986. Diet and foraging behavior of *Natrix maura*. Herpetol. J. 1:53-61.
- HALPERN, M. 1992. Nasal chemical senses in reptiles: structure and function. In C. Gans and D. Crews (eds.), Hormones, Brain and Behavior, pp. 423-523. Univ. of Chicago Press, Chicago.
- LAMBERT, M. R. K. 1967. Observations of the herpetofauna of Corsica. Brit. J. Herpetol. 3:303-306.
- LANZA, B. 1955. Notizie su alcuni Anfibi e Rettili dell'Italia centrale e della Sardegna, con cenni sulla probabile presenza di un Urodelo nelle acque della Grotta del Bue Marino (Nuoro). Monit. Zool. Ital. 63:300-308.
- MAGNUSSON, W. E. 1996. Tail and hand waves: a come-on for predators? Herpetol. Rev. 27:60.
- MASON, R. T. 1992. Reptilian pheromones. In C. Gans and D. Crews (eds.), Biology of the Reptilia. Vol. 18, pp. 114-228. Univ. of Chicago Press, Chicago.
- NORUSIS, M. J. 1988. SPSS/PC+ Advanced Statistics Vers. 2.0. SPSS Inc., Chicago.
- PHILLIPS, J. A., AND A. C. ALBERTS. 1992. Naive ophiophagous lizards recognize and avoid venomous snakes using chemical cues. J. Chem. Ecol. 18: 1775-1783.
- SCHWENCK, K. 1993. The evolution of chemoreception in squamate reptiles: a phylogenetic approach. Brain Behav. Ecol. 41:124-137.
- . 1995. Of tongues and noses: chemoreception in lizards and snakes. Trends Ecol. Evol. 10:7-12.
- THOEN, C., D. BAUWENS, AND R. F. VERHEYEN. 1986. Chemoreceptive and behavioral responses of the

- common lizard *Lacerta vivipara* to snake chemical deposits *Anim. Behav.* 34:1805-1813
- VAN DAMME, R., AND A. M. CASTILLA. 1996. Chemosensory predator recognition in the lizard *Podarcis hispanica*: effects of predator pressure relaxation *J. Chem. Ecol.* 22:13-22.
- VAN DAMME, R., D. BAUWENS, A. M. CASTILLA, AND R. F. VERHEYEN. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia* 80:516-524
- VAN DAMME, R., D. BAUWENS, D. VANDERSTIGHELEN, AND R. F. VERHEYEN. 1990a. Responses of the lizard *Lacerta vivipara* to predator chemical cues: the effect of temperature *Anim. Behav.* 40:298-305
- VAN DAMME, R., D. BAUWENS, A. M. CASTILLA, AND R. F. VERHEYEN. 1990b. Comparative thermal ecology of the sympatric lizards *Podarcis tiliguerta* and *Podarcis sicula*. *Acta Oecol.* 11:503-512.
- VAN DAMME, R., D. BAUWENS, C. THOEN, D. VANDERSTIGHELEN, AND R. F. VERHEYEN. 1995. Responses of naive lizards to predator chemical cues. *J. Herpetol.* 29:38-43

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