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Behavioral responses to plant toxins by two omnivorous lizard species

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Abstract

An ability to detect plant toxins and thereby avoid eating chemically defended plants would be very beneficial for omnivorous and herbivorous lizards. We studied the ability of the omnivorous *Podarcis lilfordi* to detect compounds belonging to three classes of common plant toxins, as well as responses indicating aversion. Solutions of the alkaloid quinine, saponin, and the phenolic coumarin, as well as distilled water (odorless control), were presented to lizards on cotton swabs. The lizards detected all three toxins as indicated by significantly decreased tongue-flick rates and tongue-flick attack scores in comparison with distilled water. Several other variables revealed aversion to saponin, including a low number of individuals that bit swabs, avoidance of swabs after tongue-flicking, performance after tongue-flicking the swab of repeated short-excursion tongue-flicks that were directed away from the swab and did not contact any substrate, failure to respond at all in the next trial, and wiping the snout on the floor of the terrarium. Reasons for apparent differences in tongue-flicking behavior between *P. lilfordi* and two other omnivorous lizard species are discussed. We also showed experimentally that saponin depresses the tongue-flick rate in the omnivorous Bonaire whiptail lizard, *Cnemidophorus murinus*. Tongue-flicking enables at least one lizard species to detect specific chemicals representing three major classes of plant toxins. It is hypothesized that this ability is a widespread adaptation to reduce ingestion of plant toxins.

Keywords: Behavior; Plant toxins; Herbivory; Chemical senses; Tongue-flicking; Squamata

1. Introduction

Animals that eat a wide range of plant foods are exposed to plant toxins that vary greatly qualitatively and quantitatively among plant species and over time within species. Some herbivorous mammals sample foods subsequently avoid those that are toxic and associate the postingestive feedback with food flavors sensed by gustation and olfaction [1]. Omnivorous and herbivorous lizards encounter plants defended by numerous types of toxins to which the lizards are, to some degree, vulnerable [2,3] and may learn to avoid toxic plants [4].

An ability to detect chemically defended plants by responding to chemical cues sampled by tongue-flicking, prior to biting or by rejection of bitten food prior to swallowing, could be a mechanism for avoiding intoxication. Actively foraging insectivorous lizards are capable of locating and identifying prey using lingually sampled chemical cues [5–7] and some herbivorous lizards are known to identify plant foods using chemical cues [8,9], hinting that lizards might be able to evaluate plant toxin levels using the chemical senses. However, very little is known regarding the ability of such lizards to detect the major types of plant toxins, such as alkaloids, saponin, and phenolics. Alkaloids serve as chemical defensive compounds against herbivores, present in about 15% of plant species [10]. Many are bitter-tasting and highly toxic [10]. Saponins are glycosidic triterpenoids that are not very toxic orally to humans, but produce foams [10] that are aversive (WEC, personal observation). Many phenolic compounds are effective defensive agents against herbivores that have unpleasant tastes and may be hallucinogenic or toxic to humans [10].

The omnivorous teiid lizard *Cnemidophorus arubensis* avoids eating common plants that contain high concentrations of alkaloids, saponin, and phenolics, but eats a plant species that contains potentially toxic levels of a cyanogenic

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compound [2,11]. At least two closely related lizard species are capable of detecting the alkaloid quinine: *C. arubensis* and *Cnemidophorus murinus* ate small pieces of sponges soaked in tomato juice, but rejected them if low concentrations of quinine were added [12].

The sampling mechanism is uncertain, but the lizards probably detected quinine by chemical sampling rather than by visual cues. Tongue-flicking is very likely the primary means of sampling. When a lizard protrudes its tongue, the tongue is projected through a volume of air and usually contacts a substrate before being withdrawn. Lingually sampled chemicals are transferred through the vomeronasal ducts to the vomeronasal organ, but may come into contact with taste buds on the tongue or in oral mucosa. Thus, vomerolfaction, gustation, or both might be important for detection of lingually sampled plant toxins.

C. arubensis and *C. murinus* were more likely to tongue-flick when quinine was present than when it was absent, and more likely to lick and bite the sponges when quinine was absent [12]. However, tongue-flicking was recorded from a distance by filming or videotaping [12]. The lizards might have performed short-excursion tongue-flicks, which indicate intense chemosensory investigation [13,14], prior to feeding that were more difficult to detect than were tongue-flicks of greater extension and frequency that are likely to have occurred while evaluating a potential food item for possible rejection. Our unpublished observations of *C. murinus* show that this species consistently tongue-flicks swabs bearing chemicals from palatable insect prey and plant foods.

Here, we describe studies of responses by two omnivores: (1) the Balearic lizard *P. lilfordi*, a lacertid [15], to chemicals representing the classes of plant toxins mentioned above and (2) the Bonaire whiptail lizard *C. murinus*, a teiid, to an alkaloid and saponin. The presence and concentrations of plant toxins in plants available to the Balearic lizard and in its diet have not been studied. Nevertheless, this lizard is appropriate for study of possible detection of plant toxins because it consumes plants from diverse families likely to be chemically defended [16]. Alkaloids, saponin, and phenolics are widespread plant toxins to which *P. lilfordi* is very likely to be exposed. Quinine was selected as a readily available alkaloid known to suppress feeding by lizards, including *C. murinus* [11,12]. Saponin and coumarin, the latter a phenolic compound, were the other potentially noxious stimuli tested as representatives of classes of plant defensive chemicals known to occur in the diet of *C. murinus* [2].

Based on avoidance of plants containing alkaloids, saponin, and phenolics by *C. arubensis*, we predicted that (1) *P. lilfordi* would tongue-flick and bite less frequently in response to cotton swabs bearing plant toxins than to distilled water and (2) *C. murinus* would tongue-flick less in response to quinine and saponin on ceramic tiles than to deionized water. Quinine and saponin are appropriate compounds for testing because they are known to occur in the diet (saponin [11]) or to have aversive properties (quinine [12]). The appropriateness of coumarin is uncertain because its toxicity to lizards and inclusion in lizard diets are unknown. It was selected arbitrarily based on ready availability and low cost.

The prediction that lizards bite less frequently in response to the plant toxins than to distilled water is much easier to test in *P. lilfordi* than it would be in most lizard species because this species frequently bites cotton swabs bearing water, although less frequently than those bearing food chemicals [17]. Most species bite frequently only in response to chemical stimuli from palatable foods [18–20].

2. Methods

2.1. Animals and maintenance

Adult male *P. lilfordi* ($n = 24$) were collected on the islet of Aire adjacent to Menorca, Balearic Islands, Spain. They were transported to a laboratory on Menorca where they were housed individually in transparent plastic terraria ($40.5 \times 25.0 \times 26.5$ cm). The sidewalls of the terraria were covered with white paper to reduce disturbance to the lizards due to movements of the experimenters and by lizards in adjacent terraria. The bottom of each terrarium was covered by indoor–outdoor carpet. Light through a laboratory window maintained the natural regional light cycle. Incandescent heat lamps suspended above one end of each cage provided additional light and heat, permitting thermoregulation. Ambient temperature during testing was 29–32 °C. Body temperatures were not measured during this experiment, but lizards measured in these conditions at other times were able to attain temperatures greater than 35 °C. Water was continuously available. Lizards were tested 1 day after being captured, and were not fed prior to the experiment. The lizards were released on Aire after the experiment.

C. murinus were collected on Bonaire Island, Netherlands Antilles, and transported to the laboratory at Indiana University–Purdue University at Fort Wayne. They were housed individually in glass terraria ($50 \times 28 \times 30$ cm), each containing a carpet, a plastic shelter, and a water bowl. The ambient temperature was 29 °C, and heat lamps provide the opportunity to thermoregulate. Light was provided by fluorescent bulbs on a 1410-h LD cycle. The lizards were fed crickets and plant foods.

2.2. Experimental procedures and variables

Responses to plant toxins by *P. lilfordi* were studied by presenting them to lizards in aqueous solutions on the cotton tips of wooden applicators (15 cm). The stimuli tested were distilled water, which served as an odorless control to assess responses in the absence of the experimental stimuli, quinine (1 g/200 g distilled water), saponin (1 g/10.48 g distilled

water), and coumarin (1 g/9 g of distilled water). The concentration of quinine was selected to be greater than the level known to be detected by *C. arubensis* and *C. murinus* [12]. Because responses to the other substances had not been studied, their concentrations were selected for this first study based on solubility. Differences in responses to the substances might be in part attributable to their different concentrations. A low concentration of quinine was used because lizards are known to be sensitive to low concentrations [12]. For these first tests, the saponin concentration was higher than for the other chemicals. Due to low solubility, much of the coumarin was undisolved; the solution was saturated. A pungency control was not used because chemosensory responses by *P. lilfordi* to cologne, the usual pungency control, do not differ from those to water [17].

Immediately before testing, which took place in home cages, stimuli were prepared by immersing the swab in one of the solutions or in distilled water. Excess liquid was removed by flicking the wrist holding the applicator. Because coumarin did not completely dissolve, some individuals were possibly exposed to undetected particles of it adhering to the swab. To begin a trial, an experimenter positioned a cotton swab 1.0–1.5 cm anterior to a lizard's snout, moving slowly to avoid inducing escape attempts or unresponsiveness. The trial began with the first tongue-flick directed to the swab. If a lizard did not bite the swab, the trial lasted 60 s. If the lizard bit the swab, the trial was terminated at the time of the bite.

The variables analyzed were number of tongue-flicks, latency to bite, number of individuals that bit, number of individuals that performed short tongue-flicks directed away from the swab yet not to a substrate, number of individuals that avoided swabs after tongue-flicking, and the tongue-flick attack score for experiments having repeated measures designs (=TFAS(R)) [21–23]. Numbers of tongue-flicks, the biting variables, and TFAS(R) are the variables typically recorded in studies of food chemical discrimination. Number of short tongue-flicks directed away from the swab (but not to a substrate), avoidance of the swab after tongue-flicking, and wiping the snout on the ground were examined as possible indicators of aversion to stimuli.

TFAS(R) combines data on tongue-flicking and biting to give the best single index of response strength to food chemicals. Calculation of TFAS(R) depends on whether a lizard bites the swab [21]. If the lizard does not bite the swab, the TFAS(R) for that trial is the number of tongue-flicks in 60 s. If it bites, TFAS(R) is given by the sum of two terms: one term is the number of tongue-flicks and the other term is calculated from latency to bite. The tongue-flick term is the maximum number of tongue-flicks performed by that individual in response to any of the stimuli in a single trial [23]. Using the maximum number ensures that a bite is weighted more heavily than any number of tongue-flicks. This is appropriate in studies of responses to food chemicals because bites reflect predation attempts [22,23]. The other term is 60 minus latency to bite in seconds. This term weights bites earlier in trials more heavily than those later in trials, because latency reflects the rapidity of food identification.

Because *C. murinus* usually fled from the investigator before coming close enough to have any chance to respond to swabs, they were tested by placing the chemicals on ceramic tiles. The stimuli tested were quinine (1 g in 200 g deionized water), saponin (1 g in 50 g deionized water), and deionized water. A lower concentration of saponin was used in this study because *P. lilfordi* responded strongly to a higher concentration. The stimuli were prepared by immersing a swab in the liquid to be tested, and then using the swab to spread it uniformly over the upper surface of a $15 \times 15 \times 1$ cm ceramic tile. The tile formed the floor of small test chamber having transparent walls on two sides, which was placed before a pane of one-way glass. To conduct a trial, an experimenter placed a lizard in the test chamber, withdrew to a blind to view the lizard, and recorded the number of tongue-flicks to the tile in the 2-min interval starting with the first tongue-flick that touched the tile.

2.3. Statistical analyses

Twenty-four individuals of *P. lilfordi* and 20 of *C. murinus* were tested in experiments having repeated measures (randomized blocks) designs with a minimum intertrial interval of 30 min. The preferred statistical tests for tongue-flicks, latency to bite, and TFAS(R) were parametric analyses of variance for single-factor experiments with repeated measures [24], followed by Newman–Keuls tests for significance of differences between pairs of means if the main effects were significant. However, the assumptions of normality and homogeneity of variance were not met in some cases. If the variances were significantly heterogeneous using Hartley's F_{max} tests, the data were logarithmically transformed. If the variances of the transformed data retained heterogeneity or the data departed greatly from normality, the analyses were conducted nonparametrically using Friedman two-way analyses of variance [25]. If the main effects were significant, differences among pairs of conditions were tested for significance using nonparametric multiple comparisons procedures [25].

Data on number of individuals that bit, number of individuals that performed short tongue-flicks directed away from swabs, and number of individuals that did not respond in the next trial after a given type of stimulus were analyzed using Cochran Q tests. For variables having significant main effects, the significance of differences between pairs of stimuli was assessed by binomial tests. Raw probabilities are reported for these binomial tests, but significance was tested using a sequential Bonferroni procedure to adjust significance levels for the number of tests conducted [26]. All significance tests were two-tailed, with a=.05. Data in the text are presented as mean ± S.E.

3. Results

3.1. P. lilfordi

Twenty-three individuals responded in all four conditions; the other individual was discarded after failure to respond after a first trial with saponin. The mean numbers of tongue-flicks were lower in response to all three plant defensive chemicals than to distilled water, but the differences were substantial only for saponin and quinine (Fig. 1). The main stimulus effect was highly significant ($\chi^2 = 27.79$, $df = 3$, $P < 1 \times 10^{-5}$). There were significantly fewer tongue-flicks in the saponin condition than in each of the other conditions ($P < .01$ for coumarin and distilled water and $P < .03$ for quinine). None of the other differences between pairs of stimuli were significant. With saponin removed from the analysis, the assumptions for a more powerful parametric analysis were met. The main effect of tongue-flicks for transformed data was significant ($F = 4.10$; $df = 2, 44$; $P < .024$). The only significant difference between pairs of stimuli was that the lizards tongue-flicked less in response to quinine than to distilled water ($P < .016$).

Latency to bite was relatively more uniform across groups than were tongue-flicks (Fig. 2). The main stimulus effect on latency to bite was significant ($\chi^2 = 13.44$, $df = 3$, $P < .0038$), but the only significant difference between pairs of stimuli was that latency to bite was significantly greater for saponin than for distilled water ($P < .05$, one-tailed). In a parametric analysis of transformed data on latency to bite with saponin excluded, latency did not differ among conditions ($F = 1.90$; $df = 2, 44$; $P > .10$).

Numbers of individuals that bit were zero for saponin, four for quinine, six for coumarin, and nine for water. The main effect of number of inidividuals that bit was significant ($Q = 15.55$, $df = 3$, $P < .005$). The only significant difference between pairs of stimuli was that a significantly greater number of individuals bit in response to water than to saponin ($P < .0039$).

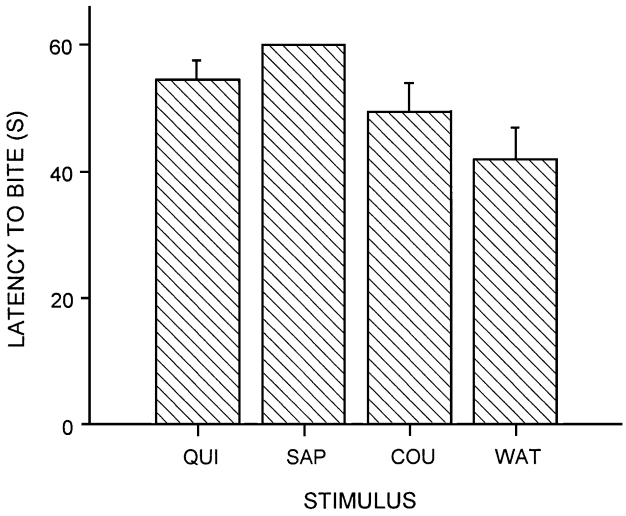

Fig. 2. Mean latency to bite swabs in 60-s trials by *P. lilfordi* in response to swabs bearing quinine (QUI), saponin (SAP), coumarin (COU), and distilled water (WAT) in 60-s tests. Error bars represent 1.0 S.E.

The greatest resolution of relative response strengths was obtained with TFAS(R) (Fig. 3). The stimulus effect of TFAS(R) was highly significant ($\chi^2 = 45.84$, $df = 3$, $P < .001$). Paired comparisons revealed significantly greater TFAS(R) in the distilled water condition than in the quinine ($P < .01$) and saponin ($P < .001$) conditions. TFAS(R) was also significantly greater in the coumarin condition than the saponin condition ($P < .05$). Although TFAS(R) was numerically greater in response to water than coumarin and to quinine than saponin, these differences were not significant using the nonparametric analysis.

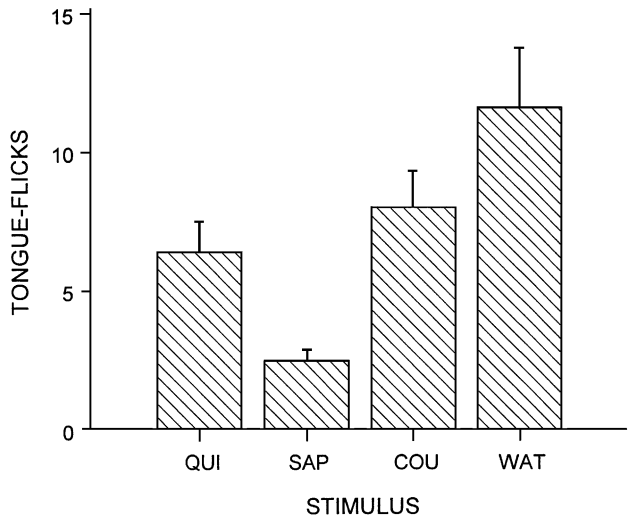

Fig. 1. Mean tongue-flicks by *P. lilfordi* responding to quinine (QUI), saponin (SAP), coumarin (COU), and distilled water (WAT) in 60-s swab tests. Error bars represent 1.0 S.E.

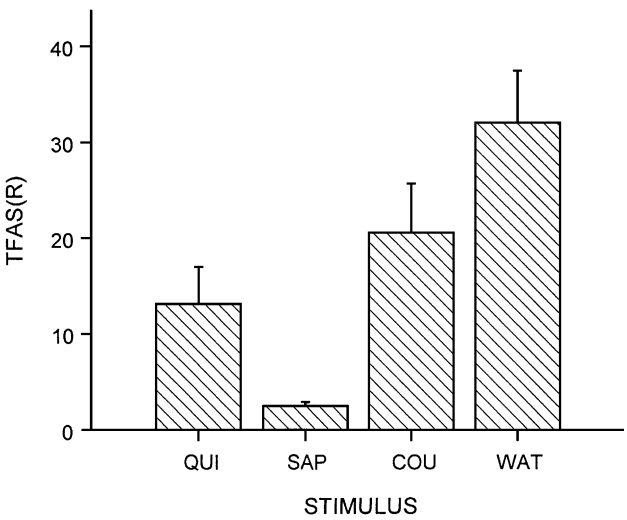

Fig. 3. Mean tongue-flick attack scores [TFAS(R)] by *P. lilfordi* responding to quinine (QUI), saponin (SAP), coumarin (COU), and distilled water (WAT) in 60-s swab tests. Error bars represent 1.0 S.E.

With saponin excluded, the stimulus effect was significant using transformed data ($F = 6.73$; $df = 2, 44$; $P < .029$). TFAS(R) was significantly greater in response to distilled water than to quinine ($P < .0022$) as in the nonparametric analysis. In contrast to its nonsignificance in the less powerful nonparametric analysis, TFAS(R) was significantly greater in the water condition than in the coumarin condition ($P < .033$). The difference between quinine and coumarin was not significant ($P > .10$).

Other behaviors that varied among conditions were the occurrence of short tongue-flicks that did not touch a swab, wiping the labials with the tongue, avoidance of the swab by moving or turning away after tongue-flicking, wiping the snout on the floor of the terrarium, and failing to respond in the next trial after being tested with a particular stimulus. All of the behaviors mentioned in the preceding sentence were most frequent in response to saponin. Two lizards in the saponin condition wiped their snouts on the terrarium floor after tongue-flicking saponin, but none did so in response to other stimuli.

The number of individuals that performed short tongue-flicks directed away from the swab and/or performed labial licks was much greater in the saponin condition than in any of the other conditions (saponin—19, coumarin—2, quinine and distilled water—0), and differed significantly among them ($Q = 51.81$, $df = 3$, $P < .001$). The number of individuals performing these behaviors was significantly greater in response to saponin than to the remaining stimuli (binomial $P = 3.82 \times 10^{-6}$ for distilled water and quinine and $P = 1.53 \times 10^{-5}$ for coumarin). Other differences between pairs of stimuli were not significant. (Quantitative data for these behaviors are 18.0 ± 3.0 for saponin and 0.4 ± 0.3 for coumarin.)

The number of individuals that avoided the swab after tongue-flicking also varied significantly among stimuli ($Q = 45.00$, $df = 3$, $P < .001$). Fifteen individuals avoided swabs in the saponin condition and none in the other conditions (binomial $P < 6.11 \times 10^{-5}$ each). Of the original 24 lizards, only 23 completed the experiment, because one individual stopped responding entirely after its first trial with saponin. Five other individuals did not respond in the next trial after being tested with saponin and had to be retested later. Nonresponsiveness after being tested with a particular stimulus was unique to saponin in this experiment. Frequency of failure to respond in the immediately succeeding trial varied significantly among stimuli ($Q = 18.00$, $df = 3$, $P < .001$). In the trial following saponin, lizards failed to respond significantly more frequently than in trials following all of the other conditions combined (binomial $P < .00049$).

3.2. C. murinus

One of the 20 lizards was discarded because it did not respond within 30 min in its second trial. The remaining 19 lizards performed 9.9 ± 1.8 (range 2–27) tongue-flicks in response to saponin, 13.9 ± 2.7 (range 2–42) to quinine, and 17.1 ± 2.7 (range 4–56) to deionized water. Numbers of tongue-flicks for the transformed data differed significantly among stimulus conditions ($F = 4.81$; $df = 2, 36$; $P < .015$). The lizards performed significantly fewer tongue-flicks in response to saponin than to deionized water ($P < .011$). The other differences were not significant.

4. Discussion

P. lilfordi and *C. murinus* detect some common plant toxins sampled lingually and the former exhibits behavioral signs of aversion to one of them. The omnivorous *C. arubensis* and *C. murinus* avoid consuming plants having high concentrations of toxins [2,11], and *C. arubensis* and the insectivorous *Anolis carolinensis* [27] refrain from eating palatable food adulterated by an alkaloid [12]. In conjunction with these findings, the results suggest that omnivorous (and presumably herbivorous) lizards chemically sample possible plant foods to detect toxins. By rejecting items that contain high concentrations of toxins, lizards could avoid intoxication.

Our knowledge regarding abilities of lizards to detect plant toxins and their use of information about toxin concentrations to avoid or limit intoxication is rudimentary. Several novel findings from this study suggest a sophisticated use of chemical cues to assess the toxicity of plant foods. An omnivorous lizard species, *P. lilfordi*, can detect an alkaloid at low concentrations by tongue-flicking, and is capable of detecting representatives of the two other major classes of plant toxins, saponin and phenolic compounds. For another omnivore, *C. murinus*, the ability to detect saponin is demonstrated. That saponin and the phenolic coumarin inhibit chemosensory investigation and related responses suggests that these substances may also inhibit feeding.

Because the concentrations of alkaloids in available plants and in the diet of *C. arubensis* and *C. murinus* and undoubtedly other plant-eating lizards vary throughout the year and among localities, the degree of tolerance for alkaloids might also change [12,28]. Omnivorous and herbivorous lizards may employ lingual chemical sampling to assess concentrations of alkaloids and other plant toxins and base decisions regarding consumption on current values of temporally variable toxin levels and perhaps on their own temporally variable tolerance levels. Research on this hypothesis could be rewarding. Temporal variation in tolerance might explain the lack of evidence for *C. murinus* in the present study for an ability to detect quinine, which was detected by *C. arubensis* at an even lower concentration [12]. However, it seems more likely that the lizards detected the quinine, but that this was not apparent because the stimuli were on tiles, which offer no focal point for tongue-flicking.

P. lilfordi responded differently to each of the three model toxins. Saponin strongly affected the chemosensory and biting behaviors. Its aversiveness was indicated in

several ways, including significant reductions in numbers of tongue-flicks, tendency to bite swabs, and TFAS(R). Other indicators of aversion were unique for saponin and significantly greater for saponin than all other stimuli. Saponin was the only compound that (1) elicited repeated short-excursion tongue-flicks directed away from the swab, (2) elicited avoidance of the swab after tongue-flicking by moving away or turning the head away, and (3) was associated with failure to respond in the following trial. Wiping of the snout on the substrate after tongue-flicking saponin by two individuals was the most dramatic aversive response. These findings suggest that *P. lilfordi* could avoid eating plants defended by high concentrations of saponin, as do the teiids *C. arubensis* and *C. murinus* [2,11]. The absence of overt signs of aversion to saponin by *C. murinus* may reflect the lower concentration in the test stimuli, perhaps diluted further by spreading from swab to tile.

The evidence that coumarin is aversive to *P. lilfordi* was that TFAS(R) was significantly depressed in relation to distilled water. Consumption of plants containing high concentrations of phenolic compounds might be avoided by chemosensory detection of the phenolics, but the appropriateness of coumarin as a model phenolic plant toxin for lizards is uncertain. Detailed chemical analyses of the types of phenolic compounds in plants available to lizards and study of their possible roles in excluding defended plants from the diet are needed to evaluate the significance of the reduced responsiveness to coumarin. However, the present data show that *P. lilfordi* detects a phenolic compound that inhibits chemosensory responses, although fairly weakly. Other phenolics, such as those present in plants eaten by omnivorous teiids [2], might be more aversive than coumarin.

Detection of the alkaloid quinine and depression of chemosensory investigation by it are indicated by significantly lower numbers of tongue-flicks and tongue-flick attack score than for distilled water. These findings extend the ability of omnivorous lizards to detect quinine at low concentrations to the family Lacertidae. The results for *P. lilfordi* differ from those for the teiids, because the rate of tongue-flicking by teiids was greater when quinine was present in potential food than when it was not [12], whereas quinine did not significantly affect the tongue-flick rate by *C. murinus* to tiles. This apparent discrepancy might indicate a real difference in responses of two teiids and *P. lilfordi*, but are more likely effects of differences in experimental procedures. Our results showed no significant effect of quinine on tongue-flick rate in *C. murinus*, but a slight numerical decrease relative to water. One possibility is that *C. arubensis* briefly performed short-excursion tongue-flicks before eating in trials lacking tomato juice, but that these tongue-flicks were difficult to detect.

Another possibility is that the airborne odor of tomato juice elicited feeding without prior tongue-flicking, but that contact with quinine required additional assessment by tongue-flicking to determine whether the food was acceptable. The two species of *Cnemidophorus* appear to be able to locate food using airborne chemical cues. This ability was demonstrated in *P. lilfordi* [17] after it was noted that these lizards could be trapped by placing pieces of fruit in boxes. The *C. murinus* and the lacertids *Gallotia caesaris* and *G. simonyi* also can be trapped by placing pieces of fruit in opaque plastic tubes, the latter two species being especially attracted by tomato (our unpublished observations). Schall [12] proposed that the teiids detected quinine from a distance, presumably by airborne chemical cues, but quinine lacks a strong odor to humans and is not volatile.

Our results do not permit conclusions regarding the relative aversiveness of the three compounds examined because the concentrations tested were very different. Quinine has aversive effects at very low concentrations (Refs. [12,27], this paper). The concentrations of saponin and perhaps coumarin in this study that were greater than lizards are likely to encounter in plants. Further work is needed to ascertain responses to concentrations of saponin and phenolics typical of defended plants.

Omnivorous and herbivorous species from diverse lizard families are capable of identifying plant food by lingually sampling plant chemicals [8,29–31]. An ability to assess nutritional quality of plants, including their toxic properties, is very likely widespread among lizards that consume plants, although the ability of omnivores to detect plant toxins has been demonstrated only in Lacertidae and Teiidae (Ref. [12], this paper). Because the insectivorous *A. carolinensis* can detect quinine and *Acanthodactylus dumerili* associates olfactory cues with unpalatability of aposematically colored locusts [32], lizards may be able to avoid intoxication by using chemical cues to detect certain classes of defensive toxins present in both plants and animals. Testing this hypothesis offers an interesting avenue for future research on mechanisms of avoiding food poisoning. Related hypotheses about relationships between the specific toxins found in local plants and animals, about responsiveness by lizards to them, and about effects of experience on responsiveness are also relevant to avoiding intoxication.

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