## ORIGINAL ARTICLE

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# Tasty figs and tasteless flies: plant chemical discrimination but no prey chemical discrimination in the cordylid lizard *Platysaurus broadleyi*

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Abstract Lizards use visual and/or chemical cues to locate and identify food. The ability to discriminate prey chemical cues is affected by phylogeny, diet, and foraging mode. Augrabies flat lizards (*Platysaurus broadleyi*) are omnivorous members of the lizard clade Scleroglossa. Within Scleroglossa, all previously tested omnivores are capable of both prey and plant chemical discrimination. At Augrabies Falls National Park, P. broadleyi feed on both insects (black flies) and plant material (figs), and as scleroglossans, are predicted to discriminate both plant and prey chemicals. However, *Platysaurus broadleyi* use visual, not chemical cues, to detect and capture black flies, which occur in large concentrations in the study area. We tested free-ranging individuals for the ability to discriminate insect and plant chemicals from controls. There was a significant stimulus effect such that lizards tongue-flicked fig-labelled tiles significantly more than the remaining stimuli, spent more time at the fig-labelled tile, and attempted to eat fig-labelled tiles more often than tiles labelled with control or insect stimuli. Platysaurus broadleyi is exceptional in being the first lizard shown to possess plant chemical discrimination but to lack prey chemical discrimination. We suggest that an absence of prey chemical discrimination may be a consequence of foraging behaviour and environmental effects. Because insect prey are highly clumped, abundant, and aerial, profitable ambushing using visual cues may have relaxed any selective pressure favouring insect prey chemical

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W. E. Cooper Jr Department of Biology, Indiana University–Purdue University, Fort Wayne, IN, 46805, USA discrimination. However, a more likely alternative is that responses to figs are gustatory, whereas as prey chemical discrimination and plant chemical discrimination are usually mediated by vomerolfaction.

**Keywords** Chemical discrimination · Plant chemicals · Prey chemicals · Selection · Figs

## Introduction

Many lizards employ lingual sampling of chemical cues to locate prey or to sample plant material in cases of herbivory (Cooper 1990, 1994a, 1994b, 1995). Within insectivorous lizards, the ability to detect prey chemicals correlates with foraging mode such that ambush (sit-andwait) foragers lack prey chemical discrimination (PCD) while active foragers use PCD to locate hidden prey (Cooper 1994b). Data from many lineages show this relationship to be widespread and stable within most families (Cooper 1995). When foraging mode is not stable within a family, it still correlates with ability to detect prey chemicals in the predicted way (Cooper 1995, 1997). For example, the genus *Mabuya* represents a rare instance of intrageneric differences in foraging mode (Cooper and Whiting 2000). M. striata sparsa is an active forager capable of PCD; M. acutilabris is an ambush forager incapable of PCD (Cooper 2000a). This result and recent phylogenetic tests support a tight link between PCD and foraging mode, supporting an adaptive adjustment of PCD accompanying switches in foraging mode (Cooper 1995).

In the past few years numerous species of insectivorous, herbivorous, and omnivorous lizards have been experimentally tested for prey and plant chemical discrimination (e.g. Cooper 2000b, 2000c, 2000d; Cooper and Habegger 2000). A consistent pattern has emerged. Insectivores do not respond to plant cues regardless of foraging mode, whereas omnivores and herbivores, even those derived from ambushing insectivores, exhibit both prey and plant chemical discrimination (Cooper 2002, 2003). There are two major taxonomic groups of lizards, Iguania and Scleroglossa, the latter including Gekkonoidea and Autarchoglossa. Within Iguania and Iguania plus Gekkonoidea (a broader group of ancestral ambush foragers), convergent evolution of both plant and prey chemical discrimination has occurred among plant eaters (W.E. Cooper, unpublished data). A single phrynosomatid species, *Sceloporus poinsettii*, is the sole known exception. It is an omnivore that lacks prey and plant chemical discrimination (Cooper et al. 2001). In Scleroglossa, correlated evolution of plant diet and plant chemical discrimination has occurred (Cooper and Vitt 2002).

Omnivorous species derived from ambush foragers are thus predicted to exhibit both prey and plant chemical discrimination. Here we report the first exception to this relationship. Platysaurus broadleyi is a small (max. snout-vent length 84 mm) member of the scleroglossan family Cordylidae, which is characterized by ambush foraging (Cooper et al. 1997). Most species of *Platy*saurus are omnivorous (Broadley 1978). P. broadleyi feeds primarily on black flies (Simulium spp.) at Augrabies Falls National Park but readily eats Namaqua figs (Ficus cordata) when they are available (Whiting and Greeff 1997; Greeff and Whiting 2000). Furthermore, P. *broadleyi*, although classified as an ambush forager when hunting for animal prey (Cooper et al. 1997), adjusts its foraging behaviour in relation to resource type and availability (Greeff and Whiting 2000). When black flies occur at high density, P. broadleyi ambushes from short attack distances; when feeding on figs, P. broadleyi moves and tongue flicks more frequently (Whiting and Greeff 1997; Greeff and Whiting 2000). Black flies are available throughout most of the year, although flies occur in reduced numbers during winter months. Fig trees produce fruit throughout the year, because of their dependence on fig wasp pollinators, but as a result individual trees in a population will fruit at different times (Compton 1993).

The objective of our study was to test the omnivorous P. broadleyi for ability to discriminate insect (fly) and plant (fig) chemicals from control stimuli. The relationship between foraging mode and PCD is stable within cordyliform lizards studied to date, but only three species representing three different genera have been studied (Cooper and Steele 1999). Only one species of flat lizard, *P. pungweensis*, has been tested for PCD. As predicted, *P. pungweensis* could not detect insect prey chemicals, but it was not tested for chemical discrimination of any plant material (Cooper and Steele 1999). Because P. broadleyi is an omnivore, it is predicted to exhibit both prey and plant chemical discrimination. In the field, P. broadleyi tongue flicks frequently when searching for figs beneath fig trees (M.J. Whiting and W.E. Cooper, personal observation) and also when evaluating figs (Whiting and Greeff 1997). However, it hunts for the extremely abundant black flies visually, ambushing those that approach closely, and does not locate them by tongue flicking (Greeff and Whiting 2000; M.J. Whiting and W.E. Cooper, personal observations). Absence of tongue flicking during searching for prey casts some doubt on the relationship between omnivory and PCD and therefore prompted testing of PCD for both prey and fig chemicals in these lizards.

## Methods

#### Study area

We studied responses by adult *P. broadleyi* in the field during spring (5–7 November 2000) at Augrabies Falls National Park (28°35'S, 20°20'E) (hereafter Augrabies), Northern Cape Province, South Africa. The area is xeric and is characterised by hot summers (max. 42.9°C) and cold winters (min. –2.9°C; Branch and Whiting 1997). The xeric effect is, however, ameliorated by the Orange River, in which large numbers of *P. broadleyi*'s primary prey, the black fly (*Simulium* spp.), breed. For detailed descriptions of the study area, see Branch and Whiting (1997), Whiting and Greeff (1997), and Greeff and Whiting (2000). Lizards at Augrabies are habituated to people and allow close approach.

#### Experimental design and analyses

We tested PCD on free-ranging lizards using an independent groups design in which each lizard was tested for a single treatment only once. Laminated cardboard squares (5×5 cm; hereafter tiles) were treated with the following substances: (1) extract from ripe figs; (2) crushed flies (Simulium spp.), the lizard's natural prey; (3) cologne (Ego, Adrenalin scent) as a pungency control; and, (4) rainwater as an odourless control. [See Cooper (1998) for a detailed review of selection of controls and procedures for testing PCD.] We smeared each substance uniformly across the tile and took care not to include solid objects such as fig seeds, fig skin, or insect body parts. Care was taken to ensure that tile preparation was as consistent as possible. The tile was air dried for at least 30 min prior to conducting trials, to ensure that no visible moisture remained on the tile. We used a balanced design in which 80 lizards were tested (n=20 per group). Lizards were not marked, but we avoided pseudoreplication by systematically moving through lizard habitat such that lizards were only sampled once. Lizards occur at high density in the study area and we were able to conduct trials rapidly, reducing the probability of sampling a lizard twice. Lizards tested were all active. Tests were conducted during morning hours, the prime activity period, although lizards will feed throughout the day if conditions are favourable. At the time of study, flies were readily available, although ripe figs were patchy and not available to all lizards.

A stimulus tile was placed a few metres from the lizard, depending on the nature of the habitat. We avoided testing lizards near fig trees or fly concentrations, thereby controlling for feeding context. Besides that, lizards were randomly selected. After the lizard approached the tile, the number of tongue-flicks performed was counted for 2 min starting from the first tongue-flick or until the lizard left the tile before 2 min elapsed. This method has the advantage of guaranteeing that the stimulus has been sampled. We recorded the time from the first tongue flick until the lizard left the tile or 120 s if it did not leave during the trial.

Because the tongue-flick data exhibited pronounced heterogeneity of variance and nonnormality, they were analysed using the nonparametric Kruskal–Wallis analysis of variance. When the experiment-wide test revealed significant differences among stimuli, differences between pairs of stimuli were tested for significance using Tukey-type nonparametric multiple comparisons (Zar 1996). We assessed differences among treatments in numbers of individuals that tongue-flicked more than twice by a 4×2  $\chi^2$  analysis followed by 2×2  $\chi^2$  for differences between pairs of means. Differences among stimuli in numbers of individuals that attempted to eat the tiles were tested for significance using binomial tests. Raw probabilities are reported for the chi-square and binomial tests, but significance tests were made using a sequential Bonferroni adjustment (Wright 1992) because six paired comparisons were made. Tests of significance were conducted with  $\alpha$ =0.05 and were two-tailed except when otherwise indicated and justified by onetailed predictions regarding stronger response to fig stimuli than control stimuli. Because no significant PCD was detected, we used data from a previous experiment to estimate statistical power required to detect PCD (Zar 1996). Using data on the insectivorous *Acanthodactylus boskianus*, the phi coefficient was 2.86.

## Results

Tongue-flick frequency

Except in the fig treatment, a large majority of lizards tongue-flicked only once (*n*=36) or twice (*n*=13), leaving only 11 of 60 individuals that tongue-flicked more than twice (3 in the cologne group, 2 in the water group, and 6 in the fly group). In contrast, 19 of 20 individuals tongue-flicked more than twice in the fig group. Significantly more individuals tongue-flicked tiles labelled with fig stimuli than with cologne ( $\chi^2$ =25.86, *df*=1, *P*<0.0001), water ( $\chi^2$ =28.97, *df*=1, *P*<0.0001), or fly ( $\chi^2$ =18.03, *df*=1, *P*<0.0001) stimuli. No other differences between pairs of treatments were significant.

Mean number of tongue-flicks was very low at five or fewer tongue-flicks per minute in all treatments, but numbers of tongue-flicks per trial differed significantly among stimulus treatments (H=37.50, df=3, P<0.0001; Fig. 1). Paired comparisons revealed that the lizards tongue-flicked significantly more times when responding to fig stimuli than to each of the remaining stimuli (P<0.001 each). There were no differences between any of the other stimulus pairs (P>0.10 each). Thus, no strong response to prey chemicals was detected although the power to detect PCD was greater than 0.99.

'Tile eating'

Seven lizards tried to eat the tile labelled with fig extract, and one lizard attempted to eat a fly-labelled tile. No lizards attempted to eat tiles labelled with either control.



**Fig. 1** Mean (±1 SE) tongue-flicks (TF) performed during sampling of tiles labelled with the four stimuli, by *Platysaurus broadleyi* 

Assuming an equal probability of 'tile eating' in all four groups, lizards attempted to eat the fig-labelled tile significantly more often than tiles labelled with control stimuli (binomial P=0.0078 each, one-tailed), but the number of lizards biting tiles in the fig and fly conditions did not differ significantly (P>0.10, two-tailed).

## Discussion

Platysaurus broadleyi showed a strong preference for figlabelled tiles. Significantly more tongue-flicks were directed towards fig-labelled tiles compared to fly and control tiles. Furthermore, lizards were more likely to attempt to 'eat' fig tiles compared to control tiles (one lizard attempted to eat a fly tile). There was no indication of PCD despite ample statistical power to detect it in the tongue-flick data. These results contrast with previous studies testing the predicted relationship between diet and PCD. In omnivores and herbivores derived from active foragers, PCD is already present when diets are expanded to include plants, so only plant chemical discrimination evolves while prey chemical discrimination is retained (Cooper 2002). However, in herbivores and omnivores derived from ambush foragers, prey and plant chemical discrimination typically coevolve (Cooper 2003).

*P. broadleyi* is the first species lacking PCD that has been shown to discriminate plant chemicals. Consideration of lizard diet, foraging behaviour, and foraging mode may shed light on this result. For example, as a result of their mating system, insect prey (primarily *Simulium* spp.) at Augrabies are highly clumped along the fast-flowing sections of a major river, providing a spatially and temporally predictable and abundant food source for lizards. Lizards may simply follow a humidity gradient to the river as a means of locating flies, or they may encounter aggregations by chance initially, and then relocate them using cognitive means. Whatever means they use to locate fly swarms, the presence of large aggregations of aerial, mobile insects favours ambush foraging by lizards using visual cues. P. broadleyi at Augrabies make more movements and spend more time moving than most sit-and-wait foragers (Cooper et al. 1997; Greeff and Whiting 2000) but still conform to an ambush foraging mode. Therefore, it is possible that an absence of PCD may be partly explained by relaxation of any selective pressures favouring location of insect prey by chemical means. Further investigation of insect PCD in other populations of P. broadleyi, where prey is more scattered, could be informative. We also need to know more about prey selection in P. broadleyi over a wide geographic area. If their diet is dominated by aerial insects regardless of habitat, then relaxation of selection pressures for insect PCD may still persist. Finally, it is possible that PCD does exist, but that our experimental protocol failed to detect it. We think this is unlikely because of the great success of previous studies of lizard PCD using tongue-flick scores (reviewed in Cooper 1994a, 1994b, 1995, 1997, 1998).

Environmental influences are also likely to affect discrimination of plant prey chemicals. When P. broad*levi* forage beneath fig trees, they move significantly more than when they forage for insects (Greeff and Whiting 2000). They also tongue-flick more frequently and upon locating a fig, they often (but not always) sample the fig by tongue-flicking prior to eating it (Whiting and Greeff 1997). Ripe figs are characterised by a high water content (Compton et al. 1996) and their relative softness allows the lizards to break them into manageable pieces for consumption [adult males eat entire figs; juveniles and females tear figs into pieces (Whiting and Greeff 1997)]. The suitability of a fig for consumption is therefore a function of its hydration. Dried figs become hard, change colour to brown, and are not eaten by lizards (Whiting and Greeff 1997). Figs are also a high-energy food source (Greeff and Whiting 1999). When lizards locate a fruiting fig tree, large numbers of lizards aggregate beneath trees and return daily until all the figs have been consumed (Whiting and Greeff 1999; M.J. Whiting, personal observation). In light of the benefits of locating and selecting ripe, high-quality figs, discrimination of fig chemicals is therefore likely to be adaptive.

Study of prey and plant chemical discrimination in additional species and populations of Platysaurus may help elucidate the importance of plant consumption and prey density to acquisition of these abilities. Although 11 of 14 taxa for which dietary data exist eat some plant matter (Broadley 1978; Whiting and Greeff 1997), the extent of omnivory is largely unknown in the absence of volumetric data. The lack of PCD in P. pungweensis (Cooper and Steele 1999) is not informative because data on prey density and the extent of plant consumption are unavailable. Plant chemical discrimination is expected only in species for which plants form more than an incidental portion of the diet. To assess the possible importance of abundant, visually detectable prey to the dissociation of prey and plant chemical discrimination, tests could be conducted for PCD in omnivorous species or populations of *Platysaurus* that exhibit plant chemical discrimination but have a markedly less abundant prey supply than *P. broadlevi* at Augrabies Falls.

In some instances, we observed lizards licking figlabelled tiles. In lizards, licking is frequently associated with nectar and fruit feeding (e.g. Eifler 1995; Cooper and Pérez-Mellado 2001; Cooper et al. 2002) and is normally triggered by a gustatory response (Schwenk 1985; Cooper and Pérez-Mellado 2001). P. broadleyi tongue-flick figs (Whiting and Greeff 1997) and in this study, lizards tongue-flicked, licked, and bit fig-labelled tiles, suggesting the possibility that *P. broadlevi* may be employing both vomerolfaction and gustation. The sense of taste in lizards is likely more prevalent than previously believed and may play an important role in chemical discrimination (Schwenk 1985; Stanger-Hall et al. 2001). For example, Anolis carolinensis is an insectivorous polychrotid lizard that uses gustation, not vomerolfaction, to discriminate prey chemicals (Stanger-Hall et al. 2001). In addition, behavioural evidence suggests a role for gustation in detecting sucrose in the omnivorous lacertid *Gallotia caesaris* (Cooper and Pérez-Mellado 2001).

More behavioural tests are needed to disentangle the roles of gustation and vomerolfaction in prey and plant chemical discrimination, especially in omnivores and herbivores (Schwenk 1985; Dearing and Schall 1992; Cooper and Pérez-Mellado 2001; Stanger-Hall et al. 2001). However, lack of PCD is consistent with the observation that both PCD and plant chemical discrimination require vomerolfaction in the herbivore *Dipsosaurus dorsalis* (Cooper and Alberts 1991). Our favoured hypothesis is that figs are recognised by taste rather than vomerolfaction. Otherwise, PCD would likely occur due to similarities in chemical cues indicating nutritional quality in plants and animals.

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