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Use of heterospecific cues by the lizard *Platysaurus broadleyi* for food location

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Abstract Flat lizards (*Platysaurus broadleyi*) at Augrabies Falls National Park, South Africa, are restricted to rocky terrain where the predominant tree is the Namaqua fig (*Ficus cordata cordata*). *P. broadleyi* readily feeds on Namaqua figs when they are available, and the lizards sometimes form large (maximum recorded = 134) congregations under fruiting fig trees. The distance lizards travel to fruiting trees also exceed normal daily foraging distances. Location of fruiting fig trees by a lizard can have a high pay-off because figs are energetically rich and trees fruit irregularly and asynchronously, resulting in a resource that is available, but unpredictable in time and space. The prediction that bird activity in fig trees provides a cue to the presence of ripe figs was tested experimentally. By placing cages containing birds and empty control cages in trees devoid of fruit, we demonstrated that *P. broadleyi* are drawn to fig trees with high bird congregations. We also tested if the presence of a fig tree was necessary to draw lizards to bird congregations by placing cages containing birds and empty control cages in a matched-pairs design on rock away from trees. Namaqua fig trees were not necessary to draw lizards to bird congregations.

Key words *Platysaurus broadleyi* · Birds · Heterospecific cues · Lizard · Sensory bias

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Introduction

When high-quality food resources vary spatially and temporally, a strategy that reduces searching time and predation risk should be favoured. To forage efficiently, an animal should also track changes in its environment (Krebs and Inman 1992), information which in some cases can be obtained directly while foraging (Cuthill et al. 1990). The information-processing scheme used by animals during foraging may be considered both a constraint on foraging and part of their phenotype, and is thereby subject to selection (Real 1992). Many animals rely on specific cues such as chemicals (Halpern 1992; Cooper 1994; Kaufman et al. 1996), sound (Tuttle and Ryan 1981), mechanical vibrations (Brownell 1977; Kaufmann 1986) and visual stimuli (Drummond 1985; Kaufman et al. 1996) to reduce searching time for food.

With a few exceptions, the role of heterospecific cues in location of resources has received little attention. Lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) use circling vultures to locate carcasses (Smithers 1983); and numerous anecdotal observations exist for associations between hornbills and various animals during hunting (reviewed in Kemp 1995). The Boran people of Kenya and the greater honey-guide (*Indicator indicator*) are involved in a facultative mutualistic symbiosis for the location of honey (Isack and Reyer 1989). This association involves an elaborate two-way communication system in which either species can initiate a search for honey. Among insects, parasitoid wasps are dependent on a variety of cues to locate hosts (Godfray 1994). Initial host searching is dependent on chemicals emitted by the host, and they soon learn to associate their hosts with their host's host.

The Augrabies flat lizard, *Platysaurus broadleyi* [formerly *Platysaurus capensis* (part) (Branch and Whiting 1997); adult snout-vent length range: 64–84 mm] is restricted to rocky outcrops in north-west South Africa and southern Namibia (Branch and Whiting 1997) and occurs sympatrically with the Namaqua fig (*Ficus cor-*

data cordata), which is also restricted to rocky terrains (van Greuning 1990; Berg and Wiebes 1992). Males are territorial and therefore offer the females no resources, although a resource defence polygyny appears to exist for that component of the population defending territories in areas of extreme insect abundance (at the river where black flies emerge) (M.J. Whiting, unpublished data). *F. c. cordata* is the dominant (sometimes the only) tree in this otherwise sparsely vegetated habitat. Individual trees are irregularly spaced. Like most other monoecious fig species (Berg and Wiebes 1992), fruiting is synchronous within a tree, but asynchronous between trees: during the month of our field work, for example, only 4 of 90 trees (4.4%) were fruiting. Hence, a specific tree produces fruit for a few weeks only, but the population as a whole fruits all year round. Preliminary field observations indicated that *P. broadleyi* is largely insectivorous, but both sexes readily feed on ripe figs (Whiting and Greeff 1997). When *F. c. cordata* trees are in fruit, large concentrations of lizards gather under them to feed on fallen ripe figs (this paper). Because figs are an energetically rich food source (Janzen 1979), lizards that locate ripe edible figs gain a high pay-off. Because of the asynchronous fruiting, ripe figs are spatially and temporally unpredictable. Either random or systematic searching for trees with ripe figs would be energetically costly, with no guarantee of success, and might also increase predation risk. These problems can be circumvented if lizards are able to use specific cues to locate fruiting fig trees. Such cues may either be the fruits themselves, or indirect phenomena that coincide with the period of fruiting.

P. broadleyi forages beneath fruiting trees using fig colour and size to discriminate between ripe edible and unripe or desiccated figs too hard to eat (Whiting and Greeff 1997). When figs are ripe, large congregations of birds gather to feed on them. This may act as an indirect cue, signalling the presence of ripe figs. In as much as *P. broadleyi* appears to have a strong sensory bias for moving objects (Whiting and Greeff 1997), the birds' constant fluttering could provide a conspicuous signal to the lizards.

Here we tested two hypotheses: (1) lizards use bird congregations in fig trees as a cue to the presence of ripe figs, and (2) the presence of a fig tree is necessary to draw lizards to bird congregations. Data were also collected on lizard aggregations under fig trees, as well as a conservative estimate of the distance lizards travelled to fig trees.

Methods

All experiments were conducted during April–May 1996 (the non-breeding season), at Augrabies Falls National Park (hereafter Augrabies) (28°35′ S, 20°20′ E), Northern Cape Province, South Africa. Conditions at Augrabies are xeric, although this is ameliorated by the Orange River. At Augrabies, the majority of lizards occur on rock along the Orange River margin, where insect prey are extremely dense. Namaqua fig trees occur in the same rocky terrain at a density of about 2–5 individuals/0.5 ha in the study area, and are the dominant, sometimes the only, tree species.

Lizard congregations under fruiting trees

To assess whether lizards were congregating under fruiting trees, we counted all individuals within a 5 m radius of the tree trunk, during a 7-min search. Searches were sometimes terminated before 7 min to reduce the likelihood of counting the same lizard twice. (We were able to confidently survey lizards without marking individuals, thereby reducing disturbance due to catching and marking lizards.) We used a matched-pairs design in which the same tree was sampled during a single fruiting and non-fruiting phase. Six trees were sampled three times in each condition (fruiting vs non-fruiting), while a seventh tree was sampled once in each condition. Means were used for statistical analysis. A Wilcoxon signed-rank test (one-tailed) was used to test the prediction that fruiting fig trees would have larger lizard aggregations than non-fruiting fig trees (because lizards are known to feed on figs).

Lizard foraging distance

Lizards observed in this study were not marked. However, to obtain a crude measure of the distance travelled to fruiting trees, we measured the distance (m) of lizard faecal pellets containing fig seeds to the nearest fruiting fig tree. Lizard faeces were easily distinguished from bird faeces containing fig seeds due to their characteristic oblong shape and associated uric acid deposit. Also, no other lizard species at the study area consumed figs. Although the environment was xeric, faeces did not last much longer than a few days to 2 weeks. We selected what we considered to be fresh faeces, stuck to rock, to ensure we estimated the correct minimum distance to the nearest fruiting tree.

Bird activity in trees as a foraging cue

We tested the prediction that lizards are attracted to high bird activity in trees by placing a cage (90 × 114 × 94 cm) containing birds in a fig tree; on a separate day, an empty control cage was used in the same tree ($n = 5$). All trees were devoid of figs. The mean number of birds/cage was 5.8 (range 5–6). Birds used were predominantly redeyed bulbuls (*Pycnonotus nigricans*) and pale-winged starlings (*Onychognathus nabouroup*), both of which feed on ripe *F. c. cordata* figs. Five trials were performed in separate trees, and the sequence of trials was alternated such that the control cage was presented first in three of the five trials. Every 20 min during an 80-min period, the number of lizards within a 5-m circumference of the tree was counted. All trials were conducted during morning hours (0900–1130 hours) when lizards were most active. Based on the lizard's strong response to movement (Whiting and Greeff 1997), we tested the a priori prediction that more lizards would be attracted to cages containing birds than to empty control cages, using a matched-pairs design (Wilcoxon signed-rank test, one tailed).

Fig trees and signal context

Finally, we tested whether lizards are attracted to bird congregations even when birds are not in trees. We placed cages containing birds and empty control cages on shelf rock away from *F. c. cordata* trees (at least 50 m). Four identical wire cages (0.9 × 0.9 × 0.9 m) were constructed, and locally caught birds, predominantly *P. nigricans* and *O. nabouroup*, were used in two cages, while the other two served as controls. Five birds/cage were used in five trials and six birds/cage were used in the remaining five trials. We conducted trials at ten locations, presenting caged birds versus empty control cages in alternate sequence. Differences in the number of lizards attracted to cages containing birds compared to empty control cages were assessed using a Wilcoxon signed-rank (matched pairs) test (two tailed).

All means are reported ± 1 SE. Differences were considered significant at $\alpha < 0.05$.

Results

Significantly (Wilcoxon, $Z = 2.28$, $P = 0.008$) more lizards were counted under fruiting trees (mean = 30.38 ± 17.3, 8.3–134) than non-fruiting trees (mean = 9.9 ± 5.1, 1.7–40) (Table 1). A total of 18 faecal pellets containing fig seeds were recovered for a mean distance of 120.0 ± 9.6 (57–187) m to the nearest fruiting fig tree. The mean number of lizards within 5 m of the cages (in trees) containing birds was significantly (Wilcoxon, $Z = 1.89$, $P = 0.03$; $n = 5$) greater than for empty control cages (Table 2). The stimulus created by bird activity was independent of context: significantly (Wilcoxon, $Z = 2.13$, $P = 0.02$; $n = 10$) more lizards were within 3 m of cages containing birds away from trees than from empty control cages in the same location (Table 3).

Discussion

P. broadleyi formed large aggregations under fig trees while figs were still available. During fruiting, insect abundance may increase, allowing for the possibility that lizards were attracted to a discrete prey patch rather than an available fruit crop. However, compared to foraging behaviour away from trees, lizards catch fewer insect prey, and spend more time actively searching debris for fallen figs (unpublished data). Also, interference competition is high, such that lizards frequently attempt to steal figs from other individuals (Whiting and Greeff 1997).

It is well known that lizards use visual cues (in addition to olfactory cues in some species) during foraging and may travel great distances to prey patches (Janzen and Brodie 1995; Whiting and Greeff 1997). The neotropical *Ctenosaura similis* travels unusually great distances (> 100 m) to flowering trees (references in Janzen and Brodie 1995). In fact, faecal pellets from *C. similis* suggest that individuals travel as much as 500 m (Travest 1989). The mean distance (114 m) of *P. broadleyi* faeces containing fig seeds from the nearest fig tree is a conservative measure of the distance lizards travelled to fruiting fig trees. During normal insectivorous foraging, lizards travel mean distances < 50 m (M.J.Whiting, unpublished data). Therefore, lizards exceeded normal foraging distances to feed on fig crops. Utilizing a cue to fruit availability eliminates the need for potentially expensive searching behaviour that in all probability (4.4% of trees were in fruit at the time of study) will be unsuccessful.

Table 1 Mean ± 1 SE and range (in parentheses) of the number of lizards counted under fruiting and non-fruiting fig trees. Fig trees 1–6 were sampled three times in both fruiting and non-fruiting phases, while tree 7 was sampled once in each phase. (Significantly more lizards under fruiting than non-fruiting trees: $P = 0.008$; see text)

Tree no.	Fruiting	Non-fruiting
1	17.67 ± 4.91 (9–26)	4.33 ± 0.67 (3–5)
2	14.00 ± 1.53 (1–16)	2.33 ± 1.86 (0–6)
3	11.00 ± 1.15 (9–13)	8.00 ± 0.58 (7–9)
4	18.00 ± 2.52 (13–21)	1.67 ± 1.20 (0–4)
5	8.33 ± 0.33 (8–9)	8.00 ± 1.53 (6–11)
6	9.67 ± 1.45 (7–12)	5.00 ± 1.73 (2–8)
7	134	40

Table 2 Mean ± 1 SE and range (in parentheses) of the number of lizards attracted to cages containing birds and empty control cages, set up as matched pairs. The experiment tested the hypothesis that lizards might use the presence of birds to locate fruiting Namaqua fig trees. (Significantly more lizards were attracted to cages with birds than to empty controls: $P = 0.03$; see text)

Cage with birds	Empty control cage
26.2 ± 3.02 (21–38)	3.4 ± 0.75 (2–6)
5.0 ± 0.89 (3–8)	1.8 ± 0.37 (1–3)
32.4 ± 2.54 (26–41)	14.4 ± 2.11 (10–20)
21.0 ± 0.84 (19–23)	10.4 ± 0.51 (9–12)
11.0 ± 1.58 (8–17)	6.8 ± 0.8 (5–9)

Table 3 Mean ± 1 SE and range (in parentheses) of lizards attracted to cages containing birds versus empty control cages, set up as matched pairs, to test if the presence of fig trees was necessary to draw lizards to bird congregations. (Significantly more lizards were attracted to cages with birds than to empty controls: $P = 0.02$; see text)

Cage with birds	Empty control cage
2.8 ± 0.92 (1–6)	0.2 ± 0.20 (0–1)
22.6 ± 4.93 (11–34)	5.2 ± 0.73 (3–7)
4.8 ± 1.91 (0–9)	0.4 ± 0.40 (0–2)
0.4 ± 0.40 (0–2)	0.0 ± 0.00 (0–0)
3.6 ± 1.33 (0–7)	2.8 ± 0.80 (1–5)
2.4 ± 0.68 (1–5)	1.2 ± 0.58 (0–3)
2.8 ± 0.73 (0–4)	1.6 ± 0.40 (1–3)
0.6 ± 0.24 (0–1)	1.5 ± 0.68 (0–4)
0.6 ± 0.40 (0–2)	0.2 ± 0.20 (0–1)
1.0 ± 0.00 (1–1)	1.0 ± 0.45 (0–2)

Regardless of whether a lizard locates a fruiting fig tree through a random event, or if it associates high bird activity with ripe figs, the pay-off (location of ripe fruit) is the same. We did not explicitly test if lizards were associating bird activity with fruiting trees. Previous observations and experiments have demonstrated that movement is a strong stimulus to *P. broadleyi* (Whiting and Greeff 1997). This may explain why individuals were also attracted to birds in cages away from trees. Caged birds continually flapped, suggesting that movement alone or in combination with another cue may attract lizards. *P. broadleyi* is also known to cue in on the behaviour of nearby conspecifics (Whiting and Greeff 1997), although this is more likely to be important for resource location at shorter (< 5 m) distances. Copying conspecifics may be rewarding when the food source is highly concentrated and not defendable, as figs beneath a tree. Therefore, a number of signals may all culminate in the high lizard concentrations at fruiting trees, but birds are likely to be the initial signal triggering the congregation.

We envision that the use of passive cues can have three evolutionary outcomes depending on the type of interaction between the emitter and the receiver. When both species benefit, as is the case in the honey-guide and human interaction, this signal system can become ritualized. When there is competition between species, one may expect the emitter to become more reluctant to send the signal. Even though the signal is passive at first, the emitter may adopt behaviours which reduce the possible extent of signal exploitation. Lastly, in cases with neutral interactions, the signal should remain unchanged.

In a rain forest in Gabon, Gautier-Hion and Michaloud (1989) found that figs were infrequently eaten because of their unpredictable fruiting patterns and low densities. Further, figs were generally eaten by wide-ranging animals, such as bats. Augrabies is similar because the available crop of ripe figs is low at any one time, and is also highly unpredictable. The figs do not appear to form a major component of the lizard's diet, but because of their energetic quality and the relatively high abundance at which they occur when a tree is in fruit, the pay-off for locating a fruiting tree is potentially high. By responding to an indirect cue that signifies resource availability, lizards are able to facultatively exploit *F. c. cordata* fruit crops. In so doing, they may avoid unnecessary energy expenditure and increased risk of predation imposed by random or systematic searching. Also, because fruiting trees are a spatially and temporally diffuse resource, such searching behaviour is likely to be futile.

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