CHEMOSENSORY PREDATOR RECOGNITION IN THE LIZARD *Podarcis hispanica:* EFFECTS OF PREDATION PRESSURE RELAXATION

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Abstract—We compared the behavior of two subspecies of *Podarcis hispanica* lizards in cages that had been chemically marked by a saurophagous snake, the viper *Vipera latastei*. One of the subspecies (*P.h. atrata*) has experienced a relaxation from predation pressure by this viper, as snakes were eradicated from the island it inhabits over 100 years ago. Nevertheless, individuals from *P.h. atrata* responded to the snake's chemicals similarly to individuals from a population of *P.h. hispanica*, currently sympatric with *V. latastei*. Lizards exhibited more stress-indicating behaviors (foot shakes, tail vibrations, sudden starts), became less mobile, and tongue-flicked more while moving in a snake-inhabited terrarium than when in a clean, unfamiliar terrarium.

Key Words—Antipredator behavior, chemoreception, lizards, Lacertidae, Reptilia, predation, relaxation, snakes.

INTRODUCTION

Predation is an important selective force that can shape the morphological, behavioral, and life-history characteristics of prey animals. Studies on a variety of species [e.g., spiders (Riechert and Hedrick, 1990), fish (Magurran and Seghers, 1990; Gelowitz et al., 1993), salamanders (Dowdy and Brodie, 1989; Ducey and Brodie, 1991), snakes (Sweet, 1985), and mammals (Owings and Coss, 1977)] have demonstrated that geographical variation in predation pressure is reflected in parallel variation in antipredator behavior of prey animals; prey animals from predator-free or -poor habitats fail to recognize predators in staged

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encounters (Magurran, 1986; Magurran and Seghers, 1990; Gelowitz et al., 1993; Mathis and Smith, 1992) or show inappropriate responses to predator stimuli (Breden et al., 1987; Dowdey and Brodie, 1989; Herzog and Schwartz, 1990; Riechert and Hedrick, 1990). These intraspecific differences in anti-predator behavior may arise from differential experience within the lifetime of an individual (Magurran, 1989; Olla and Davis, 1989; Jaervi and Uglem, 1993), from natural selection acting upon genetic variation (Huntingford, 1982; Breden et al., 1987; Riechert and Hedrick, 1990), or from a combination of both (Giles and Huntingford, 1984; Magurran, 1990).

In this paper, we compare the ability of two subspecies of the lacertid lizard *Podarcis hispanica* to detect chemicals from the saurophagous snake *Vipera latastei*. Predator recognition is a necessary first step of adequate antipredator behavior. The vomeronasal system of reptiles offers good opportunity to study the ability to recognize predatory cues, without the need to actually confront the animals with the predator itself. Reptiles have been shown to react to chem-icals left behind by predators with an increased rate of tongue extrusions (Chiszar et al., 1978; Thoen et al., 1986; Van Damme et al., 1990, 1995). The intensified movements of the forked tongue probably facilitate delivery of chemical sub-stances to the ducts leading to Jacobson's organ (Parsons, 1970). Tongue-flick rate can therefore be used as a quantitative bioassay of interest in a variety of stimuli, including food and predator chemical cues.

One of the lizard subspecies under study, *P.h. atrata*, is endemic to the Mediterranean archipelago of the Columbretes Islands (Castellón, Spain). A large population of *Vipera latastei* inhabited the main island of this archipelago but was completely eradicated when a lighthouse was constructed by the end of the 19th century. In spite of several herpetological expeditions, not a single live snake was observed after 1886 (Castilla et al., 1987). The other subspecies, *P.h. hispanica*, lives on the nearby mainland of Spain (ca. 50 km away) and is still sympatric with *V. latastei*. Our objective was to test whether the recent relaxation of the predation pressure in *P.h. atrata* has resulted in the loss of the ability to recognize viper chemicals. If *P.h. atrata* still reacts to the snake chemicals, this strongly suggests that the chemosensory recognition of predator cues is genetically based, since none of the individuals has ever been in contact with snake predators. Alternatively, lizards may respond to chemicals that the viper has in common with other predators now present on the island. If *P.h. atrata* fails to recognise the stimuli, recognition is either based on expe-rience and/or has been lost in the island population.

METHODS AND MATERIALS

Typically, *Podarcis hispanica* is a small [snout-vent length 40–60 mm], slender, flattened wall lizard living on rocks, stony slopes, walls, and other

habitats dominated by vertical elements. Like most other lacertids, *P. hispanica* has an active-searching foraging mode, a predominantly arthropod-based diet, and a diurnal activity pattern. It should be noted, however, that the species exhibits substantial variation in body dimensions and habitat preferences throughout its distributional range in Iberia and northwest Africa (Salvador, 1986). The population of *P.h. hispanica* sampled here has the typical characteristics described above. These lizards lived on garden walls and in a small park and were almost exclusively seen on stony substrates elevated more than 0.5 m above ground. Adult SVL ranged between 40 and 55 mm ($\overline{X}$ = 46.9 mm; SD = 3.7 mm; N = 27). The subspecies *P. hispanica atrata*, from Columbretes Islands, is aberrant in its large adult body size (range 52–71 mm; $\overline{X}$ = 60.5 mm; SD = 4.2 mm; N = 44). Although lizards from this population climb regularly, they are most frequently seen on flat, horizontal surfaces, often at ground level.

   Vipera latastei is a rather small (adult SVL 50–60 cm), stocky snake from the Iberian Peninsula and northwest Africa. It prefers sunny, stony, and slightly vegetated slopes and open deciduous forest. The snake feeds on rodents, lizards, and bird nestlings, killing its prey by injecting neurotoxic and hemorraghic venom (Gruber, 1989).

   We caught 10 adult *Podarcis hispanica atrata* (four males and six females) on the bigger island of the Columbretes archipelago (Columbrete Grande) and 10 *P.h. hispanica* (six males and four females) from the nearby mainland (Castellón, Spain) and transported them to the laboratory in Antwerp, Belgium. Lizards were housed in five large terraria and daily were given ample amounts of food (crickets and mealworms) and water. Two 150-W spotlights suspended above both extremes of each terrarium provided light and heat for 10 hr/day. Individuals from both populations were kept apart. A male viper (*Vipera latastei*, SVL 45 cm) was obtained from the province of Burgos (Spain) and was kept in a cage located in a separate room. We took care that none of the lizards was in visual or chemical contact with this viper outside experimentation.

   We followed the experimental procedure outlined in Thoen et al. (1986) and Van Damme et al. (1990) to assess the lizards' responses to snake chemical cues. We introduced each individual lizard successively into two small terraria. These terraria were identical in dimensions (25 × 25 cm), substrate (sand, mosses, and stones), illumination, and heating (provided by a 150-W spotlight suspended 22 cm above the substrate). One of the cages (hereafter referred to as the viper situation) had previously been inhabited by the viper. After the snake had resided in the cage for at least 12 hr, we removed it and replaced it by a lizard. The other test terrarium was free from any viper chemicals; we used it to monitor lizard behavior in an unfamiliar but predator-free situation. The order in which a lizard was tested in the control and the viper situation was decided by chance. Since *P. hispanica* is known to react to chemicals left behind

on the substrate by conspecifics (Gómez et al., 1993), we changed the sand and vegetation and rinsed the stones from the testboxes after each experiment.

We observed the lizards' behavior from behind a one-way mirror. Observations started about 10 sec after transfer of the lizard to the test box and lasted 15 min. We distinguished the following behavioral acts and locomotor patterns. (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. This is the locomotor type typically observed in unrestrained lizards. (3) Slow motion: very slow movement accompanied by jerky or waving movements of the forelimbs. (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 ventrum resting on the substrate; this pattern can be accompanied by movements of 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 upwards. (7) Start: sudden jump, most often followed by a quick, short run. (8) Foot shake: the raised forelimbs are alternately and rapidly moved up and down. (9) Tail vibration: the entire tail, or its posterior portion, is moved rapidly from side to side.

We used a BASIC program run on a personal computer to record the lizards' behavior. The program assigns a key to each of the behavioral acts distinguished and checks every second which key on the computer keyboard is being pressed by the observer. At the end of an observation period, the program lists for every second the behavior performed by the lizard, the number of tongue flicks, starts, foot shakes, and tail vibrations.

We used 2 × 2 factorial repeated measures analysis of variance on the total duration or frequency of behavioral acts to test for differences between treatments (viper/control) and populations. Lizards clearly extruded their tongues more frequently while moving than when basking or resting. Therefore, if we want to use tongue-flick frequency as a bioassay for predator recognition, we have to correct for the amount of time the lizard spent moving. We did this by introducing the total duration of walk and slow motion as a covariate into the analysis of variance.

Lizard activity typically consists of alternating mobile (foraging, exploration) bouts and stationary periods (basking, resting). We suspected that the length and frequency of these bouts might differ between treatments and/or populations. There is a practical difficulty in delimiting a locomotion bout, because lizards in general do not move in a continuous way, but now and then pause for a couple of seconds before resuming their itinerary. We used an algorithm described by Sibly et al. (1990) to distinguish between these short stops within a locomotion bout and "real" stationary periods. In this method, two regression models (a one-process model and a two-process model) are fitted

to a $\log_e$ frequency distribution of gap lengths. A gap is every interval between two successive movements. The one-process model assumes that all events are generated by a single Poisson process, and thus that behavior cannot be split into bouts. The two-process model considers events to be generated by one of two random Poisson processes, a fast process operating within bouts and a slow process generating new bouts. In our case, the two-process model clearly fitted better to the data than the one-process model. We derived a bout-criterion interval (Slater and Lester, 1982) of 28 sec, which means that gaps between real locomotory bouts must at least be this long. If the interval is shorter than 28 sec, the gap is considered as a short pause within a movement. Using this criterion, we calculated for each observational period the average locomotory bout length and frequency, the length of the interval between bouts, and the number and frequency of pauses within locomotion bouts. These new behavioral parameters were compared between treatments and populations using repeated-measures analysis of variance. Since the number of pauses is clearly dependent on the time spent moving, we corrected for this by introducing total bout duration (mean bout length × frequency) as a covariate into the analysis. All statistical analyses were performed with the SPSS/PC + statistical package (Norusis, 1990).

RESULTS AND DISCUSSION

Lizards of both populations reacted to the former presence of *Vipera latastei* in the test terrarium by an increased number of starts, foot shakes, and tail vibrations (Table 1). These behaviors are typically displayed by lizards in conflict situations, during encounters with conspecifics (Verbeek, 1972), potential prey, or predators (Nuyten and Van Wezel, 1984; Thoen et al., 1986; Van Damme et al., 1990, 1995). Since the presence or absence of predator chemicals constitutes the only difference between our two test situations, we assume that the increase in these stress-indicative behaviors in the viper situation represents a shift in motivational status towards enhanced awareness and possibly fear.

We found significant treatment × population interaction effects for the number of foot shakes and tail vibrations. This suggests that although lizards from both populations respond to viper chemicals, the predator-sympatric *P. hispanica hispanica* reacted more vigorously than the predator-allopatric *P. hispanica atrata*. This differentiation was, however, not evident in the other stress-indicative behavioral components (the number of tongue-flicks and starts).

In contrast to *Lacerta vivipara* (Thoen et al., 1986; Van Damme et al., 1990, 1995), *Podarcis hispanica* did not tongue-flick more in the viper situation than in the control situation. This finding is deceptive, however, because tongue-flick frequency is clearly higher during locomotion, and lizards moved significantly less in the viper situation than in the control situation. After correction

TABLE 1. BEHAVIOR OF LIZARDS FROM POPULATIONS ALLOPATRIC (COLUMBRETES) AND SYMPATRIC (CASTELLÓN) WITH *Vipera latastei*[a]

Variable	P.h. atrata Columbretes		P.h. hispanica Castellón		P		
	Control	Viper	Control	Viper	Treat	Pop	Pop × treat
Walk	461.4 ± 142.4	193.9 ± 172.8	248.0 ± 198.0	205.2 ± 146.5	0.009	0.03	0.004
Slow motion	7.8 ± 9.9	4.0 ± 9.8	58.5 ± 84.9	4.3 ± 5.1	0.07	0.05	0.07
Bask	56.7 ± 29.0	92.0 ± 69.8	110.6 ± 97.9	101.3 ± 47.5	0.16	0.53	0.31
No move	310.1 ± 143.8	587.7 ± 260.6	436.8 ± 253.0	557.8 ± 182.6	0.22	0.04	0.05
Stand up	50.1 ± 42.0	3.7 ± 3.6	21.8 ± 33.1	15.4 ± 17.6	0.31	0.01	0.02
Dig	13.9 ± 17.5	18.7 ± 35.9	24.3 ± 32.5	16.0 ± 27.6	0.35	0.87	0.58
Tongue flicks	226.1 ± 45.1	162.6 ± 124.1	277.2 ± 117.8	220.1 ± 110.9	0.04	0.15	0.90
Starts	0.6 ± 1.07	0.9 ± 1.5	2.8 ± 2.0	3.5 ± 4.8	0.015	0.82	0.58
Foot shakes	0.1 ± 0.3	0.3 ± 0.6	0.2 ± 0.4	4.3 ± 5.0	0.02	0.02	0.02
Tail vibrations	0.1 ± 0.3	0.3 ± 0.7	0.2 ± 0.4	4.3 ± 5.0	0.02	0.02	0.02
Locomotory bouts	2.8 ± 1.5	5.7 ± 3.6	4.6 ± 2.9	5.7 ± 1.5	0.02	0.32	0.18
Bout length	394.7 ± 279.7	174.5 ± 149.6	90.5 ± 127.3	59.9 ± 44.8	0.03	0.003	0.06
Gap length	57.1 ± 27.7	51.8 ± 16.3	75.3 ± 39.8	96.3 ± 59.5	0.56	0.14	0.27
Stops	44.6 ± 12.2	29.9 ± 16.2	18.1 ± 16.1	17.4 ± 14.0	0.09	0.002	0.05
Stop length	6.9 ± 2.4	8.6 ± 2.4	8.3 ± 1.5	10.4 ± 4.5	0.24	0.20	0.45

[a]Lizards were observed in a terrarium that had been previously inhabited by a snake (viper) and in an unfamiliar, but clean, terrarium (control). Presented are the number or duration (seconds) of behavioral acts observed during 15-min observation periods. Values are means (±SD, $N = 10$ for both populations). The last three columns give the P values for the effects of population, treatment, and the interaction between population and treatment, as derived from repeated-measures analysis of variance.

for the amount of time spent moving (walk + slow motion), lizards of both populations extruded their tongues more often in the viper situation than in the control terrarium (Figure 1, $F = 8.38$, $df = 1$ and 17, $P = 0.01$). This finding suggests that lizards perceive chemical clues indicating the presence of the viper and that these stimuli invoke an enhanced utilization of the chemoreceptive apparatus.

We found no population or treatment × population interaction effects for the corrected tongue-flick frequency (both $P > 0.2$). We conclude that the ability to detect viper chemicals must be genetically based in *P.h. atrata*, since none of the lizards from this subspecies had any experience with predatory snakes before. Furthermore, 100 years of relaxed predation pressure have not resulted in the loss of the ability for chemoreceptive recognition. Alternatively, lizards may respond to chemicals that the viper has in common with other predators present in its habitat. Little is known regarding the degree of specificity of responses by the lizard to such chemicals. In the case of *P.h. atrata*, however, this alternative explanation seems unlikely, since the Columbretes Islands are
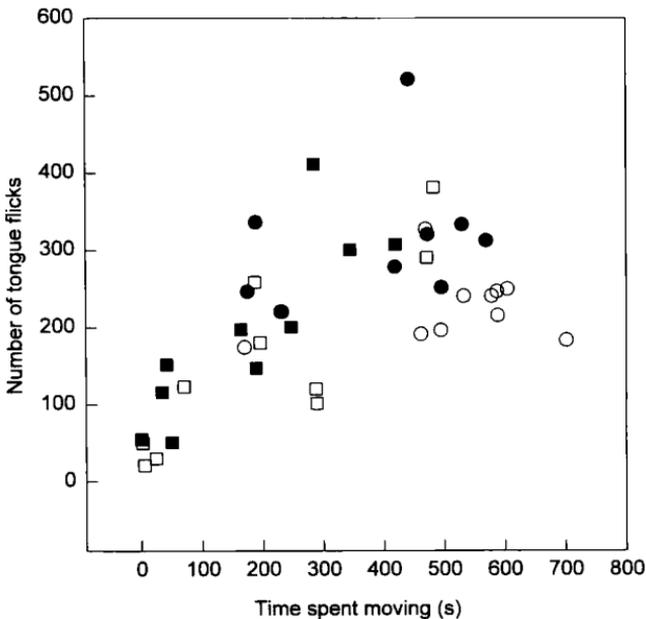

FIG. 1. Number of tongue flicks performed by the lizard *Podarcis hispanica* as a function of the time spent moving. Lizards were observed for 15 min in terraria previously inhabited by a viper (filled symbols) and in unfamiliar but clean terraria (open symbols). Circles represent individual lizards from a predator-allopatric population (*P.h. atrata*), and squares refer to lizards from a predator-sympatric population (*P.h. hispanica*).

currently nearly devoid of potential predators. There are no snakes or mammals and no typical saurophagous birds such as corvids or shrikes (Castilla et al., 1987), leaving only two species of gulls (*Larus cachinnans michahellis* and *Larus audouinnii*) as potential predators of lizards. These gulls primarily predate or scavenge on fish and marine invertebrates (Cramp, 1983), but it is not impossible that they occasionally attack a lizard.

Locomotion patterns differed between populations and treatments. In the control situation, *P.h. atrata* showed a much higher tendency to explore the cage than *P.h. hispanica* and thus obtained higher mobility scores (Table 1). This difference in mobility between populations was largely due to the longer mean duration of locomotion bouts performed by the island subspecies (Table 1). Although we cannot present quantitative data to support this, the observed differences in locomotory activity seem to persist outside our experimental situations. Both in the field and in their home cages in the laboratory, individuals of *P.h. atrata* can be seen moving about far more often than their conspecifics from the mainland. Although it is tempting to ascribe this difference to the higher predation risk on the mainland, many other factors involved in the cost-benefit balance of locomotory activity (e.g., body dimensions, prey density, social context, etc.) may also be involved.

Locomotion in *P. hispanica* is not smooth and continuous, but consists of a pattern of bursts of movement alternating with pauses. Although seemingly widespread among lizard species (see Avery et al., 1987, and references therein), the exact ecological significance and/or the physiological basis of this jerky motion pattern remains obscure. In our experiments, the number of pauses per unit time traveled and the mean duration of pauses did not differ between species or treatments. Therefore, we have no reasons to suppose that the frequent stops are a part of the antipredator behavior of *P. hispanica*.

We conclude that the lizard *P. hispanica* is capable of detecting the former presence of a predatory snake, the viper *V. latastei*, presumably through chemosensory perception of chemicals left behind on the substrate. The ability is still present in individuals from a population that has experienced relaxation from predation by snakes during the past 100 years. In *P.h. atrata*, the response to the viper's former presence may constitute another example of a "ghost of predation past" (Peckarsky and Penton, 1988; cf. Connell, 1980) or may reflect responses to chemicals common to a range of predatory species. Assuming that the ability to detect predator chemicals is genetically based, it may not be surprising that it has survived in the viper-free population. The rate at which vestigial characters disappear from a population is likely to be a negative function of the costs of expressing the character, and we cannot think of any substantial costs involved in this case. It would be interesting to study predator recognition abilities in populations that are liberated from specific predators for longer periods of time.

REFERENCES

AVERY, R.A., MUELLER, C.F., JONES, S.M., SMITH, J.A., and BOND, D.J. 1987. Speeds and movement patterns of European lacertid lizards: A comparative study. *J. Herpetol.* 21:324–329.

BREDEN, F., SCOTT, M., and MICHEL, E. 1987. Genetic differentiation for anti-predator behaviour in the Trinidad guppy, *Poecilia reticulata*. *Anim. Behav.* 35:618–620.

CASTILLA, A.M., JIMENEZ, J., and LACOMBA, I. 1987. Los reptiles de Columbretes, pp. 181–194, *in* A. Matilla (ed.). Islas Columbretes. Contribución al estudio de su medio natural. Generalitat Valenciana, Valéncia.

CHISZAR, D., SCUDDER, K., KNIGHT, L., and SMITH, H.M. 1978. Exploratory behavior in prairie rattlesnakes (*Crotalus viridis*) and water moccasins (*Agkistrodon piscivorus*). *Psychol. Rec.* 28:363–368.

CRAMP, S. 1983. Handbook of the Birds of Europe, the Middle East and North Africa, Vol. III. Waders to Gulls. Oxford University Press, Oxford.

CONNELL, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.

DOWDEY, T.G., and BRODIE, E.D.J. 1989. Antipredator strategies of salamanders: Individual and geographical variation in responses of *Eurycea bislineata* to snakes. *Anim. Behav.* 38:707–711.

DUCEY, P.K., and BRODIE, E.D.J. 1991. Evolution of antipredator behavior: Individual and populational variation in a neotropical salamander. *Herpetologica* 47:89–95.

GELOWITZ, C.M., MATHIS, A., and SMITH, R.J.F. 1993. Chemosensory recognition of northern pike (*Esox lucius*) by brook stickleback (*Culaea inconstans*): Population differences and the influence of predator diet. *Behaviour* 127:105–118.

GILES, N., and HUNTINGFORD, F.A. 1984. Predation risk and interpopulation variation in antipredator behaviour in the three-spined stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* 32:264–275.

GÓMEZ, A., FONT, E., and DESFILIS, E. 1993. Chemoreception in the Lacertidae: Exploration and conspecific discrimination in the Spanish wall lizard, *Podarcis hispanica*, pp. 213–230, *in* E.D. Valakos, W. Böhme, V. Pérez-Mellado, and P. Maragou (eds.). Lacertids of the Mediterranean Region. Hellenic Zoological Society, Athens.

GRUBER, U. 1989. Die Schlangen Europas. Franckh'sche Verlagshandlung, Stuttgart.

HERZOG, H.A., and SCHWARTZ, J.M. 1990. Geographical variation in the anti-predator behaviour of neonate garter snakes, *Thamnophis sirtalis*. *Anim. Behav.* 40:597–601.

HUNTINGFORD, F.A. 1982. Do inter- and intraspecific aggression vary in relation to predation pressure in sticklebacks? *Anim. Behav.* 30:909–916.

JAERVI, T., and UGLEM, I. 1993. Predator training improves the anti-predator behaviour of hatchery reared Atlantic salmon (*Salmo salar*) smolt. *Nord. J. Freshwat. Res.* 68:63–71.

MAGURRAN, A.E. 1986. Predator inspection behaviour in minnow shoals: Differences between populations and individuals. *Behav. Ecol. Sociobiol.* 19:267–273.

MAGURRAN, A.E. 1989. Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*). *Ethology* 82:216–223.

MAGURRAN, A.E. 1990. The inheritance and development of minnow anti-predator behaviour. *Anim. Behav.* 39:834–842.

MAGURRAN, A.E., and SEGHERS, B.H. 1990. Population differences in predator recognition and attack cone avoidance in the guppy *Poecilia reticulata. Anim. Behav.* 40:443–452.

MATHIS, A., and SMITH, R.J.F. 1992. Avoidance of areas marked with a chemical alarm substance by fathead minnows (*Pimephales promelas*) in a natural habitat. *Can. J. Zool.* 70:1473–1476.

NORUSIS, M.J. 1990. SPSS/PC+ Statistics for the IBM PC/XT/AT and PS/2. SPSS, Chicago.

NUYTEN, K., and VAN WEZEL, H. 1984. Twee gedragsstudies aan de levendbarende hagedis (*Lacerta vivipara*): Waarneming en herkenning van een predator en van vrouwtjes als paringspartner. BSc thesis. University of Nijmegen.

OLLA, B.L., and DAVIS, M.W. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*). *Aquaculture* 76:209–214.

OWINGS, D.H., and COSS, R.G. 1977. Snake mobbing by Californian ground squirrels: Adaptive variation in ontogeny. *Behaviour* 62:50–69.

PARSONS, T.S. 1970. The nose and Jacobson's organ, pp. 99–191, *in* C. Gans, and T.S. Parsons (eds.). Biology of the Reptilia, Vol. 2. Academic Press, New York.

PECKARSKY, B.L., and PENTON, M.A. 1988. Why do *Ephemerella* nymphs scorpion posture: A "ghost of predation past"? *Oikos* 53:185–193.

RIECHERT, S.E., and HEDRICK, A.V. 1990. Levels of predation and genetically based anti-predator behaviour in the spider, *Agelenopsis aperta. Anim. Behav.* 40:679–687.

SALVADOR, A. 1986. *Podarcis hispanica* (Steindachner, 1870)—Iberische Mauereidechse, pp. 71–82, *in* W. Böhme (ed.). Handbuch der Reptilien und Amphibien. Aula-Verlag, Wiesbaden.

SIBLY, R.M., NOTT, H.M.R., and FLETCHER, D.J. 1990. Splitting behaviour into bouts. *Anim. Behav.* 39:63–69.

SLATER, P.J.B., and LESTER, N.P. 1982. Minimising errors in splitting behaviour into bouts. *Behaviour* 79:153–161.

SWEET, S.S. 1985. Geographic variation, convergent crypsis and mimicry in gopher snakes (*Pituophis melanoleucus*) and western rattlesnakes (*Crotalis viridis*). *J. Herpetol.* 19:55–67.

THOEN, C., BAUWENS, D., and VERHEYEN, R.F. 1986. Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. *Anim. Behav.* 34:1805–1813.

VAN DAMME, R., BAUWENS, D., VANDERSTIGHELEN, D., and VERHEYEN, R.F. 1990. Responses of the lizard *Lacerta vivipara* to predator chemical cues: the effect of temperature. *Anim. Behav.* 40:298–305.

VAN DAMME, R., BAUWENS, D., THOEN, C., VANDERSTIGHELEN, D., and VERHEYEN, R.F. 1995. Responses of naive lizards to predator chemical cues. *J. Herpetol.* 29:38–43.

VERBEEK, B. 1972. Ethologische Untersuchungen an einiger europäische Eidechsen. *Bonner Zool. Beitr.* 23:122–151.