Anim. Behav., 1986, **34**, 1805–1813

Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits

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Abstract. Behavioural cues were used to assay the capacity of common lizards to detect chemical deposits of snakes. The lizards were observed in cages that had been previously inhabited either by one of two species of snake that feed on lizards (the viper *Vipera berus* and the smooth snake *Coronella austriaca*), or the grass snake (*Natrix natrix*), which does not feed on lizards. As a control, the lizards were tested both in a clean cage and in one sprayed with a pungent odorant. The lizards responded to the snakes' chemicals by increased tongue-flick rates, with the highest rates being given in response to the deposits of their predators. The chemosensory examination of the snakes' odours induced a shift in general behaviour in response to the predator, but not to the non-predator chemical cues. This behavioural response consisted mainly of a disruption of the locomotor patterns. Our findings strongly suggest that lizards detected and distinguished between the chemicals deposited by three species of snake. Behavioural performances were highly variable among individual lizards in all trials, but the relative scores of individuals tended to be similar in response to different stimuli.

Although it is generally acknowledged that many lizards primarily orient visually, many species frequently extrude their tongues in a snake-like manner. In many lizard families, the Jacobson's organs are well developed (Parsons 1959, 1970) and the forked tongue probably facilitates delivery of chemical substances to the ducts leading to the vomeronasal organs. Hence, it is not surprising that a growing body of evidence indicates that the assimilation of chemical information from the environment serves various functions in lizards. It has been demonstrated or suggested that chemoreception is involved in the detection of conspecifics (Duvall 1979, 1981; Duvall et al. 1980; Gravelle & Simon 1980; Bissinger & Simon 1981), sex recognition and courtship (Greenberg 1943; Cooper & Vitt 1984), exploration (Gehlbach 1979; Bissinger & Simon 1981; Simon et al. 1981) and maternal care (Duvall et al. 1979); see Madison (1977) and Simon (1983) for reviews. Although the detection and recognition of predators through olfactory cues has been well documented in, amongst others, rodents (Griffith 1920; Stoddart 1980a), deer (Müller–Schwarze 1972) and snakes (Bogert 1941; Chiszar et al. 1978; Weldon 1982), it has not yet been demonstrated in lizards. Berry (1974) suggested that chuckwallas (*Sauromalus obesus*) might detect chemical deposits of predators, but no cogent evidence supported this suggestion. In an experimental study, Simon et al. (1981) were unable to demonstrate that chemoreception was involved in the detection of a snake predator by an iguanid lizard. Nevertheless, snakes are known to deposit chemicals that facilitate intraspecific communication (e.g. Madison 1977; Ross & Crews 1978; Andrén 1982; Ford 1982; Garstka et al. 1982), so that their prey might have evolved the ability to detect these substances and consequently the presence of the snakes releasing them.

We here describe results of experiments that were designed to determine whether the common lizard can detect chemical cues deposited by a sympatric snake predator, and whether this lizard can distinguish between the chemicals of a non-predatory and of two predatory snakes. We use the rate of tongue extrusions as an index of the chemoreceptive response to the snakes' odours. This measure has been widely used as a quantitative index of interest in novel stimuli, and in chemicals from prey and predators, for both lizards and snakes (e.g. Arnold 1981; Simon et al. 1981; Weldon 1982). We observed that an increase in chemosensory examination was accompanied by a shift in the lizards' behaviour; our major objective is therefore to describe and analyse the observed behavioural response to the predator's chemicals.

MATERIALS AND METHODS

Animals and their Maintenance

The common lizard is a small (adult body length 45–65 mm), diurnal, insectivorous lizard which is found over a wide range in Europe and Central Asia. This ground-dwelling species, which behaves like a typical heliotherm, most frequently inhabits well-vegetated and rather humid places.

During the first half of April 1983, we captured 10 adult males of this species and also one adult male common viper (*Vipera berus*) in a small field in the military property 'het Groot Schietveld', Brasschaat (51°20′N, 4°30′E), in Antwerp, Belgium. An adult female smooth snake (*Coronella austriaca*) and an adult female grass snake (*Natrix natrix*) were collected near Spontin (50°18′N, 5°00′E) in Namur, Belgium. The latter two snake species do not occur in the vicinity of the lizard collecting area.

The lizards were housed, two or three to each cage, in soil-filled plastic terraria (60 × 35 × 22 cm) containing some heather (*Calluna vulgaris*). House crickets *Acheta domestica* and water were provided ad libitum. The snakes were maintained individually in identical cages. All cages were heated for 6–8 h/day by one 75-W bulb, suspended about 30 cm above the substrate.

Experimental Procedure

We initially attempted to determine whether the lizards were able to detect chemical cues deposited by the sympatric common viper. This snake is a diurnal predator, mainly of small rodents and lizards, including the common lizard (Vølsoe 1944; Pielowski 1962; Presst 1971). Since a clear-cut response was evident from preliminary observations, we also attempted to examine whether the lizards responded to some specific quality of the odour of the viper or to some substance shared by predatory snakes or snakes in general. Ideally, this test would involve confrontation of the lizards with the chemicals of both a second, sympatric predatory snake and a sympatric non-saurophagous snake. The absence of snakes, other than the viper, from the lizard collecting area and nearby regions, prevented this experimental set-up. Instead, we chose two colubrid snakes, the smooth snake and the grass snake, which are allopatric with the population of our lizards, but which coexist with common lizards over extensive parts of Western and Northern Europe. The smooth snake preys regularly on lizards (Spellerberg & Phelps 1977), whereas the grass snake is mainly a predator of fish and amphibians (Steward 1971).

Our experimental procedure consisted of introducing an individual lizard successively to five terraria, each of which had been treated in a specific way.

(1) Clean control: an unfamiliar, untreated terrarium.

(2) Civet control: an unfamiliar cage wherein we spread some 'scatol' before each test. This is a strong-smelling, concentrated extraction derived from the mucous glands of the civet cat (*Viverra civetta*), and which is used as a raw material in the production of perfumes (Cerbelaud 1951). This liquid was chosen, rather than a chemically produced commercial odorant, because of its organic composition.

(3) Viper: the cage in which the viper had been housed.

(4) Smooth snake: the cage in which the smooth snake had been housed.

(5) Grass snake: the cage in which the grass snake had been housed.

The snakes were removed from their terraria 5 min before each test and replaced after its termination. Every individual lizard was tested once in each experimental cage. Trials were performed in the order: civet control, smooth snake, clean control, viper, grass snake.

The test cages were of the same dimension as the home cages, and we took special care to make the appearance of all terraria used in this study as similar as possible. During the course of the tests, the terraria were heated by two 75-W incandescent light bulbs, suspended 22 cm above the substrate.

Observations

Observations started circa 10 s after transfer of the lizard to the appropriate test box. Its behaviour was then observed continuously for 20 min from behind a one-way mirror. We distinguished between the following behavioural acts and locomotor patterns.

(1) Tongue-extrusion (= 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. This is the locomotor pattern typically observed in unrestrained lizards.

(3) Slow motion: the lizard proceeds by very slow, stalking movements, most often accompanied by jerky or waving movements of the forelimbs. In extreme, though not exceptional, cases, the lizard proceeds as if observed by the light of a stroboscopic bulb.

(4) Run: very fast movement, often over only a short distance.

(5) Stand up: lizard stands in an upright position against the wall of the vivarium and performs scratching movements with the forelegs.

(6) No move: lizard stands still, its ventrum resting on the substrate; this pattern can be accompanied by movements of head, tail or forelimbs.

(7) Bask: lizard rests under light bulb with the ribs spread laterally; one or more feet are often tilted upwards.

(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.

Tongue-extrusions were counted by a hand held counter and the total number was read at the end of each test. The occurrence of Starts, Foot shakes, Tail vibrations (frequency) and the other behavioural acts (duration) were recorded continuously by use of an event recorder (Esterline Angus, 20 channels). Because of a mechanical defect, most Foot shakes were not recorded, preventing us from presenting quantitative data on this behaviour.

The locomotor patterns Run and Stand up were observed only sporadically and therefore exhibited extremely skewed frequency distributions (preponderance of zero-values). As this may induce statistical complications, we added these data to the records of Walk.

Data Analysis

We used one-way analysis of variance (ANOVA) and Duncan's new multiple range test (DNMRT) to evaluate differences in the mean duration and frequency of the behavioural acts among experimental situations.

In order to obtain an integrated picture of the behavioural responses to the test situations, we used a principal component analysis. This multivariate analysis reduces the dimensionality of the original space by creating component axes and provides a useful way of defining relationships between the original variables.

RESULTS

Tongue-flicking rates differed markedly among experimental treatments (Table I, ANOVA: $P < 0{\cdot}001$). The lizards extruded their tongues most often in the cages that had been inhabited by the viper and smooth snake; they did so least in both control tests. In the grass snake cage, lizards performed significantly more tongue-flicks than in the control experiments, but fewer than in the predators' cages.

In addition to the above response, some striking differences in general behaviour among the experi-

Table I. Scores (frequency or duration) of distinct behavioural acts of common lizards in different treatments (mean ± SE, $N = 10$, test duration = 20 min)

	Clean control	Civet control	Viper	Smooth snake	Grass snake	ANOVA
Tongue-extrusions†	344·4 ± 45·2^{a}	326·2 ± 55·9^{a}	522·9 ± 36·4^{b}	528·8 ± 43·2^{b}	412·6 ± 40·0	*
Crawl‡	558·2 ± 81·4	445·0 ± 77·3^{a}	221·9 ± 39·4	388·0 ± 50·6	485·8 ± 75·6^{a}	**
Slow motion‡	6·4 ± 2·7^{a}	10·7 ± 7·1^{a}	249·1 ± 39·1	78·6 ± 21·1	11·1 ± 6·2^{a}	**
No move‡	492·8 ± 56·9	688·0 ± 93·0	537·7 ± 47·7	511·1 ± 87·9	505·4 ± 85·2	NS
Bask‡	143·2 ± 67·2	56·3 ± 36·7	191·3 ± 39·2	222·3 ± 74·0	197·7 ± 54·9	NS
Start†	0·0^{a}	1·3 ± 0·6^{b}	8·4 ± 1·8^{c}	2·4 ± 0·6^{b,c}	0·5 ± 0·3^{a}	**
Tail vibration†	0·0^{a}	0·4 ± 0·2^{a}	1·5 ± 0·5^{b}	3·3 ± 1·0^{b}	0·3 ± 0·2^{a}	**

Superscripts common in a row denote values that do not differ significantly (Duncan's multiple range test).
† Frequency/20 min.
‡ Duration (s/20 min).
* $P < 0{\cdot}01$; ** $P < 0{\cdot}001$.

mental treatments were obvious (Table I). In the two control, and in the grass snake, terraria, the lizards basically alternated periods of rest (No move) with basking and bouts of activity, during which they walked and occasionally ran through the cage. Slow motion was rarely seen in these experiments. In contrast, Slow motion was a major component of the lizards' behaviour in the viper and smooth snake cages. The data indicate that lizards moved almost exclusively by Slow motion during the first 8–10 min of the viper tests (Fig. 1). Thereafter, they gradually shifted towards a more frequent use of ordinary Walk. In the smooth snake cage, the animals mainly used Slow motion during the initial 5 min of the test (Fig. 1), and then alternated Slow motion with Walk, whereas they afterwards moved almost exclusively by Walk. It is worth mentioning that in both predatory snake terraria, Slow motion was observed almost immediately after the onset of the experiments (Fig. 1). This suggests that the predator-released chemicals were detected by the initial tongue-flicks and induced both a shift in locomotory behaviour and an increased and prolonged examination of odours in the environment. A further striking difference among test situations was the relatively high frequency of Tail vibrations and Starts in the tests of viper and smooth snake (Table I). Foot shakes were also seen almost exclusively in the cages of the predators, although we are unable to provide quantitative support for this statement.

A principal component analysis was used to

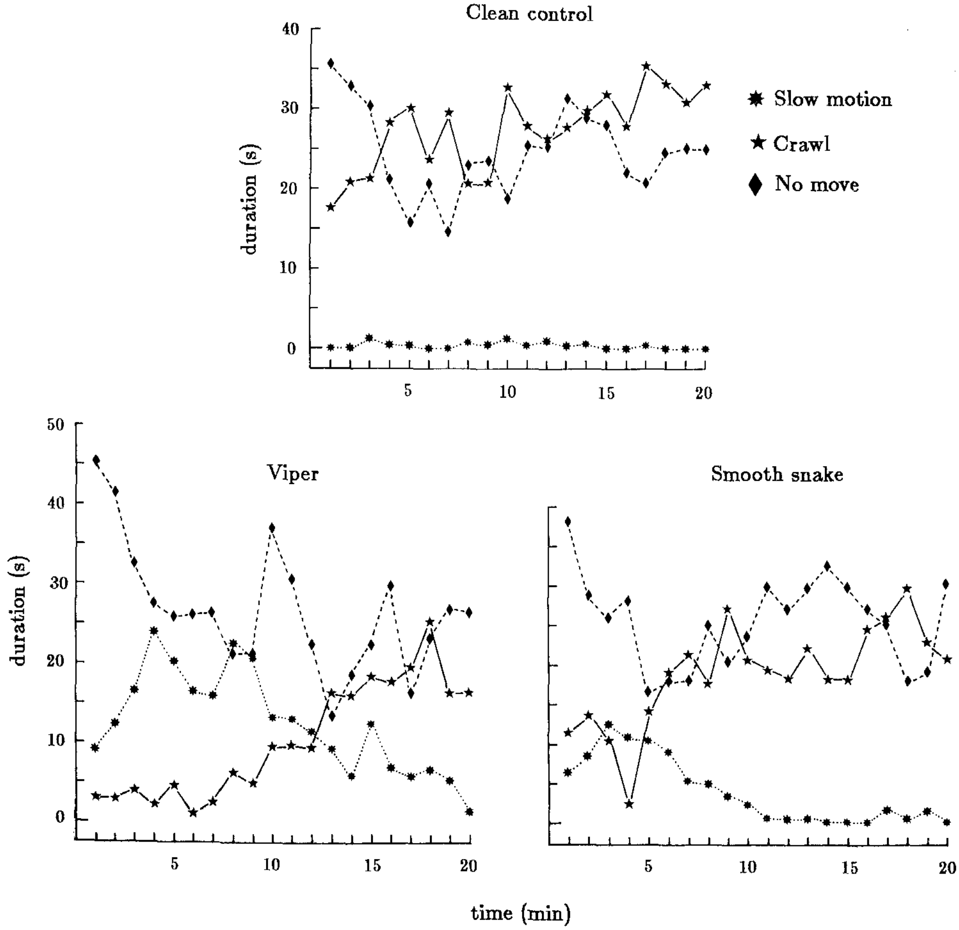

Figure 1. Mean duration of three behavioural acts of common lizards (Slow motion, Walk and No move) as a function of time in three experimental treatments.

quantify the general behaviour in the different experimental treatments. In this analysis, the raw data were the total duration or frequency scores of the distinct behavioural variables during the 20-min course of the individual tests. The Tongue-extrusion frequency was not entered as a variable, since it is considered to be an index of the intensity of examination of the environment by the perception mechanism that discriminates among stimuli and so ultimately induces the behavioural response.

The five extracted principal axes were all significant and respectively accounted for 40·5, 29·0, 16·6, 11·3 and 2·7% of the total variation. The alignment of the experiments along the component axes was studied by considering the projections of the individual tests on these axes (Fig. 2). The scores on the first principal component differed according to the experimental treatment (ANOVA: $F=18{\cdot}914$, $df=4, 45$, $P<0{\cdot}001$). The tests with the grass snake cage and both controls had low and comparable scores on this axis, whereas the tests with the viper cage obtained the highest values. The trials with the smooth snake cage scored intermediate values, which differed significantly from all others (DNMRT, $P<0{\cdot}05$; Fig. 2). This first principal axis was positively correlated with the frequency of Tail vibrations ($r=0{\cdot}508$, $P<0{\cdot}001$) and Starts ($r=0{\cdot}857$, $P<0{\cdot}001$) and the total duration of Slow motion ($r=0{\cdot}893$, $P<0{\cdot}001$), and was negatively correlated with the duration of Walk ($r=-0{\cdot}756$, $P<0{\cdot}001$). The experimental treatments can therefore be aligned along a behavioural gradient which is characterized by a transition of moving by Walk towards the extensive use of Slow motion, and by the graduate occurrence and increased frequency of Tail vibrations and Starts. The positions of the projections on the second to fifth major axes did not differ among stimuli situations (ANOVA, all $P>0{\cdot}10$). These axes therefore lack value in delineating responses of lizards towards the experimental treatments.

Although most of the observed behavioural variation reflects differences among experimental situations, a considerable inter-individual variation occurs within each treatment. Thus the behavioural scores in the principal axes space (Fig. 2) indicate both a large variance within, and a considerable overlap of, the behavioural responses among experimental treatments. Since our experimental procedure examined the responses of the same individual in different conditions, we could test for consistent behavioural differences among individuals. The rank orders of the behavioural scores on the first major axis of individual lizards were significantly correlated among experimental treatments (Kendall coefficient of concordance: $W=0{\cdot}473$, $P<0{\cdot}02$). The rank orders of the number of Tongue-extrusions in the different trials also contained a significant individual component

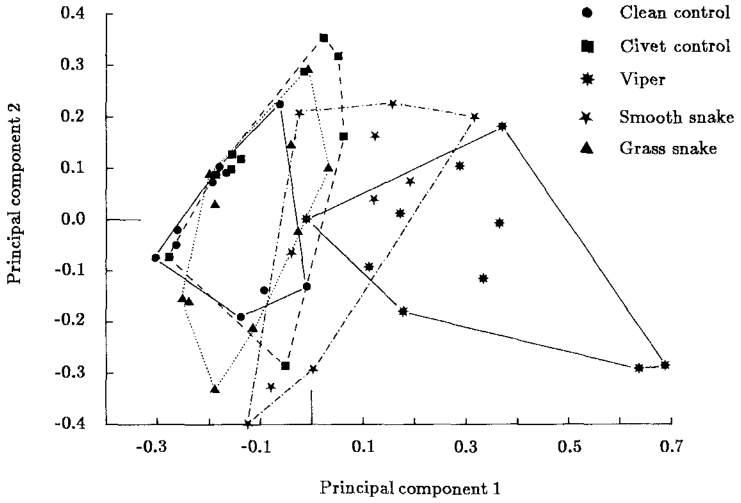

Figure 2. Projections of the behavioural scores in the individual tests on the PC1, PC2 space obtained by a principal component analysis.

(KCC, $W=0{\cdot}398$, $P<0{\cdot}05$). Thus both the relative tongue-flick rates and the relative scores of individual lizards on the behavioural gradient depicted by the first principal axis, tend to be similar in different stimulus situations.

DISCUSSION

Our results clearly indicate that the common lizard can detect chemical cues deposited, either actively or passively (see below) by two species of predatory snakes. However, detection of the snakes' chemicals does not in itself imply that they were actually identified as such. The observed variation in chemosensory and behavioural responses at least suggests that lizards distinguish between an unfamiliar odour (civet), the chemicals of a non-predatory snake and the odours of two predatory snakes. Lizards extruded their tongues more often in an unfamiliar, untreated cage (clean control) than in their home cages (mean number of tongue-flicks/20 min = 79·1, SD = 20·4, $N=10$; Thoen 1984), indicating exploration of novel situations (DeFazio et al. 1977; Gehlbach 1979; Bissinger & Simon 1981; Simon et al. 1981). Although we did not quantify the behaviour of the lizards in their home cages, no obvious behavioural response to the experimental control cage was observed, except for an apparent increase in time spent moving. In the presence of the civet odour, neither the tongue-flick rate, nor the general behaviour differed markedly from that observed in the untreated cage. The lack of responses towards commercial odorants has been established in both reptiles and mammals (e.g. Courtney et al. 1968; Duvall 1981), indicating that these odours either remain undetected or elicit no further chemoreceptive interest.

Lizards exhibited higher rates of tongue-extrusions in the grass snake test than in either of the control treatments. Hence, chemical substances deposited by this non-saurophagous snake were seemingly detected and examined. However, the lizards did not react by behavioural responses similar to those observed in the predator cages. Given that they actually detected the deposits of the grass snake, lizards apparently discriminated between chemicals of this non-predatory snake and odours of predatory ones. We observed similar tongue-extrusion rates and behavioural postures in the tests with the viper and the smooth snake. However, some striking quantitative differences in behaviour were evident between these two tests. The results suggest that lizards distinguish between the chemicals left by these two predators, which may differ in composition, and/or in concentration. An alternative explanation would attribute the differential response to unfamiliarity of our lizards to the odours of the allopatric smooth snake. This interpretation is, however, not supported by results from similar experiments with lizards that are sympatric with this snake, which confirmed the differential responses observed in this study (Thoen 1984, unpublished data). In short, our experiments demonstrate that common lizards respond differently to, and therefore seemingly distinguish between, the chemicals of three snake species.

Our most obvious result is the shift in general behaviour induced by the detection of predator chemicals. Various studies have documented the behavioural effects of the presentation of predator odours in a variety of animals. Responses vary from a disruption of locomotion, such as the 'freezing' behaviour of rats (Griffith 1920; Courtney et al. 1968), increased awareness and withdrawal behaviour in squirrels (Henessy & Owings 1978), deer (Müller-Schwarze 1972) and mice (Stoddart 1980a), to the adoption of stereotyped postures in rattlesnakes (Bogert 1941; Cowles & Phelan 1958; Weldon & Burghardt 1979) and fish (George 1960 cited in Stoddart 1980b). In the common lizard presentation of predator chemicals induces an extensive use of the Slow motion locomotor pattern and the display of Starts, Tail vibrations and Foot shakes. The behavioural pattern Slow motion was seen almost exclusively in cages which had previously held predatory snakes. Recent work in our laboratory has established that lizards also shift towards Slow motion when they can see (but not smell) a viper (Nuyten & Van Wezel 1984). It may be worth mentioning that we had never before observed Slow motion movements in unrestrained lizards, despite our extensive field and laboratory experience with this species (in an area where predatory snakes are absent). These observations provide both positive and negative evidence for considering this behavioural characteristic as a typical response towards predator stimuli. Tail vibrations and Foot shakes are usually observed during social encounters in this lizard, and can be considered to be appeasement displays (Verbeek 1972; own observations). We speculate that intraspecific interactions and the presence of predator stimuli are both conflict situations, to which a lizard may respond by displaying similar stereotyped postures. In general, we suggest that the transition in behaviour observed in our experimental series probably represents an underlying shift in motivational state, which might range from indifference or an exploratory tendency in the control and grass snake trials, towards extreme awareness and possibly fear in the predator cages.

It is tempting to speculate on the nature of the chemicals that are detected by the lizards. Potential candidates are the sex pheromones that many snakes, including the viper (Andrén 1982), rely on for species and sex recognition (review in Madison 1977). The production of these skin secretions seems to be related to reproductive condition in both garter snakes (Garstka et al. 1982) and vipers (Andrén 1982). We have recently established that common lizards respond to viper deposits, irrespective of the sex, age and reproductive state of the snake (D. Bauwens, C. Thoen & D. Vanderstighelen, unpublished data), suggesting that lizards respond to chemicals other than the vipers' sex attractants. We suggest that chemicals that are not functional in snake communication might be involved. Blood-borne lipids and proteins have been shown to percolate through the skin of garter snakes (Crews & Garstka 1982; Garstka et al. 1982). However, we need further study of the production of chemicals by snakes and of the responses of lizards towards the deposits of various types of experimentally treated snakes to examine this possibility.

The behaviour of individual lizards varied considerably in all our treatments. A significant fraction of this variance could be attributed to consistent inter-individual differences in both chemosensory examination and behavioural response, and hence possibly in motivational state. These differences were preserved across experimental trials. This was a most unexpected finding, not least because the behavioural scores integrate the duration and frequency of distinct behavioural acts performed over a 20-min test period. Environmental factors are therefore expected to induce considerable variation in behaviour both within and among experimental trials. The study of individual consistency of behaviour in natural populations has been a largely neglected subject (Arnold & Bennett 1984). Nevertheless, the available studies have demonstrated a considerable degree of individual constancy of complex behaviours and whole-animal performances such as the feeding and antipredator responses of snakes (Arnold 1981; Arnold & Bennett 1984), running speed in lizards (Bennett 1980; Huey & Hertz 1984), swimming speed in toads (Miller & Camilliere 1981) and body temperatures maintained by lizards (DeWitt 1967; Christian et al. 1985). Our results, although based on a small sample, complement these findings and encourage further studies of the repeatability and inheritance of the responses of lizards to snake odours.

From our present knowledge it is impossible to judge the possible adaptive significance of the lizards' chemoreceptive and behavioural responses to the snake deposits. It may be argued that by moving slowly and unobtrusively, lizards reduce the risk of being detected by a nearby snake predator. However, our experiments provide no evidence that the snakes themselves are actually located, but only demonstrate that their deposits can be detected. Detection of a 'marked' site may eventually reduce the risk of predation, provided that the snake remained in the vicinity. These comments call for a detailed consideration of the spatial behaviour of these snakes and of the volatility and persistence in time of their deposits.

ACKNOWLEDGMENTS

We are grateful to Raoul Van Damme, Dirk Vanderstighelen, Kees Nuyten and Henk Van Wezel for their comments on a previous draft of the manuscript, their help in capturing and maintaining the animals and many other kindnesses. The style of the manuscript was greatly improved by the helpful comments of Carl Gans and Katelijne Flies. This work was supported by a grant of the I.W.O.N.L. (to C.T.), preparation of the manuscript was aided by a grant of the N.F.W.O. (Krediet aan navorsers).

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(Received 12 August 1985; revised 30 October 1985; MS. number: 2740)