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PREY CHEMICALS DO NOT AFFECT GIVING-UP TIME AT AMBUSH POSTS BY THE CORDYLID LIZARD PLATYSAURUS BROADLEYI

WILLIAM E. COOPER, JR.^{1,3} AND MARTIN J. WHITING²

¹Department of Biology, Indiana University-Purdue University at Fort Wayne, Fort Wayne, IN 46805, USA ²School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

ABSTRACT: Lizards that forage from ambush do not exhibit prey chemical discrimination, but might enhance foraging efficiency by staying longer at ambush posts bearing chemical prey cues. By presenting chemical stimuli to free-ranging lizards, we tested whether *Platysaurus broadleyi* had longer giving-up time (i.e., time at an ambush post) in the presence of insect prey stimuli. The lizards remained no longer at tiles labelled by prey chemicals than control substances, but giving-up times were greater at tiles labelled by a plant food (fig). Ambush foragers may not use prey chemicals to assess the quality of ambush posts.

Key words: Ambush; Behavior; Cordylidae; Food chemical discrimination; Foraging mode; Giving-up time; Prey chemical discrimination; Squamata

FORAGING mode in insectivorous/carnivorous lizards is tightly linked with the use of the chemical senses to locate, identify, and evaluate food. Active foragers tongue-flick repeatedly while moving through an area searching for food, whereas ambush foragers do not (Evans, 1961). With one exception (Cooper, 1999), only active foragers exhibit prey chemical discrimination, a differentially stronger response to prey chemicals that is shown by a combination of elevated tongue-flicking for chemosensory sampling and biting of objects bearing prey chemical cues in relation to weaker responses to control stimuli (Cooper, 1994a,b, 1997, 2000). Examination of evolutionary shifts between foraging modes has revealed correlated evolution between foraging mode and prey chemical discrimination, whereas shifts from active foraging to ambush foraging are accompanied by loss of prey chemical discrimination and shifts from ambush foraging to active foraging are accompanied by acquisitions of

Because ambush foragers wait motionless at ambush posts for prey to move into their visual fields, tongue-flicking substrates to detect chemical prev cues is likely to have little or no value. It has also been suggested that tongue-flicking might disrupt crypsis maintained by immobility, a primary defense of ambush foragers (Vitt, 1983), increasing the probability of revealing a lizard's presence to prey and predators (Cooper, 1995, 1997). Field observations of ambush-foraging lizards reveal extremely low rates of tongue-flicking at ambush posts. Cooper et al. (1994) found that four phrynosomatid species averaged only one tongue flick per 53.4 min while at ambush posts and 96% of all tongue-flicks to substrates occurred immediately upon arrival at a new site. The latter suggests the possibility that such lizards might evaluate ambush posts based on the presence of prev chemicals.

prey chemical discrimination (Cooper, 1995, 1997). The earliest lizards probably were ambush foragers that lacked prey chemical discrimination (Cooper, 1995, 1997).

³ Correspondence: e-mail, cooperw@ipfw.edu

Ambush foraging lizards, when experimentally tested with chemical cues on cotton swabs or ceramic tiles, exhibit no chemical discrimination of prey. However, it is possible that the lizards can detect and identify prey chemicals based on one to a few tongue-flicks, but they do not respond more strongly to them than to other stimuli because additional tongue-flicks provide no further information and/or attacks are triggered by visual, not chemical, cues. Ambush foragers do not find and immediately attack prey using chemical cues sampled by tongue-flicking, but it remains possible that they might evaluate ambush posts by sampling for prey chemicals. If the intensity of prey chemical cues at an ambush post is positively correlated with abundance, prey chemicals might be used by ambushers as a cue to remain longer at the post.

The idea that food is distributed heterogeneously in the environment and that animals respond to spatial clumping of food gave rise to optimal patch use theory as the major foci of optimal foraging theory (Pyke et al., 1977). The simple idea that predators should remain longer in patches with higher expected feeding rates is the starting point for theories about optimal patch use. The length of time spent in a patch before leaving is called "giving-up time." Many studies of optimal patch use have focused on when it is optimal for an individual to abandon an ambush post or foraging patch for a new one (e.g., Munger, 1984). However, little attention has been given to what cues animals may use to identify ambush posts and whether these cues also influence giving-up times. Chemical cues might provide ambush foragers information about the rate at which currently absent prey are likely to move into positions that are visually detectable from the ambush post. If so, giving-up times should be longer at ambush posts bearing chemical cues than at similar posts that do not.

We tested the hypothesis that ambush foragers have longer giving-up times when prey chemicals are present. The Augrabies flat lizard *Platysaurus broadleyi* is an omnivore that is primarily insectivorous except when fig fruits are available (Whiting and Greeff, 1997). When foraging for animal prey, *P. broadleyi* ambushes (Cooper et al., 1997). Unlike other omnivorous lizards, this species exhibits plant chemical discrimination, but not prey chemical discrimination (M. Whiting and W. Cooper, unpublished data). The Augrabies flat lizard moves between ambush posts somewhat more frequently than most ambush foragers (Cooper et al., 1997). Casual observations showed that a higher proportion of individuals of this species tongueflick upon arriving at new ambush posts than do phrynosomatid lizards studied previously (Cooper et al., 1994). Thus, *P. broadleyi* provides a likely species for researching the effect of prey chemicals on giving-up times in an ambusher following lingual sampling of prey chemicals and control stimuli.

MATERIALS AND METHODS

We studied adult *P. broadleyi* in the field during November 2000 (early summer) in a dense population at Augrabies Falls National Park (28° 35′ S, 20° 20′ E; hereafter Augrabies), Northern Cape Province, South Africa. The region is xeric and has hot summers (maximum: 42.9 C) and cold winters (minimum: -2.9 C) (Branch and Whiting, 1997). However, food is abundant at the study site because it is adjacent to the Orange River where large numbers of the black fly (Simu*lium* spp.) breed and fig trees periodically provide abundant fruit. More detailed descriptions of the study area can be found in Branch and Whiting (1997), Whiting and Greeff (1997), and Greeff and Whiting (2000). It is exceptionally easy to study P. broadleyi at Augrabies because they are abundant, easy to observe on the bare stone substrate of most of the area, and allow close approach due to habituation to people.

We examined the effect of the presence of food chemicals on giving-up time, defined as the duration between arrival at the site and departure. The experimental sites were laminated cardboard squares (5×5 cm; hereafter referred to as tiles), each of which bore one of four stimuli: (1) extract of ripe fig fruit, (2) crushed flies (*Simulium* spp.), (3) cologne (Ego, Adrenalin scent) as a pungency control, and (4) rain water as an odorless control. To prepare a tile, a stimulus was smeared uniformly across a tile and solid objects such as fig seeds, fig skin, or insect body parts were excluded. The tile was dried for at least 30 min prior to use.

To begin a trial, the experimenter placed a stimulus tile a few meters from a lizard, the

distance varying somewhat with the nature of the habitat. Once the lizard approached the tile, the time spent at the tile was recorded, beginning with the first tongue-flick that touched the tile and ending when the lizard moved to another site. Lizards typically tongue-flicked immediately upon arrival at the tile. The givingup time was measured in this way to maximize any possible effect of chemical stimuli by ensuring that the chemical stimuli had been sampled by tongue-flicking. If the lizard did not leave the tile within 120 s, 120 s was recorded as the maximum giving-up time. Eighty individuals were tested, 20 with each of the four stimulus treatments. We avoided pseudoreplication by systematically moving through lizard habitat, testing each lizard only once. Due to the high density of lizards at Augrabies, trials could be conducted rapidly, avoiding confusion among individuals due to movements over a lengthy interval between tests.

The data were analyzed using analysis of variance for a single-factor experiment having an independent groups design (Zar, 1996). Data were examined for heterogeneity of variance using Levene's test and for non-normality using a Kolmogorov-Smirnov goodness-of-fit test. Logarithmic transformation was required to meet the assumption of homogeneity of variances and normality. Following detection of a significant main effect, comparison between pairs of treatments means were conducted using Newman-Keuls tests (Winer, 1962). Significance tests were two-tailed, with $\alpha = 0.05$. Statistical power was estimated as in Zar (1996).

Results

Most lizards (95%, n = 76) moved away from the stimulus before 120 s had elapsed (Table 1). The variances of the raw givingup times were significantly heterogeneous (Levene's $F_{3,76} = 5.05$, P < 0.0031). The logarithmically transformed data had homogeneous variances (Levene's $F_{3,76} = 1.31$, P =0.277) and did not depart significantly from normality ($D_{0.05,80} < 0.074$, P > 0.10), allowing us to use the parametric ANOVA procedure. The main stimulus effect for the giving-up time was significant ($F_{3,76} = 7.88$, P = 0.00012). Pairwise comparisons revealed that lizards spent significantly longer sampling fig-labelled tiles compared to cologne (P = 0.0043), water

TABLE 1.—Descriptive statistics (mean ± SE, range in parentheses) of sampling duration in seconds for *Platysaurus broadleyi*. Tiles were labelled with four stimuli: fig extract, crushed flies, water (odorless control), and cologne (pungency control). Sample sizes were 20 per group.

Fig	Fly	Water	Cologne
38.1 ± 8.9 (6-120)	$\begin{array}{c} 22.2 \pm 6.9 \\ (2120) \end{array}$	$\begin{array}{c} 12.0\pm3.6\\(1\!-\!\!52)\end{array}$	8.05 ± 1.6 (2-25)

(P = 0.0038), and fly (P < 0.013). No other differences between stimulus pairs were significant. When the analysis was restricted to the fly treatment and the two control treatments, there was no significant difference among treatments using a one-tailed test based on the prediction of greater giving-up time in the fly treatment $(F_{2,57} = 1.73, P = 0.187,$ two-tailed). The power to detect a difference between giving-up times was >0.95.

DISCUSSION

The lack of any effect of prey chemicals on giving-up time suggests that P. broadleyi did not use chemical cues to evaluate ambush sites. Because the statistical power to reject the hypothesis of no difference was high, it is unlikely that a real effect of lingually sampled prey chemicals on giving-up time went undetected. Our results strongly suggest that lizards do not lingually sample prey chemicals on ambush posts to make decisions about how long to remain at ambush posts. It is possible, but quite unlikely, that visual distractions by prey undetected by the experimenter might have overridden responses to prey chemicals. All available evidence continues to suggest the unimportance of prey chemical cues for locating and identifying prey by ambushforaging lizards.

That the lizards remained at fig-labelled tiles significantly longer than tiles labelled with the remaining stimuli is consistent with the finding that *P. broadleyi* exhibits plant chemical discrimination as indicated by increased tongue-flicking and biting. Whether ripe figs are located by visual or chemical cues, the figs are likely to still be in the immediate vicinity of their chemical cues. Search for figs may be indicated by the longer giving-up time. For mobile insects, especially aerial blackflies, that are abundant throughout the area, there may be little correlation between the presence of prey chemicals and the prey themselves. If so, there would be little or no advantage to staying longer at sites where prey chemicals are detected, even if the lizards could detect and identify prey chemicals. Thus, the question of whether ambush foragers can identify prey chemicals remains unanswered, although the lower abundance of vomeronasal chemoreceptor cells in ambushers than in active foragers (Cooper, 1997) suggests that prey chemical discrimination may be absent or less well developed in ambush foragers than in active foragers. Whatever the perceptual abilities of ambush foragers may be with respect to prey chemicals, it is becoming increasingly clear that any such abilities are not used to enhance foraging success.

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