Omnivorous lacertid lizards (*Gallotia*) from El Hierro, Canary Islands, can identify prey and plant food using only chemical cues

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Abstract: We studied lingual and biting responses to food chemicals by two species of omnivorous lacertid lizards, the Canary Island endemics *Gallotia simonyi* (the giant lizard of El Hierro) and *Gallotia caesaris* (Boettger's lizard), to ascertain their ability to discriminate between prey and plant food chemicals on the one hand and control stimuli on the other. We recorded frequencies of tongue-flicking and latency to bite in 60-s trials in which chemical stimuli on cotton-tipped applicators were presented to the lizards. Both species exhibited prey-chemical discrimination, as indicated by elevated tongue-flick rates and higher proportions of individuals biting in response to surface chemicals from crickets. Both species exhibited plant-chemical discrimination, as indicated by significantly greater tongue-flick rates and biting frequency in response to chemicals from tomato fruit than to the control stimuli. Juvenile *G. simonyi* responded much more strongly to chemical stimuli from tomato fruit than from leaves of *Psoralea bituminosa*, which is not a preferred food for juveniles. The findings are consistent with the hypothesis that chemosensory discrimination evolves in omnivorous lizards to permit evaluation of food quality, resulting in correspondence between plant diet and plant-chemical discrimination, both being absent in insectivores. The results are also consistent with the hypothesis that prey-chemical discrimination is retained and plant-chemical discrimination evolves in the omnivorous lizards derived from actively foraging insectivores.

Résumé : Nous avons examiné les réponses linguales et maxillaires aux substances chimiques alimentaires chez deux espèces de lézards lacertidés omnivores endémiques des îles Canaries, le Lézard géant d'El Hierro (*Gallotia simonyi*) et le Lézard de Boettgers (*Gallotia caesaris*) dans le but de vérifier leur capacité de discriminer d'une part les substances chimiques des proies et des plantes, et d'autre part les stimulus de contrôle. Nous avons noté la fréquence des coups de langue et le temps de latence avant la morsure au cours de tests de 60 s où les lézards étaient exposés à des stimulus chimiques présentés sur des cotons-tiges. Les lézards des deux espèces ont su distinguer les stimulus chimiques reliés aux proies; ils ont augmenté la fréquence de leurs coups de langue et une plus grande proportion des individus ont réagi par des morsures aux substances chimiques provenant de la surface de grillons. Les lézards des deux espèces ont également été capables de faire la discrimination entre les substances chimiques des plantes; la fréquence de leurs coups de langue et de leurs morsures ont augmenté significativement plus en présence de tomates qu'en présence de stimulus témoins. Les jeunes *G. simonyi* ont réagi beaucoup plus fortement aux stimulus chimiques des tomates qu'à ceux de feuilles de *Psoralea bituminosa* qui ne constituent pas une nourriture de prédilection pour les juvéniles. Ces résultats corroborent l'hypothèse selon laquelle la discrimination chimique évolue chez les lézards omnivores de façon à permettre l'évaluation de la qualité des aliments, ce qui donne lieu à des correspondances entre le régime alimentaire végétarien et la discrimination des substances chimiques des plantes, caractéristiques qui sont absentes chez les insectivores. Ces résultats appuient l'hypothèse selon laquelle, chez les lézards omnivores issus de lignées insectivores à quête active de nourriture, la discrimination chimique des proies demeure alors que la discrimination chimique des plantes se développe.

[Traduit par la Rédaction]

Introduction

To reliably obtain adequate energetic and nutritional intake, animals must have sensory capacities adequate to detect foods in the context of the search methods used. Evolutionary relationships may be expected to link discriminative abilities to diet and foraging behavior. Chemosensory responses by lizards to food are being studied intensively as a model system of these relationships. Many squamate reptiles can identify prey using only chemical cues sampled by tongue-flicking (Cooper 1994*a*, 1994*b*), but little is known regarding responses to plant chemicals or their relationship to diet. Food-chemical discrimination is mediated by vomerolfaction (Halpern and Frumin 1979; Cooper and Alberts 1991). Chemicals from substrates adhere to the protruded tongue, are carried into the mouth when the tongue is retracted, and are transferred to vomeronasal ducts at the roof of the mouth to the vomeronasal organs (Halpern 1992).

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Prey-chemical discrimination and its relationships to foraging and diet have been the focus of much research in snakes (e.g., Burghardt 1970*a*; Arnold 1981*a*; Cooper 1994*a*) and lizards (Cooper 1995, 1997, 1999, 2000*a*). All snakes are capable of prey-chemical discrimination (e.g., Burghardt 1970*a*; Cooper 1990), and chemical cues from preferred foods elicit the strongest responses (Burghardt 1970*b*). Dietary specialization in snakes facilitated establishment of a correspondence between diet and chemosensory responsiveness. Within populations, snakes respond most strongly to cues from preferred prey (e.g., Burghardt 1970*b*; Cooper et al. 1990). Geographic dietary variation, too, is matched by variation in responsiveness, with strongest responses to locally preferred foods (Burghardt 1970*b*; Arnold 1981*a*, 1981*b*; Cooper et al. 2000*a*).

For insectivorous lizards, foraging mode strongly influences prey-chemical discrimination (Cooper 1995, 1997). Active foragers tongue-flick while moving through the habitat searching for food (Evans 1961) and can thereby locate prey (Bogert and Martín del Campo 1956; Auffenberg 1984). All active foragers tested discriminate prey chemicals from control substances. Insectivorous ambush foragers tongue-flick infrequently (Evans 1961; Bissinger and Simon 1979), usually at the conclusion of infrequent moves (Cooper et al. 1994), and do not exhibit prey-chemical discrimination (Cooper 1994*a*). Only one species that has been called an ambush forager, the lacertid *Acanthodactylus scutellatus* (Perry et al. 1990), is known to be capable of prey-chemical discrimination (Cooper 1999). This species was derived from actively foragers, moves more frequently than the large majority of species of ambush foragers, and has a reduced capacity for prey-chemical discrimination compared with an actively foraging congener (Cooper 1999). Whether there is a relationship between diet and prey-chemical discrimination in lizards is uncertain.

Most lizard species are generalist predators (Pough 1973; Iverson 1982). They were traditionally called insectivores, but eat a much wider variety of small prey (e. g., Pianka 1986; Vitt and de Carvalho 1995). As expected from its diverse diet, the omnivorous *Podarcis lilfordi* responds strongly to chemical cues from diverse animal prey (W.E. Cooper, Jr. and V. Pérez-Mellado, unpublished data). The broad relationship between diet and response strength remains unknown.

Most lizard species eat little or no plant material (Iverson 1982). The responses to plant chemicals of those that eat plants are of interest to ascertain whether (*i*) chemosensory response in lizards corresponds to dietary preferences, (*ii*) plant-chemical discrimination is typical of omnivorous and herbivorous species, and (*iii*) responses to chemical cues from plants and animals are related to the foraging mode used to hunt animal prey. Prey- and plant-chemical discriminations occur in plant eaters from both major lizard lineages, Iguania (Cooper and Alberts 1990, 1991, 1993; Cooper 2000*c*; Cooper and Flowers 2001) and Scleroglossa (Cooper 2000*d*, 2000*e*, 2000*f*; Cooper et al. 2000*b*), but more comparative data are needed on the points raised.

Because prey-chemical discrimination was present in the omnivores that had insectivorous, actively foraging ancestors, maintenance of correspondence between diet and chemosensory response requires that plant-chemical discrimination be acquired upon addition of plants to the diet. For plant eaters that had ambush foragers as ancestors, plant-chemical discrimination might evolve for the purpose of assessing nutritional quality, and prey-chemical discrimination might also evolve once the lizards are freed from the need to remain immobile while waiting for prey at ambush posts where repeated tongue-flicking cannot aid in locating prey.

We present data on chemosensory responses to animal and plant foods of omnivorous *Gallotia*, lacertids endemic to the Canary Islands. *Gallotia simonyi*, the giant lizard of El Hierro (>200 mm snout–vent length (SVL)), is a critically endangered species that eats a variety of plants species and parts, including seeds, and diverse arthropods and vertebrates (Pérez-Mellado et al. 1999). *Gallotia caesaris*, a smaller species (ca. 100 mm SVL) that occurs syntopically with *G. simonyi*, also eats small animals, flowers, fruit, and buds (Barbadillo et al. 1999). Given that the sister-genus of *Gallotia*, *Psammodromus* (Harris et al. 1998), consists of insectivorous active foragers (Iverson 1982; Pérez-Mellado 1982; Pollo and Pérez-Mellado 1988; Arnold 1993), these genera are the sister-group of other lacertids, and that the sister-group of Lacertidae, Teiidae, consists of active foragers (Cooper 1994), the ancestral conditions for Lacertidae were active foraging and insectivory. Thus, their relationships to other lacertids permitted us to test the predictions that chemical discriminations by *G. simonyi* and *G. caesaris* has been retained from ancestral active foragers for prey and added for plants.

Material and methods

Animals and maintenance

Gallotia simonyi from several clutches hatched in September 1999 in the Lagartario (Centro de Recuperación del Lagarto Gigante de El Hierro), a breeding facility to propagate this endangered species for release into its former habitat, were studied in the laboratory at the breeding facility in late June 2000. The SVL and mass of these juveniles, based on measurement of 27 individuals in May 2000, were 67.6 ± 1.0 mm and 7.8 ± 0.4 g (mean ± 1.0 SE), respectively. Adults of *G. caesaris* were collected on 29 June 2000 on a rocky slope on El Hierro, Canary Islands, adjacent to the small remaining range of the endangered *G. simonyi*. They were captured in cylindrical opaque plastic traps, which were leaned against large rocks to permit access by the lizards to the open upper end and were baited with pieces of tomato. The traps were slick high enough to prevent lizards from escaping by climbing or jumping. They were also tested at the Lagartario.

Gallotia simonyi were housed two per cage in large wooden terraria (ca. 60 × 60 × 50 cm) with glass fronts. *Gallotia caesaris* were housed two per cage in plastic terraria (40 × 26 × 26 cm). The sides of each plastic cage were covered by white paper to reduce distraction by the surroundings and disturbance by movements of the investigators. The light cycle was natural for the region, provided by a window. The thermal cycle was that of the region with additional heat supplied by incandescent bulbs suspended in the wooden terraria or above the plastic terraria. During experiments the room temperature was 28–29°C and the cage temperature 1 cm above floor level was 31–34°C. The lizards had the opportunity to thermoregulate by basking and were active during trials. They were placed in cages overnight prior to testing and were not fed there until after the experiments, when they ate readily.

Stimuli and experimental design

Adult crickets (*Gryllus bimaculatus*) were the source of animal-prey stimuli for both lizard species. Leaves of the plant *Psoralea bituminosa* (Leguminosae) were the source of plant cues for

G. simonyi, but were not used for *G. caesaris* after it was found that they did not elicit strong responses from *G. simonyi*. Tomato fruit was a source of plant stimuli for both species. The former two species are used frequently as lizard food by the staff of the Lagartario and are eaten in the field (Pérez-Mellado et al. 1999). Tomato was selected as a fruit stimulus that had been found to be effective in attracting *G. caesaris* and *G. simonyi* to traps. *Gallotia simonyi* is known to consume at least one other species of Solanaceae (Pérez-Mellado et al. 1999). In addition to these organismic stimuli, we examined responses by the lizards to odorous and odorless control stimuli. Cologne (Mennen Skin Bracer, Spice Scent®) acted as a control for responses to a pungent nonfood substance. It was diluted with deionized water (3:1 deionized water: cologne by volume) to eliminate possible negative effects of undiluted cologne on responses (Dial and Schwenk 1996; Cooper 1998*a*, 1998*b*). The odorless control was deionized water.

Stimuli were prepared by dipping the cotton tip of a 15 cm long wooden applicator into deionized water and then adding other stimuli if necessary. The only exception was that swabs were dipped directly into diluted cologne without prior wetting. Excess water or cologne was removed by flicking the wrist. To add food stimuli to a moistened swab, the swab was rolled firmly over the surface of a cricket, leaf, or cut surface of a tomato.

To begin a trial, an experimenter approached a lizard's cage and slowly brought the cotton swab into a position 1–2 cm anterior to the lizard's snout. The appropriate individual to be tested within a cage was recognized from easily detected size differences between cage mates. Beginning with the first tongue-flick, the experimenter recorded the number of tongue-flicks directed to the swab in 60 s, the occurrence of biting and latency to bite in seconds, as well as any licking behavior. Licks occurred only after preliminary tongue-flicks and presumably reflect a feeding behavior rather than chemosensory investigation. Thus, it would have been feasible to treat the first lick as the equivalent of a bite, stop the trial when the first lick occurred, and calculate a variable equivalent to the tongue-flick attack score for repeated-measures experiments, TFAS(R), but with either a bite or a lick as the variable other than tongue-flicks. Because a feeding behavior receives heavier weighting than any number of tongue-flicks, counting licks as tongue-flicks would not affect the rankings used for analysis.

All experiments employed repeated-measures designs and a minimum intertrial interval of 30 min. Two experiments were conducted with *G. simonyi*. In experiment 1, the responses of 20 individuals to chemical cues from cricket, *P. bituminosa* leaves, cologne, and deionized water were examined from 15:00 to 18:40 on 29 June 2000. Three individuals were dropped from the analysis because they failed to respond in any trial and repeatedly fled, giving a sample size of 17. The sequence of trials was partially counterbalanced among individuals to avoid possible bias due to the sequence of stimulus testing. In experiment 2, conducted from 10:45 to 12:00 on 30 June 2000, the stimuli tested were tomato and deionized water. Four of the 20 individuals were dropped because of nonresponsiveness, giving a sample size of 16. Trial sequence was completely counterbalanced, with response to each stimulus being tested first in half of the individuals. The responses of *G. caesaris* to chemical stimuli from cricket, tomato, cologne, and deionized water were observed on 30 June 2000 from 13:20 to 16:40. The sequence of stimulus presentation was partially counterbalanced among the 20 individuals tested.

Variables and analyses

The variables analyzed for all experiments were the number of tongue-flicks, number of individuals that bit, and tongue-flick attack score (TFAS). TFAS(R) is the best overall indicator of response strength (Burghardt 1967, 1970*a*; Cooper and Burghardt 1990; Cooper 1998*a*). It is a composite variable that combines the effects of tongue-flicks and biting, weighting biting more heavily because it is a feeding response. If a lizard does not bite in a trial, its TFAS(R) is the number of tongue-flicks in that trial. If the lizard bites, TFAS(R) is the maximum number of tongue-flicks by that individual in any one of its trials in that experiment plus (60 minus latency to bite in seconds). The number of individuals that failed to tongue-flick in a given condition also was analyzed for experiment 1 with *G. simonyi*.

The preferred method of analysis for tongue-flicks and TFAS(R) is parametric analysis of variance for a single-factor experiment having a repeated-measures (randomized blocks) design (Winer 1962), but variances of these variables are often heterogeneous and their distributions are sometimes non-normal. Data were examined for heterogeneity of variance as approximated by Hartley's $F_{\max}$ tests. Because (*i*) variances were significantly heterogeneous for both the raw data and logarithmically transformed data ($\log(x + 1)$) and (or) (*ii*) the data exhibited extreme departure from normality in all cases, nonparametric tests were used. Main effects were assessed for significance using Friedman's two-way analysis of variance. If the main stimulus effects were significant, comparisons between pairs of stimulus condition means were made following procedures described by Zar (1996). Data in the text are presented as the mean ± 1.0 SE.

Differences among conditions in the numbers of individuals that bit and the numbers of individuals that failed to tongue-flick were examined using Cochran's *Q* tests. If significant main effects were found, binomial tests were used for comparisons between pairs of conditions. Significance levels were adjusted lower by a sequential Bonferroni procedure (Wright 1992) to account for the number of possible unplanned tests. Unadjusted probabilities are reported for the binomial tests, but comparisons stated to be significant reflect the Bonferroni adjustment. Statistical tests were two-tailed, with $\alpha = 0.05$.

Results

Gallotia simonyi

Experiment 1

The yearlings exhibited much stronger responses to cricket chemicals than to the other stimuli, and responded more strongly to the plant stimuli than to the control stimuli (Table 1, Fig. 1). Furthermore, many individuals failed to tongue-flick in the control trials, but did tongue-flick in response to prey and plant cues (Table 1). The number of tongue-flicks varied significantly among conditions ($\chi^2 = 34.68$, df = 3, $P < 1.0 \times 10^{-5}$). Paired comparisons revealed that the lizards performed significantly more tongue-flicks in the cricket condition than in the plant ($P < 0.025$), cologne ($P < 0.01$), and deionized water conditions ($P < 0.01$). Numbers of tongue-flicks in response to plant stimuli were significantly greater than to cologne ($P < 0.025$) or deionized water ($P < 0.05$). The difference between the two control stimuli was minimal and nonsignificant ($P > 0.10$).

The numbers of individuals that failed to tongue-flick (Table 1) also varied significantly among conditions ($Q = 19.09$, df = 3, $P < 0.001$). Significantly more individuals tongue-flicked in the cricket condition than in the cologne ($P < 0.002$) and deionized water ($P < 0.005$) conditions. Substantially more individuals tongue-flicked at least once in the plant condition than in the cologne and deionized water conditions ($P < 0.05$ each), but the differences were not significant after Bonferroni adjustment. The difference between the control conditions was not significant ($P > 0.10$).

Table 1. Tongue-flick and bite data for two sympatric species of *Gallotia* responding to chemical stimuli from prey, palatable plants, and a control substance in 60-s swab trials.

	Cricket	Plant	Cologne	Deionized water
G. simonyi (*n* = 17)				
No. of tongue-flicks				
Mean	14.2	3.1	0.6	1.1
SE	4.1	0.6	0.2	0.4
Range	1–55	0–7	0–3	0–7
No. of individuals that bit	11	0	0	0
G. caesaris (*n* = 20)				
No. of tongue-flicks				
Mean	17.3	30.2	2.4	3.2
SE	4.8	8.6	0.6	0.7
Range	1–58	0–124	0–9	0–11
No. of individuals that bit	10	1	0	0

Note: The plant stimuli were *Psoralea bituminosa* leaves for *G. simonyi* and tomato for *G. caesaris*.

Fig. 1. Mean tongue-flick attack scores for repeated-measures experiments (TFAS(R)) for 17 juvenile *Gallotia simonyi* in 60-s swab trials. Plant stimuli were chemicals from leaves of *Psoralea bituminosa*. Error bars represent 1.0 SE.

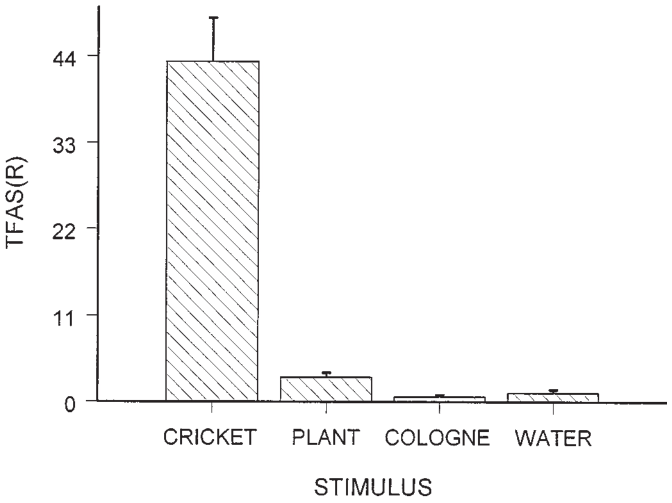
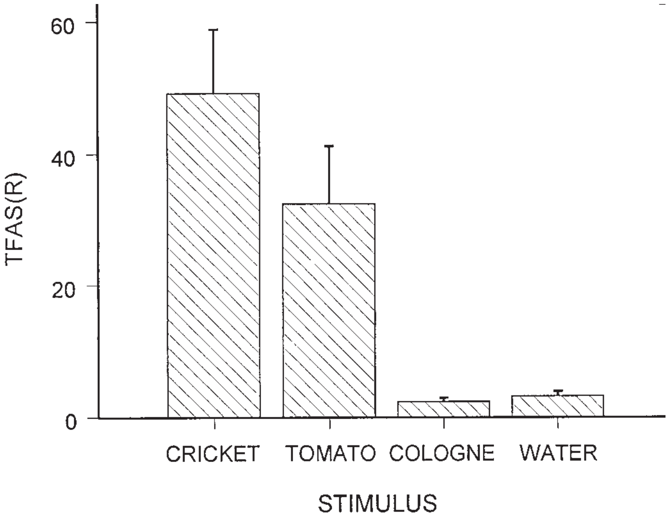


Fig. 2. Mean TFAS(R) for 20 adult *Gallotia caesaris* in 60-s swab trials. Error bars represent 1.0 SE.



Lizards bit only in the cricket condition (Table 1). The stimulus effect was significant (Q = 30.00, df = 3, $P <$ 0.001). Significantly more individuals bit in the cricket condition than in each of the other conditions ($P > 0.10$ each). No other differences were significant ($P > 0.10$ each).

TFAS(R) showed the same pattern of significance as the numbers of tongue-flicks, but the differences in response strength between the cricket condition and the remaining conditions was more pronounced (Fig. 1). TFAS(R) varied significantly among stimuli ($\chi^2 = 42.32$, df = 3, $P < 1.0 \times 10^{-5}$). P values were identical with those for tongue-flicks for all of the paired comparisons.

Experiment 2

The yearlings responded strongly to chemical stimuli from tomato fruit. Tomato stimuli elicited considerably more tongue-flicks (31.7 ± 9.2) than did deionized water (1.2 ± 2.6). Nonparametric analysis of variance showed that this difference was significant ($\chi^2 = 5.40$, df = 3, $P < 0.021$). The significance level would have been even lower except that an individual that bit in the tomato condition after only one tongue-flick tongue-flicked twice in the deionized water condition and another individual tongue-flicked only twice in each condition. All lingual protrusions were recorded as tongue-flicks, but many of them were actually licks in which the dorsal surface of the tongue contacted the swabs rather than the ventral tip of the tongue as in tongue-flicks. Ten lizards bit in response to tomato stimuli, but none bit in the deionized water condition. This difference was significant ($P < 0.002$). TFAS(R) was 48.18 ± 10.2 in the tomato condition and 1.2 ± 2.6 in the deionized water condition. This difference was significant ($\chi^2 = 8.07$, df = 3, $P < 0.0046$).

Gallotia caesaris

The lizards responded much more strongly to both cricket and tomato stimuli than to the control stimuli (Table 1, Fig. 2). The stimulus effect for the number of tongue-flicks was significant ($\chi^2 = 23.59$, df = 3, $P < 0.003$; Table 1). Cricket and tomato stimuli each elicited significantly more tongue-flicks than did cologne or deionized water ($P < 0.01$ each). No other differences between pairs of stimuli were significant

($P > 0.10$ each). In this experiment all lingual protrusions that contacted swabs were recorded as tongue-flicks, but most of the lingual protrusions in trials with tomato stimuli were licks rather than typical tongue-flicks for chemical sampling. During chemical sampling by tongue-flicking, the anteroventral lingual surface contacts substrates. In typical tomato trials, the lizards performed a few initial tongue-flicks with anteroventral contact and then began a series of lingual protrusions in which the anterodorsal surface of the tongue contacted the swab.

Half of the lizards bit in the cricket condition, but no more than one bit in any of the other conditions (Table 1). The stimulus effect for the number of lizards that bit was significant ($Q = 27.39$, df = 3, $P < 0.001$). Significantly more lizards bit in response to cricket stimuli than to tomato ($P = 0.012$), cologne ($P < 0.002$), or deionized water ($P < 0.002$). Differences between the other pairs of conditions were not significant ($P > 0.10$ each).

TFAS(R) was far greater in response to the animal and plant stimuli than to the control stimuli (Fig. 2). Mean TFAS(R) differed significantly among stimuli ($\chi^2 = 37.85$, df = 3, $P < 1 \times 10^{-5}$). Despite the greater frequency of lingual protrusions in the tomato condition, TFAS(R) was numerically greater in the cricket condition than in the tomato condition, owing to the effect of the greater number of individuals that bit in the cricket condition. However, this difference was not significant ($P < 0.11$). TFAS(R) in response to both cricket and tomato stimuli was significantly greater than to either of the control stimuli ($P < 0.01$ each). The control stimuli did not differ significantly from each other ($P > 0.10$).

Discussion

Both species of *Gallotia* discriminated prey chemicals and plant chemicals from control substances. Prey-chemical discrimination was strong in both. In *G. simonyi*, prey-chemical discrimination is indicated in experiment 1 by the significantly greater number of tongue-flicks, number of individuals that bit, and TFAS(R) in the cricket condition than in any of the other conditions, and by the significantly greater proportion of individuals that tongue-flicked at least once in the cricket condition than in the two control conditions. In *G. caesaris* the evidence for prey-chemical discrimination is the significantly greater number of tongue-flicks, number of individuals that bit swabs, and TFAS(R) in response to cricket stimuli than to cologne or deionized water.

The occurrence of prey-chemical discrimination in *G. simonyi* and *G. caesaris* conforms to the prediction that prey-chemical discrimination is retained by the omnivorous descendants of insectivorous foragers. The ability to identify prey using only chemical cues is beneficial to these species because both eat substantial quantities of insects and other prey (Pérez-Mellado et al. 1999; Barbadillo et al. 1999) in addition to plants. Furthermore, both species forage actively for prey (V. Pérez-Mellado and W.E. Cooper, Jr., unpublished observations) in a manner resembling that of actively foraging insectivorous lacertids (Cooper and Whiting 1999), which suggests that they may benefit from locating hidden and (or) immobile prey by means of chemical cues in the same way.

Plant-chemical discrimination also was demonstrated in both species, but response strength varied among plant stimuli in *G. simonyi*. In experiment 1, *G. simonyi* discriminated stimuli from *P. bituminosa* leaves from the two control stimuli, as shown by the significantly greater number of tongue-flicks (and TFAS(R)) in response to the plant stimuli than to cologne and deionized water. However, no individuals bit swabs bearing plant chemicals, and the both the mean and maximum numbers of tongue-flicks in the plant condition were quite low, much lower than in response to cricket stimuli.

The relatively weak responses to leaves may be a consequence of their unimportance in the diet of juvenile *G. simonyi*. *Psoralea bituminosa* leaves are one of the staple dietary items of adult *G. simonyi* in the Lagartario and in the field (Pérez-Mellado et al. 1999), but the juveniles unexpectedly did not eat them when given the opportunity to do so following the experiment. Because ontogenetic increases in the percentage of plant material in lizard diets have rarely been documented (Durtsche 1999), and plant-specific ontogenetic changes are unknown, a study of possible ontogenetic changes in consumption of *P. bituminosa* leaves would be valuable both as a possible example of the phenomenon and for their implications for the captive husbandry of the endangered *G. simonyi*.

In contrast to the weak, although significant, responses to *P. bituminosa* leaves, both lizard species responded strongly to chemical cues from tomato fruit. *Gallotia simonyi* responded much more strongly in experiment 2 to tomato cues than to deionized water. Coupled with the absence of differences between responses to cologne and deionized water in experiment 1, this indicates that *G. simonyi* can discriminate between tomato and control stimuli. Response strengths indicated by TFAS(R) to tomato and cricket stimuli by *G. simonyi* were comparable, reflecting the omnivorous diet.

The numbers of tongue-flicks in the tomato condition were strikingly similar in the two lizard species. TFAS(R) was slightly greater in *G. simonyi* than in *G. caesaris* because of the slightly higher proportion of individuals that bit in the former species, but visual inspection of the means and standard errors indicates that these differences are not significant. The results indicate that both species respond strongly to plant-chemical stimuli and prey-chemical stimuli, corresponding to the importance of prey and plants in their diets.

The occurrence of plant-chemical discrimination in *G. simonyi* and *G. caesaris* adds data supporting another independent origin of omnivory to the growing database that will eventually permit tests for correlated evolution of plant consumption and plant-chemical discrimination in Autarchoglossa, Scincomorpha, and Lacertoidea. In addition to the two species of *Gallotia*, plant-chemical discrimination has been detected in several other omnivorous lizards, including skinks (Cooper et al. 2000*b*; Cooper 2000*e*), a teiid (Yanosky et al. 1993), and a gerrhosaur (Cooper 2000*f*). Several species of actively foraging insectivores are known to lack plant-chemical discrimination (Cooper and Hartdegen 1999; Cooper 2000*b*; Cooper and Habegger 2000; Cooper et al. 2000*b*, 2000*c*). Thus, the available comparative data, although incomplete, are uniformly consistent with the hypothesis that plant-chemical discrimination evolves convergently in omnivores. The above comparative data also support the hypotheses that plant eaters derived from ambush foragers evolve both prey- and plant-chemical discrimination, whereas those derived from active foragers retain responsiveness to prey chemicals and evolve plant-chemical discrimination. More comparative data are needed to adequately test these hypotheses.

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