acta ethol (2002) 4:119–124
DOI 10.1007/s102110100051

ORIGINAL ARTICLE

William E. Cooper Jr · Valentín Pérez-Mellado

Responses by a generalist predator, the Balearic lizard *Podarcis lilfordi*, to chemical cues from taxonomically diverse prey

Received: 11 April 2001 / Received in revised form: 17 July 2001 / Accepted: 18 July 2001 / Published online: 14 September 2001

Abstract Specialist predators may respond strongly to sensory cues from preferred prey, but responses by generalist predators, although predicted to be less specific, are poorly known. Among squamate reptiles, diet and strength of response to chemical prey cues covary geographically in snakes that are specialist predators. There have been no previous studies of correspondence between diet and chemosensory response in lizards that are prey generalists. Actively foraging lizards discriminate between prey chemicals and control substances. It has been speculated that differential responses among prey species are unlikely in typical species that are dietary generalists. We examined this relationship in *Podarcis lilfordi*, an omnivorous lacertid that consumes a wide variety of animal prey. In experiments in which chemical stimuli were presented on cotton swabs, lizards responded more strongly to chemicals from a broad spectrum of prey types than to deionized water, an odorless control. These findings plus previous data showing that *P. lilfordi* is capable of prey chemical discrimination suggest that *P. lilfordi* can identify a wide range of potential prey using chemical cues. However, there was no evidence of differential response to stimuli among prey species, even in comparisons of prey included in the natural diet and potential prey not in the diet. The results, although limited to a single species, are consistent with the hypothesis that lizard species that are prey generalists do not exhibit the differential response strengths to chemical prey cues observed in snakes that have more specialized diets.

Communicated by R.F. Oliveira

W.E. Cooper Jr (✉)
Department of Biology, Indiana University–Purdue University,
Fort Wayne, IN 46805, USA
e-mail: cooperw@ipfw.edu
Tel.: +1-219-4816311, Fax: +1-219-4816087

V. Pérez-Mellado
Departamento de Biologia Animal, Universidad de Salamanca,
Salamanca 37071, Spain

Keywords Behavior · Chemical senses · Diet · Lacertidae · Squamata

Introduction

Responses to sensory cues used to identify and select foods can be expected to reflect dietary preferences in dietary specialists but might not vary strongly among prey types in prey generalists. Variation in response strength to chemical cues from different prey types has been best demonstrated in squamate reptiles, in particular, snakes, many of which specialize in consumption of a narrow range of prey types. Among snakes the strength of responses to chemical prey cues varies among prey types within snake populations, being strongest to locally important dietary items (e.g., Burghardt 1967, 1970a; Cooper et al. 1990). Response strength also covaries geographically with diet among snake populations, populations in each area exhibiting strongest reactions to foods that they normally eat (Burghardt 1970b; Arnold 1992; Burghardt and Schwartz 1999; Cooper et al. 2000a). Both the intra- and interpopulational data suggest that natural selection has produced the strongest responses to locally preferred prey types.

Like snakes, many lizards are capable of identifying food using only chemical cues (reviewed by Cooper 1994a, b, 1995, 1997), but whether they respond differentially among palatable prey types is virtually unknown. If the specificity of response to chemical cues from favored prey by snakes is a consequence of dietary specialization, it may be absent or greatly reduced in lizards, most of which are insectivores (Pough 1973; Iverson 1982). Most so-called insectivorous lizards are actually generalist predators of arthropods and other animals small enough to be consumed (Pianka 1986). Given the broad diet of generalist insectivores and of omnivores, it has been assumed that they would respond strongly to surface chemicals from a wide taxonomic range of prey (Cooper 2000a; Cooper and Habegger 2000a). This assumption has been one basis for studying responses to prey and plant chemicals by insectivores, omnivores, and herbivores to establish whether there is a correspondence between diet and chemosensory response in lizards (Cooper 2000a; Cooper et al. 2000b).

The assumption of strong responsiveness to chemical cues from a wide range of prey rests on weak evidence because most studies of prey chemical discrimination have used chemical stimuli from only a single prey species and the few that have tested responses to more than one prey type have used a taxonomically limited range of prey. Von Achen and Rakestraw (1984) found strong responses to chemical cues from two spider species and an orthopteran species by the scincid lizard *Eumeces fasciatus* and the anguid *Ophisaurus ventralis*, but responses did not differ significantly among prey types. Using prey cues from three different phyla, Burghardt (1973) found that mealworm extract elicited a significantly stronger response by *E. fasciatus* than did cues from neonatal mouse. Responses to neither of these prey differed from response to earthworm extract. In informal laboratory tests, Cooper (unpublished observations) has noted strong responses to chemical cues from tenebrionid beetle larvae and crickets by scincid and lacertid lizards. From all of these studies there is only the one known instance of differential response among potential prey types. Further information based on responses to a wider taxonomic diversity of prey is needed to assess the relationship between diet and chemosensory responsiveness in lizards.

Actively foraging, but not ambush foraging, insectivorous lizards are capable of discriminating prey chemicals from control substances by tongue flicking (Cooper 1995, 1997, 1999, 2000b). Recent studies show that omnivorous lizards also exhibit prey chemical discrimination (e.g., Cooper 2000c, Cooper et al. 2000b). The three chemical senses most likely to be useful for prey chemical discrimination are olfaction, gustation, and vomerolfaction. Most lizards have well-developed olfactory systems (Parsons 1970; Gabe and Saint Girons 1976) and many have numerous lingual taste buds (Schwenk 1985). The vomeronasal organs of squamate reptiles are more developed than those of other vertebrates, being relatively larger and having higher concentrations of chemoreceptor cells (Parsons 1970; Gabe and Saint Girons 1976; Cooper 1996).

Active foragers tongue flick environmental substrates, sampling nonvolatile molecules (Evans 1961). The molecules are carried into the mouth when the tongue is retracted and pass by a disputed mechanism into the openings of the vomeronasal ducts in the roof of the mouth, traveling through the ducts to the chemosensory epithelium of the vomeronasal organs (Gillingham and Clark 1981; Halpern 1992; Young 1993). The strong development of the vomeronasal organs and involvement of the tongue in prey chemical discriminations suggest the importance of vomerolfaction to prey chemical discrimination but by no means establish it. Olfaction or even taste might participate in prey chemical discriminations. However, tests of garter snakes (*Thamnophis sirtalis*) and the desert iguana (*Dipsosaurus dorsalis*) show that vomerolfaction is crucial for prey chemical discrimination (Halpern and Frumin 1979; Cooper and Alberts 1991). In the only lizard species tested, *D. dorsalis*, blocking vomerolfaction eliminates prey chemical discrimination despite the availability of olfactory and gustatory cues (Cooper and Alberts 1991). Tongue flicking is a useful index of chemosensory investigation of potential foods due to its role in sampling chemicals for vomerolfactory analysis (Cooper and Burghardt 1990a). Biting in response to food chemicals often provides further evidence that lizards have identified the chemicals as indicators of food.

Here, we report the findings of a study of tongue flicking and biting responses to chemical cues from a wide range of prey types presented on cotton swabs to the Balearic lizard *Podarcis lilfordi*, a lacertid endemic to the Balearic Islands of the Mediterranean, especially on islets surrounding Menorca and Mallorca. This species is a medium-sized omnivore that consumes many different prey types as well as flowers, nectar, and fruits (Pérez-Mellado and Corti 1993; Pérez-Mellado et al. in press). By tongue flicking, *P. lilfordi* can discriminate between chemical cues from plant and animal foods and control substances (Cooper and Pérez-Mellado 2001). In previous tests using stimuli from domestic crickets *Acheta domesticus*, *P. lilfordi* was found to discriminate between prey chemicals and control substances (Cooper and Pérez-Mellado 2001). In the present study we examined responses to known and potential prey species syntopic with the lizards or found nearby on Menorca, the ancestral source of the lizard population studied. The goal was to determine whether a prey generalist exhibits strong chemosensory discriminations among prey types, as do more dietarily specialized snakes, or exhibits relatively strong and not greatly differing responses among prey types, which would be expected for a species adapted to feeding on a broad spectrum of prey types. Tests were limited to animal prey stimuli because *P. lilfordi* is more specialized in its selection of plant foods (Pérez-Mellado and Corti 1993).

Methods

Subjects and maintenance

We collected adult *Podarcis lilfordi* on Aire, Menorca, Balearic Islands, Spain by placing cut pears in a plastic cooler and placing rocks next to the cooler to allow the lizards to climb to the opening at the top and jump into the cooler. The lizards were housed individually in translucent plastic terraria (40×26×26 or 46×26×26 cm) in the laboratory on Menorca. To reduce possible disturbance by investigators and distraction by lizards in neighboring cages, the sides of the terraria were covered by brown paper. Each terrarium contained a substrate of indoor–outdoor carpet and a water bowl. Ambient temperature was 28.6–29.6°C, and heat lamps adjacent to the cages produced a thermal gradient that permitted the lizards to thermoregulate to attain higher temperatures. The lizards were active and fed readily under laboratory conditions. A window supplied light on the natural light cycle for the region, and the incandescent bulbs used for heat provided additional light.

Water was available ad libitum. The lizards were not fed prior to the experiments but were tested during the 2 days following capture. Upon conclusion of the experiments reported here and additional work, the lizards were released at the site of capture.

Experimental procedures

We evaluated the hypotheses that *P. lilfordi* detects chemical stimuli from a wide taxonomic spectrum of prey species and that response strength varies with prey type. The prey stimuli were integumentary chemicals from ants, a beetle, a thysanuran, an isopod (*Porcellio* sp.), a slug, a snail, an earthworm, and a toad (*Bufo viridis*). Ants and beetles form important portions of the diet for *P. lilfordi* from Aire, and snails and isopods are also eaten (Pérez-Mellado and Corti 1993). Toads do not occur on Aire and might be rejected as food due to defensive chemicals; earthworms, slugs, and thysanurans have not been recorded in the diet but have limited availability and might be consumed if encountered (Pérez-Mellado and Corti 1993). Because previous experimental work had established that *P. lilfordi* is capable of discriminating between prey and control substances using only chemical cues, only deionized water was used as an odorless control for responses elicited by the experimental setting and procedures in the absence of prey cues. Significantly different responses to animal cues and deionized water would show that the animals detected chemicals from the animal species used as stimulus sources.

The stimuli were presented on the cotton tips of wooden applicators (15 cm). The first step in stimulus preparation was to immerse the cotton tip of an applicator in deionized water and remove excess fluid by flicking the wrist. For trials involving prey cues, the moist swab was rolled across the surface of a prey item with firm pressure to impart prey surface chemicals to the cotton. The concentration of chemicals cannot be controlled by this procedure and may vary among prey types. However, because the stimuli are sampled in a standardized manner from prey surfaces, stimulus strengths should accurately reflect their availability to predators on prey surfaces.

To conduct a trial an experimenter approached a lizard's cage and slowly positioned a swab 1–2 cm anterior to a lizard's snout. Unless the lizard bit the swab, the experimenter recorded the number of tongue flicks directed to the swab during a 60-s interval beginning with the first tongue flick. If the lizard bit the swab, the number of tongue flicks prior to the bite and latency in seconds to bite were recorded and the trial was terminated. If a lizard did not tongue flick within 30 s after the swab was placed before it, the experimenter gently touched the lizard's anterior labial scales with the swab to induce tongue flicking.

A randomized blocks design was used, each lizard responding to all stimuli. For the 20 *P. lilfordi* tested, the sequence of stimulus presentation was randomized among individuals to avoid bias due to testing order. The only exception to randomization was that all lizards were tested with deionized water as one of the first five trials, corresponding to the first day of testing. The responses of 2 individuals decreased greatly over trials. Both became unresponsive and were dropped from the experiment, leaving *n*=18. Because responsiveness tended to decrease due to habituation to testing conditions, inclusion of all trials with water in the first five trials is conservative in decreasing the likelihood of detecting differences between prey cues and deionized water. Five trials were conducted on 29 May 2000, and the remaining four trials were conducted on 30 May 2000. The minimum intertrial interval was 20 min.

The most important response variable was the tongue-flick attack score for experiments having repeated measures designs, TFAS(R) (Cooper and Burghardt 1990b). If the lizard does not bite the swab, TFAS(R) is the number of tongue flicks in 60 s. If it bites, TFAS(R) is the greatest number of tongue flicks by that individual in any one of the stimulus conditions plus [60 minus the latency to bite in seconds]. Because biting reflects a predation attempt, it is weighted more heavily than any number of tongue flicks unless the bite occurs at exactly 60 s.

Statistical analysis

Continuous variables analyzed were number of tongue flicks, latency to bite, and TFAS(R), all of which had homogeneous variances using Hartley's F_{max} test (Winer 1962). The significances of differences among stimuli for tongue flicks, latency to bite, and TFAS(R) were assessed using analysis of variance for a single-factor experiment having a randomized blocks (repeated measures) design (Winer 1962). Following detection of significant main stimulus effects, Newman–Keuls tests were used to determine the significance of differences between pairs of stimulus means. Differences among conditions in proportion of lizards biting swabs were tested for significance by a Cochran's *Q* test followed by sign tests of the differences among pairs of conditions (Siegel 1956). Unadjusted probabilities are reported for the sign tests, but statements regarding their significance are based on sequential Bonferroni adjustments for the number of tests (Wright 1992). Significance tests were two-tailed with $\alpha=0.05$ (unless adjusted lower).

Results

Podarcis lilfordi responded strongly to chemical cues from a wide variety of animal species including known and potential prey species. The number of tongue flicks varied little among conditions (Table 1; *F*=1.07; *df*=8, 136; *P*>0.10). Latency to bite (Table 1) varied significantly among conditions (*F*=3.69; *df*=8, 136; *P*<0.00063). Latencies were significantly shorter in response to all animal prey cues than to deionized water (probabilities: ant, 0.00044; beetle, 0.025; thysanuran, 0.0024; isopod, 0.0028; earthworm, 0.00072; slug, 0.0037; snail, 0.0062; toad, 0.0330). No pairs of prey stimuli conditions differed significantly in latency.

Table 1 Tongue flicks, latency to bite (in seconds), and number of individuals (*n*=18) that bit on both days pooled in response to chemical cues from ant (*AN*), beetle (*BE*), thysanuran (*TH*), isopod (*IS*), earthworm (*EW*), slug (*SL*), snail (*SN*), toad (*TD*), and deionized water (*DW*) in 60-s swab trials. *SE* Standard error

	AN	BE	TH	IS	EW	SL	SN	TD	DW
Tongue flicks									
$\bar{x}$	5.5	9.9	7.1	6.9	6.5	4.9	5.9	6.0	8.6
SE	1.2	1.9	1.2	1.5	2.0	1.4	1.9	1.8	1.5
Range	1–20	1–32	1–20	1–22	1–30	1–23	1–27	1–34	2–24
Latency to bite									
$\bar{x}$	11.1	22.9	15.2	14.9	12.3	16.7	18.6	26.1	40.3
SE	4.4	5.8	4.9	5.0	5.2	5.2	6.3	6.6	6.1
Range	1–60	1–60	1–60	1–60	1–60	1–60	1–60	1–60	3–60
Number that bit	16	15	15	16	15	15	13	11	7

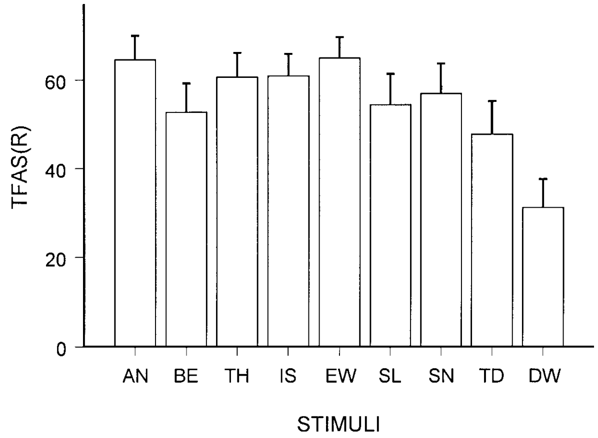

Fig. 1 Tongue-flick attack scores [TFAS(R)] by 18 adult *Podarcis lilfordi* to chemical cues from ant (*AN*), beetle (*BE*), thysanuran (*TH*), isopod (*IS*), earthworm (*EW*), slug (*SL*), snail (*SN*), toad (*TD*), and deionized water (*DW*). *Error bars* represent one SE

Although numerous individuals bit in all conditions, the number of individuals that bit (Table 1) was lower in response to deionized water than to any of the animal stimuli. Numbers of individuals that bit differed significantly among conditions ($Q=26.25$, $df=8$, $P<0.001$). None of the differences among pairs of stimuli were significant after Bonferroni adjustment, but the source of the significant main effect is clearly the differences between deionized water, which elicited the fewest bites, and stimuli from several prey types. Unadjusted P values for the comparisons with deionized water are 0.004 for beetle, slug, and thysanuran, 0.006 for *Porcellio*, ant, and earthworm, and 0.008 for snail. Toad stimuli elicited the fewest bites among animal stimuli, but the differences among animal stimuli were not significant.

TFAS(R) values were much greater in response to chemical cues from animal stimuli than from deionized water but differed little among the animal stimuli (Fig. 1). The stimulus effect was highly significant ($F=3.84$; $df=8$, 136; $P<0.00005$). TFAS(R) was significantly lower in response to deionized water than to chemical cues from ant ($P<0.0004$), beetle ($P<0.013$), thysanuran ($P<0.0016$), isopod ($P=0.004$), earthworm ($P<0.00033$), slug ($P=0.013$), snail ($P<0.0065$), and toad ($P<0.030$). All other differences had P values >0.10.

Discussion

Podarcis lilfordi is able to identify prey using only chemical cues and exhibits similar strong responses to a wide range of prey types as predicted for a prey generalist. The lizards responded much more strongly to chemical stimuli from a broad spectrum of prey species than to deionized water. The evidence for this is that the latency to bite was significantly shorter and tongue-flick attack score was significantly greater for each of the prey stimuli than for deionized water. That predatory attack occurred more quickly after sampling cues by tongue flicking in response to all types of potential prey than to the odorless control substance suggests that the lizards identified the diverse animal stimuli as indicating food. Our earlier work showed that the lizards discriminated cricket stimuli from deionized water and a pungency control, cologne, and that their responses to cologne did not differ from those to deionized water (Cooper and Pérez-Mellado 2001). Combined with the earlier finding of prey chemical discrimination, the current findings of stronger responses to all prey types than to deionized water suggest that the lizards can identify chemicals from a wide range of prey.

There is no evidence for correspondence between diet and responsiveness to prey cues or even for differential responses to stimuli among prey species. Although ants and beetles form important portions of the diet for *P. lilfordi* from Aire, responses to their chemical cues were not significantly greater than those to species that are rarely or never eaten, such as toads, earthworms, slugs, and thysanurans (Pérez-Mellado and Corti 1993). On the contrary, responses to chemical cues from thysanurans, slugs, and earthworms (Fig. 1) were strong despite the absence of these animals in the diet. Despite a lack of significant differences among stimuli, the latency to bite was greatest for ants and the number of tongue flicks was greatest in response to beetles. However, there was no hint of greater TFAS(R), the best indicator of overall response strength, in response to important foods than to infrequent or unutilized prey types.

Combined with the presence of strong responses to chemical cues from a wide variety of animal prey, the lack of strong differential responses among prey types suggests that the lizards may respond to chemical constituents shared by many prey. The chemical nature of the effective stimuli is unknown, but likely possibilities are proteins, lipids, or both, which may be widespread in animals.

The results support the hypothesis that *P. lilfordi*, a dietary generalist, exhibits little (or no) specificity of response to chemical cues from favored animal prey. This stands in marked contrast with findings for snakes having more specialized diets (e.g., Burghardt 1970a; Henderson et al. 1983; Arnold 1992; Cooper et al. 2000a), which exhibit highly significant differences in strength of responses among prey types using much smaller sample sizes. Because this is the first study designed to test responses of lizards having broad diets to chemical cues from a wide range of prey taxa, we cannot generalize our findings even to the majority of insectivorous and omnivorous dietary generalists. Although our findings are likely to be widely applicable, studies of additional species representing other lineages are desirable.

If the present findings apply to most actively foraging insectivorous lizards and omnivores derived from actively foraging ancestors, studies of diet and chemosensory responsiveness are unlikely to reveal the geographic covariation observed within species in snakes (Burghardt 1970b; Arnold 1981; Cooper et al. 2000a) or correlated evolution of diet and chemosensory responsiveness. That is not to say that prey-specific responses are absent in lizards, which are capable of responding specifically to cues from predatory snakes (e.g., Thoen et al. 1986; Dial et al. 1989; Cooper 1990; Phillips and Alberts 1992) and of identifying species, sex, reproductive condition, and familiar individuals using only pheromonal cues. It cannot be concluded from this study that the lizards cannot detect differences among chemical cues from various prey types. They might do so without responding differentially if all prey are acceptable.

There are two good possibilities for extending the findings of differential response to food chemical cues by food specialists from snakes to lizards. A correspondence between diet and chemosensory responses might occur in actively foraging insectivorous/carnivorous species that have the most specialized diets. Relatively few dietary specialists are found among actively foraging lizards, but the food niche breadth of several species of termite specialists (Pianka 1986) is narrow enough to provide good tests. Other candidates for such studies are several varanids that eat primarily vertebrates and the lacertid *Nucras tessallatus*, for which scorpions constitute over half of the diet (Pianka 1986).

Another approach would be to examine the relationship between response to plant chemicals and inclusion of plants in the diet. All information available to date suggests that insectivorous species do not discriminate chemicals from palatable plants from control stimuli, but that omnivorous and herbivorous species do so (e.g., Cooper 2000a, c, d; Cooper and Habegger 2000a, b; Cooper et al. 2000b). Unlike prey chemical discrimination, which is limited to actively foraging lineages among insectivores and carnivores, plant chemical discrimination occurs in omnivores and herbivores derived from both ambush foragers and active foragers. Ongoing comparative studies suggest that there is a strong link between plant diet and plant chemical discrimination. The categories of chemical stimuli used to identify plants have not been investigated.

Acknowledgements This study was partially supported by grants from the Plan de Movilidad de Investigadores of the University of Salamanca and by the Institut Menorquí d'Estudis, Consell Insular de Menorca, and by project PB98-0270 of the Spanish Ministry of Education and Culture. We complied with current laws of Spain in conducting the work.

References

Arnold SJ (1981) Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. Evolution 35:489–509

Arnold SJ (1992) Behavioural variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. Anim Behav 44:705–719

Burghardt GM (1967) Chemical-cue preferences of inexperienced snakes: comparative aspects. Science 157:718–721

Burghardt GM (1970a) Chemical perception of reptiles. In: Johnston JW Jr, Moulton DG, Turk A (eds) Communication by chemical signals. Appleton-Century-Crofts, New York, pp 241–308

Burghardt GM (1970b) Intraspecific geographical variation in chemical good cue preferences of newborn garter snakes (*Thamnophis sirtalis*). Behaviour 36:246–257

Burghardt GM (1973) Chemical release of prey attack: extension to naive newly hatched lizards, *Eumeces faciatus*. Copeia 1973:178–181

Burghardt GM, Schwartz JM (1999) Geographic variations on methodological themes from comparative ethology: a natricine snake perspective. In: Foster SA, Endler JA (eds) Geographic diversification of behavior: an evolutionary perspective. Oxford University Press, Oxford, pp 69–94

Cooper WE Jr (1990) Chemical detection of predators by a lizard, the broad-headed skink (*Eumeces laticeps*). J Exp Zool 256: 162–167

Cooper WE Jr (1994a) Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. J Chem Ecol 20:439–487

Cooper WE Jr (1994b) Prey chemical discrimination, foraging mode, and phylogeny. In: Vitt LJ, Pianka ER (eds) Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, N.J., pp 95–116

Cooper WE Jr (1995) Foraging mode, prey chemical discrimination, and phylogeny in lizards. Anim Behav 50:973–985

Cooper WE Jr (1996) Preliminary reconstructions of nasal chemosensory evolution in Squamata. Amphibia-Reptilia 17:395–415

Cooper WE Jr (1997) Correlated evolution of prey chemical discrimination with foraging, lingual morphology, and vomeronasal chemoreceptor abundance in lizards. Behav Ecol Sociobiol 41:257–265

Cooper WE Jr (1999) Supplementation of phylogenetically correct data by two-species comparison: support for correlated evolution of foraging mode and prey chemical discrimination in lizards extended by first intrageneric evidence. Oikos 87:97–104

Cooper WE Jr (2000a) Food chemical discriminations by an herbivorous lizard, *Corucia zebrata*. J Exp Zool 286:372–378

Cooper WE Jr (2000b) An adaptive difference in the relationship between foraging mode and responses to prey chemicals in two congeneric scincid lizards. Ethology 106:193–206

Cooper WE Jr (2000c) Correspondence between diet and food chemical discriminations by omnivorous geckos (*Rhacodactylus*). J Chem Ecol 26:755–763

Cooper WE Jr (2000d) Chemosensory discrimination of plant and animal foods by the omnivorous iguanian lizard *Pogona vitticeps*. Can J Zool 78:1–5

Cooper WE Jr, Alberts AC (1991) Tongue-flicking and biting in response to chemical food stimuli by an iguanid lizard (*Dipsosaurus dorsalis*) having sealed vomeronasal ducts: vomerolfaction may mediate these behavioral responses. J Chem Ecol 17:135–146

Cooper WE Jr, Burghardt GM (1990a) Vomerolfaction and vomodor. J Chem Ecol 16:103–105

Cooper WE Jr, Burghardt GM (1990b) A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. J Chem Ecol 16:45–65

Cooper WE Jr, Habegger JJ (2000a) Elevated tongue-flicking and biting by the insectivorous lygosomine skink *Mabuya macularia* to prey, but not plant, chemicals. Ethol Ecol Evol 12: 175–186

Cooper WE Jr, Habegger JJ (2000b) Lingual and biting responses to food chemicals by some eublepharid and gekkonid geckos. J Herpetol 34:360–368

Cooper WE Jr, Pérez-Mellado V (2001) Food chemical cues elicit general and population-specific effects on lingual and biting behaviors in the lacertid lizard *Podarcis lilfordi*. J Exp Zool 290:207–217

Cooper WE Jr, Buth DG, Vitt LJ (1990) Prey odor discrimination by ingestively naive coachwhip snakes (*Masticophis flagellum*). Chemoecology 1:86–91

Cooper WE Jr, Burghardt GM, Brown WS (2000a) Behavioural responses by hatchling racers (*Coluber constrictor*) from two geographically distinct populations to chemical stimuli from prey and predators. Amphibia-Reptilia 21:103–115

Cooper WE Jr, Al-Johany AM, Vitt LJ, Habegger JJ (2000b) Responses to chemical cues from animal and plant foods by actively foraging insectivorous and omnivorous scincine lizards. J Exp Zool 287:327–339

Dial BE, Weldon PJ, Curtis B (1989) Chemosensory identification of snake predators (*Phyllorhynchus decurtatus*) by banded geckos (*Coleonyx variegatus*). J Herpetol 23:224–229

Evans LT (1961) Structure as related to behavior in the organization of populations of reptiles. In: Blair WF (ed) Vertebrate speciation. University of Texas Press, Houston, pp 148–178

Gabe M, Saint Girons H (1976) Contribution a la morphologie comparee des fosses nasales et de leurs annexes chez lepidosauriens. Mem Mus Natl Hist Nat, Nouv Ser A 98:1–87

Gillingham JC, Clark DL (1981) Snake tongue-flicking: transfer mechanics to Jacobson's organ. Can J Zool 59:1651–1657

Halpern M (1992) Nasal chemical senses in reptiles: structure and function. In: Gans C, Crews D (eds) Biology of the Reptilia, vol 18. Brain, hormones, and behavior. University of Chicago Press, Chicago, pp 423–523

Halpern M, Frumin N (1979) Roles of the vomeronasal and olfactory systems in prey attack and feeding in adult garter snakes. Physiol Behav 22:1183–1189

Henderson R, Binder MH, Burghardt GM (1983) Responses of Hispaniolan vine snakes (*Uromacer frenatus*) to prey extracts. Herpetologica 39:75–77

Iverson JB (1982) Adaptations to herbivory in iguanine lizards. In: Burghardt GM, Rand AS (eds) Iguanas of the world. Noyes Publications, Park Ridge, N.J., pp 60–76

Parsons TS (1970) The nose and Jacobson's organ. In: Gans C, Parsons TS (eds) Biology of the Reptilia, vol 2. Morphology B. Academic Press, London, pp 99–191

Pérez-Mellado V, Corti C (1993) Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). Bonn Zool Beitr 44:193–220

Pérez-Mellado V, Perera A, Cortazar G (in press) La lagartija balear, *Podarcis lilfordi* (Günther, 1884) de I'Illa d'en Colom, Parc Natural de s'Albufera des Grau (Menorca). Situación actual y estado de conservación. Bull Cient Parcs Nat Balears

Phillips JA, Alberts AC (1992) Naive ophiophagous lizards recognize and avoid venomous snakes using chemical cues. J Chem Ecol 18:1775–1783

Pianka ER (1986) Ecology and natural history of desert lizards. Princeton University Press, Princeton, N.J.

Pough FH (1973) Lizard energetics and diet. Ecology 54:837–844

Schwenk K (1985) Occurrence, distribution and functional significance of taste buds in lizards. Copeia 1985:91–101

Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Thoen C, Bauwens D, Verheyen RF (1986) Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. Anim Behav 34:1805–1813

Von Achen PH, Rakestraw JL (1984) The role of chemoreception in the prey selection of neonate reptiles. In: Seigel RA, Hunt LE, Knight JL, Malaret L, Zuschlag NL (eds) Vertebrate ecology and systematics – a tribute to Henry S. Fitch. Museum of Natural History, University of Kansas, Lawrence, pp 163–172

Winer BJ (1962) Statistical principles in experimental design. McGraw-Hill, New York

Wright SP (1992) Adjusted p-values for simultaneous inference. Biometrics 48:1005–1013

Young BA (1993) Evaluating hypotheses for the transfer of stimulus particles to Jacobson's organ in snakes. Brain Behav Evol 41:203–209