

- * Need larger Sample Size
- * Need Advanced Exp. design that lessens human interaction w/ organisms
- * Animal Stimuli should reflect natural diet/no mice

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CORRESPONDENCE BETWEEN DIET AND FOOD CHEMICAL DISCRIMINATIONS BY OMNIVOROUS GECKOS (*Rhacodactylus*)

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Abstract—Chemosensory responses to food are correlated with geographic variation in diet of some colubrid snakes, but the influence of diet on chemosensory behavior has not been established generally in snakes or lizards. Most lizards are generalist predators of small animals, making it difficult to study effects of diet, but herbivory and omnivory have evolved in several lineages, providing an excellent opportunity to study the effects of dietary change on chemosensory behavior. Based on ecological considerations, I argue that inclusion of plants in the diet of lizards that evolved from ambush foragers lacking prey chemical discrimination might be expected to evolve responsiveness to plant food chemicals. If animal prey also are retained in the diet, then responsiveness to prey chemicals should evolve as well. I experimentally studied tongue-flicking and biting responses by omnivorous geckos of the genus *Rhacodactylus* to chemical stimuli from plant and animal foods and control substances presented on cotton swabs. The lizards exhibited significantly greater responses to plant stimuli than to control stimuli. One of two species tested responded strongly to cricket chemicals, but the other showed no significant response to mouse surface chemical stimuli. The results support the hypothesis that dietary shifts induce corresponding changes in chemosensory response, but establishment of correlated evolution between diet and food chemical discriminations in lizards will require study of many herbivores/omnivores and insectivores as controls.

Key Words—Chemosensory behavior, tongue-flicking, diet, herbivory, Squamata, *Rhacodactylus*.

INTRODUCTION

Sensory capacities must be adapted to uses of the senses. There are well known examples among vertebrates of spectacular visual acuity, ultrasonic perception,

opportunistic

omnivorous animals have greater overall chemotaxis than either extreme

Thesis →

Are mice local to new Caledonia?

Pure natural selection
& adaptation.

and electrical-field sensing associated with specialized hunting methods, but there is relatively little comparable information about evolutionary modification of chemosensory abilities and behaviors in relation to hunting techniques and diet. The best studied case is the use of vomerolfaction and perhaps other chemical senses by squamate reptiles to locate, identify, and evaluate food. Foraging mode and use of lingually mediated prey chemical discrimination are correlated in lizards (Cooper, 1995a, 1997), and there are some indications that response to chemical cues from potential foods varies with diet.

• Maybe specialist do well
for a short time & space

• Generalists do well
over a large geography
& long term

• Being a generalist presents
a disadvantage to specific
chemosensory function

• At what point in terms
of selection does it
become an advantage
to be a specialist?

Chemosensory responsiveness to prey varies geographically in several species of garter snakes of the genus *Thamnophis* and in the colubrid *Coluber constrictor*, the geographic variation corresponding to dietary differences in *T. elegans* and *C. constrictor* (Burghardt, 1970a; Arnold, 1981; Cooper et al., 2000). Surprisingly little is known about relationships between diet and responses to food chemicals in lizards, primarily because most lizard species are generalist predators of small animals, making it difficult or impossible to detect a relationship between diet and chemical sensitivity.

Herbivorous and omnivorous lizards provide an excellent opportunity to detect any influence of diet on the evolution of chemosensory response to food. Herbivory has been derived in several lizard groups from the ancestral condition of insectivory/carnivory observed in *Sphenodon* (outgroup), most iguanians, and most scleroglossans (Pough, 1973; Iverson, 1982). Responses to food chemicals by herbivores and omnivores are poorly known but may be predicted from considerations about characteristics of plant food and lizard foraging behavior. Because plants differ greatly in palatability and nutritional qualities, both interspecifically and ontogenetically, an ability to assess these features by tongue-flicking would be beneficial (Cooper and Alberts, 1990). As anticipated, the largely herbivorous iguanid *Dipsosaurus dorsalis* responds strongly to chemicals from plant food (Cooper and Alberts, 1990).

The evolutionary changes in chemosensory response predicted in a lineage that adopts herbivory or omnivory depend on the foraging mode of the insectivorous ancestor. Among insectivorous lizards, active foragers use their tongues to sample chemicals to detect and identify food, but ambush foragers do not (Cooper, 1994a,b, 1995a, 1997, 1999). Active foragers can find hidden prey by tongue-flicking. In contrast, once an ambusher has adopted a fixed ambush post, it has nothing to gain by repeated tongue-flicking at the same site. Tongue-flicking may even reveal its presence to predator or prey.

When plants become the primary dietary component of lizards, they should evolve responsiveness to plant chemicals. In species derived from ambush foragers, the lizards are freed from any constraint on tongue-flicking due to detection by prey. They may benefit from chemosensory analysis of lingually sampled chemicals, unlike their ambush-foraging ancestors. Omnivores derived from ambush foragers are also predicted to evolve lingually mediated chemosensory

* Does their prey "lead"
them to plant food?

• Ambushers have no initial prey-chemosense - visual cues
• Coevolve sense for prey & plant food

* Foragers have initial chemo-function for prey & retain it as they develop sense for herbivory

identification of both plant and animal food. In omnivores derived from active foragers, chemosensory responses to plant foods are predicted to evolve, and those to animal prey should be retained.

In this paper I report the results of a study of the ability to discriminate plant and animal prey chemicals from control substances by geckos of the genus *Rhacodactylus*. This genus consists of large gekkonid lizards of the tribe Carphodactylini, subfamily Diplodactylinae (Bauer and Henle, 1994; Good et al., 1997). They are exceptional among geckos in consuming large amounts of plant, as well as animal, food. Commonly consumed plant parts include fruit, flowers, and pollen (Mertens, 1964; Bauer and Sadler, 1994). Omnivory is derived in *Rhacodactylus* from insectivory present in the common ancestors of Gekkota, Gekkonidae, and Diplodactylinae (Cooper, unpublished data). Because importation of wild-caught *Rhacodactylus*, especially species from New Caledonia, is likely to impact natural populations in island habitats of limited extent, I studied animals in zoo collections. To evaluate the ability to discriminate plant and animal foods from control substances, I experimentally tested chemosensory responses by individuals of three species of *Rhacodactylus* to chemical stimuli presented on cotton swabs.

This is a bit problematic
Can Captivity effect
this data?
Probably not.

Where else are they
found?

METHODS AND MATERIALS

Eight *Rhacodactylus leachianus* were observed at the Dallas Zoo and Fort Worth Zoo and four *R. auriculatus* and one *R. ciliatus* at the Saint Louis Zoo. All individuals were adults. All observations were made in home cages that were off exhibit. Although all cages provided ample shelters such as rocks and hollow logs, cage sizes and types and environmental conditions varied among lizards and zoos. To control these variable effects, each individual was tested in all experimental conditions in identical environmental conditions. Each individual served as its own control in statistical analyses that eliminated effects of differences in responsiveness among individuals. All tests were conducted in daylight hours between 09:00 and 15:00 hr, which might have reduced responsiveness somewhat.

I used the swab method (Burghardt, 1970b; Cooper and Burghardt, 1990; Cooper, 1998a) to study the ability of the lizards to discriminate preferred foods from control stimuli. To prepare a stimulus, I first dipped the cotton end of an applicator into deionized water. Deionized water served as an odorless control for responses to the experimental milieu. Food stimuli were added by rolling the moist cotton across the surface of an opened banana or the integument of a neonatal albino laboratory mouse (*Mus musculus*) for *R. leachianus* or a domestic cricket (*Acheta domestica*) for the other two lizard species. While rolling the cotton over a surface, I pressed lightly to achieve transfer of chemicals. Romaine lettuce was a pungency control for responses to a detectable chemical stimulus from a nonfood

* Study seems not to
account for behavioral
variation - might be
a food preference based
on temporal circumstance

* Is there any evidence
that leachies eat
rodent prey in the wild?
* Wouldn't it be best
to test Saprophyagy?

* How would this study work using more natural food items? Pollen, nectar, flowers

or less preferred food. Banana and the animals used corresponded to the zoo diets. Insects are an important food source for *R. auriculatus*, with orthopterans present in over 25% of stomachs examined (Bauer and Sadler, 1994).

To begin a trial, I opened the door to a lizard's cage carefully to avoid startling movements or vibrations. I slowly positioned the cotton tip of an applicator 1–1.5 cm anterior to the lizard's snout. If the lizard tongue-flicked the swab within 30 sec, I recorded the number of tongue-flicks directed to the swab in the 60 sec beginning at the first tongue-flick, provided that the lizard did not bite the swab. If the lizard bit, I recorded the number of tongue-flicks before the bite and latency in seconds between the first tongue-flick and the bite. If the lizard did not respond within 30 sec, I touched its snout briefly with the swab. If it tongue-flicked within the next 30 sec, I recorded data as above. If it did not tongue-flick in the next 30 sec, zero tongue-flicks were recorded.

I tested the responses of each lizard to all four stimuli in a randomized blocks design. Trial sequences were randomized to prevent possible bias due to the sequence of stimuli tested. Intertrial intervals were at least 30 min. The variables analyzed were number of tongue-flicks and tongue-flick attack score for repeated measures designs, TFAS(R) (Cooper and Burghardt, 1990). The primary measure of response strength is TFAS(R), a composite variable that combines influences of tongue-flicks, bites, and latency to bite (Burghardt, 1970b; Cooper and Burghardt, 1990). If a lizard does not bite, TFAS(R) is the number of tongue-flicks. If it bites, TFAS(R) is the maximum number of tongue-flicks in any one condition for that individual plus (60 – latency to bite in seconds).

Tongue-flicks and TFAS(R) were tested for significance by nonparametric Friedmann two-way analysis of variance due to heterogeneity of variance and non-normality in the control conditions. When a main effect was significant, comparisons between pairs of means were made by multiple comparison procedures (Zar, 1996). Alpha was 0.05. Significance tests were two-tailed except where explicitly stated otherwise. One-tailed tests were justified where stronger responses were predicted to chemical stimuli from preferred food than to control stimuli.

RESULTS

All individuals tongue-flicked in response to animal and banana stimuli, and all but two tongue-flicked in response to romaine lettuce and deionized water (one each of *R. leachianus* and *R. auriculatus*). Responses by *R. leachianus* were greater in response to the preferred food, banana, than to other stimuli (Table 1). Numbers of tongue-flicks differed significantly among conditions ($\chi^2 = 13.65$, $df = 3$, $P < 0.005$). The number of tongue-flicks in response to banana stimuli was significantly greater than to romaine lettuce ($P < 0.05$, one-tailed) and deionized water ($P < 0.01$). No other differences were significant.

Only one individual bit a swab scented with banana. Thus, data for tongue-

* Human interaction is a factor - animals more acclimated to men are more likely to flick than those not. Not sure how to get around this, though.

* Low # of individuals worries me in regard to accurate data - low sample size.

Procedure

Problematic

Expected

TABLE 1. TONGUE-FLICKS DIRECTED TO COTTON SWABS WITH STIMULI FROM BANANA, ANIMAL PREY,^a ROMAINE LETTUCE, OR DEIONIZED WATER

Species	Tongue flicks/60 sec			
	Banana	Animal	Lettuce	Water
<i>Rhacodactylus leachianus</i> (8 tested)				
Mean	13.9	10.0	8.0	2.1
SE	2.4	1.9	2.5	1.0
Range	4–25	2–19	0–18	0–7
<i>R. auriculatus</i> (4 tested)				
Mean	32.2	41.5	10.2	5.8
SE	3.3	4.4	5.6	5.1
Range	24–40	29–49	0–20	0–21
<i>R. ciliatus</i> (1 tested)				
	20	14	2	2

^aAnimal prey: mouse for *R. leachianus*, cricket for other species.

flicks and TFAS(R) were identical, with the exception that TFAS(R) was 17.5 ± 3.4 in the banana condition. However, although the same comparisons were significant for tongue-flicks, analysis of TFAS(R) permitted an additional inference. TFAS(R) varied significantly among conditions ($\chi^2 = 15.45$, $df = 3$, $P < 0.005$). TFAS(R) was significantly greater in response to banana stimulus than to stimuli from mouse ($P < 0.05$, one-tailed), romaine lettuce ($P < 0.05$, one-tailed), and deionized water ($P < 0.01$). Differences among other stimuli were not significant. Although differences between the mouse and control conditions were not significant, responses to mouse stimulus were slightly greater than to the control stimuli.

Data for the two species tested with cricket stimuli, *R. auriculatus* and *R. ciliatus*, showed tongue-flicking at elevated rates in response to both banana and cricket stimuli (Table 1). The main stimulus effect for tongue-flicking by *R. auriculatus* was significant ($\chi^2 = 10.80$, $df = 3$, $P < 0.025$). The lizards performed more tongue-flicks in response to cricket than to romaine lettuce and deionized water ($P < 0.01$ each) and in response to banana than to romaine lettuce or deionized water ($P < 0.03$ each, one-tailed). The responses of the single individual of *R. ciliatus* showed a similar pattern of relative magnitudes of tongue-flicks rates among conditions as in *R. auriculatus*, with many more tongue-flicks in the banana and cricket conditions than in the control conditions (Table 1).

Analysis of TFAS(R) for all three species pooled produced main effects and responses to banana stimuli that were significant at lower alpha levels. The stimulus effect was significant ($\chi^2 = 23.0$, $df = 3$, $P < 0.001$). TFAS(R) in response to banana stimulus was greater than to romaine lettuce and deionized water ($P < 0.01$ each). Response strength was greater to animal stimulus than

Sample size - too heuristic

to deionized water ($P < 0.01$), but not greater than to romaine lettuce ($P < 0.06$, one-tailed). The other two differences were not significant.

DISCUSSION

Rhacodactylus leachianus discriminated between banana and the control stimuli, as indicated by the significant elevation of numbers of tongue-flicks and TFAS(R), and between banana and mouse stimuli as indicated only by the greater TFAS(R). That only one individual bit a swab bearing banana stimulus suggests that additional cues may be important to elicit feeding—perhaps visual or tactile cues. There was no indication of elevated response to the mouse stimulus although the lizards eat mice in captivity. The analysis for *R. auriculatus* revealed discrimination of both plant and animal food chemical stimuli from control stimulus. Because no individuals bit, this was indicated only by the significantly greater numbers of tongue-flicks elicited by banana and cricket stimuli than by romaine lettuce and deionized water.

The prediction that the omnivorous *Rhacodactylus* geckos exhibit lingually mediated discrimination between plant food chemicals and control stimuli was confirmed for two species. Together with the strong response to banana stimulus by the single specimen of *R. ciliatus*, the findings suggest that plant chemical discriminations may be widespread in *Rhacodactylus*. In conjunction with published data on the iguanid *Dipsosaurus dorsalis* (Cooper and Alberts, 1990, 1991; Cooper, 2000a), these findings support the hypotheses that incorporation of a substantial plant component into the diet induces evolution of chemosensory response to plant and animal foods in species derived from ambushing ancestors.

Establishment of an evolutionary correlation between herbivory and food chemical discrimination will require comparative study of numerous species of herbivores and control data on responses to plant and animal chemicals by insectivores. Nevertheless, all available data, including data for members of three families belonging to distantly related lineages, suggest that chemosensory behavior is altered to match dietary requirements as well as constraints of foraging mode. The evolutionary hypothesis has not yet been tested conclusively, but the present findings add to the comparative data base needed to test it and are consistent with it.

The prediction that *Rhacodactylus* lizards use prey chemical discrimination to evaluate cues from animal foods was verified for responses to cricket stimuli for *R. auriculatus*, but not for responses to mouse stimuli by *R. leachianus*. The reasons for the difference in discrimination of animal prey stimuli among species of *Rhacodactylus* are uncertain. One possibility is that all species are more responsive to cricket chemicals than mouse chemicals. Arthropods are the dominant prey type of nearly all geckos studied (reviewed by Bauer and Sadler, 1994). Although *R. leachianus* eat mice and other vertebrates in captivity and

* Additional cues may be visual or may be a chemosensory threshold.
Be interesting to see if they bite an actual banana

→ Could be the result of visual cues & not chemosense

* Chemosensory function is primarily a function of diet (herb, omni, carn, insect) + mode (forager or ambusher)

* Again - are rodents an actual food source in New Caledonia?

birds in the field (Mertens, 1964), grasshoppers are a favored food in captivity. Insects are important in the natural diets of some *Rhacodactylus* (Bauer and Sadler, 1994), but mice have not been reported in the natural diet and may not be commonly available in the arboreal habitat of the lizards. It is quite likely that these lizards have evolved greater responsiveness to chemical cues from insects. The strong responses to cricket chemicals by the single individual of *R. ciliatus* hint that response to insect chemicals could be widespread in the genus *Rhacodactylus*.

Another consideration is that *R. leachianus* may discriminate the mouse stimulus from the control stimulus, but that the ability was not detected in the experiment. There are at least two possible reasons for a misleading failure to detect an elevated response to mouse stimulus by *R. leachianus*. First, because the statistical power of the experiment is low due to small sample size, a real effect might have gone undetected. The mean tongue-flick rate in response to mouse stimulus was much higher than to deionized water, and six of eight individuals tongue-flicked more frequently in response to mouse stimulus than to deionized water. The difference was not significant due to one individual that tongue-flicked more in response to deionized water than to the mouse stimulus and another that tongue-flicked equally in the two conditions. Responses were also slightly higher to mouse than romaine lettuce stimulus. It seems quite likely that a greater response to mouse stimulus than to water would be revealed by using a larger sample size.

A second possible reason for the lack of apparent elevated response to mouse stimulus is the variability of responsiveness due to defensive behavior. Of the many species that I have tested successfully using the swab method, *R. leachianus* was perhaps the most difficult to study. Some species flee repeatedly or refuse to tongue-flick in the presence of an experimenter (e.g., *Hydrosaurus pustulosus*, *Ophisaurus ventralis*), requiring use of other methods. *Rhacodactylus leachianus* frequently either fled under rocks or into hollow log shelters or attempted to bite me when I tried to begin trials. Several individuals never responded to swabs and could not be used. After unsuccessful preliminary trials, I was able to collect data by presenting swabs to lizards when their heads were visible to me inside logs or at the edges of rocks that hid the rest of their bodies. Even among those that did tongue-flick, variation in defensiveness among trials due to the position or exposure of the lizard may have increased the variability of results.

Chemosensory responses by *Rhacodactylus* differ from those of all other geckos studied by the swab method. Among other geckos, several eublepharid species exhibit prey chemical discrimination and a high proportion of individuals bite swabs bearing animal food chemicals (Dial, 1978; Dial et al., 1989; Cooper, 1995b, 1998b), which is consistent with their active foraging mode (Kingsbury, 1989; Cooper, 1994a,b). However, three gekkonid species, *Gekko gecko*, *Pachy-*

Guess not!
Reveal exp. w/ avian
prey?

* possibly: attraction to
rodent prey is <
remnant of visual cues
& not chemosensory

New exp. design
is required to
eliminate human
interaction!

dactylus turneri, and *Thecadactylus rapicauda*, do not exhibit lingually mediated food chemical discrimination (Cooper, 1995b, 2000b). Because these species and a large majority of gekkonids are insectivorous ambush foragers (Cooper, 1994a,b; Cooper et al., 1999), both omnivory and lingually mediated discriminations of plant and animal foods are presumably derived characters in *Rhacodactylus*.

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