SHORT COMMUNICATION

# Influence of prey encounter and prey identity on area-restricted searching in the lizard *Pedioplanis namaquensis*

**Douglas A. Eifler · Karabo Baipidi ·
Maria A. Eifler · Drew Dittmer · Luwi Nguluka**

**Abstract** We experimentally determined that the lizard *Pedioplanis namaquensis* engages in area-restricted searching (=ARS, localized searching after encounters with food) while foraging and that prey characteristics influence ARS. Single prey items were introduced to free-ranging lizards, and their subsequent search effort was characterized using first passage times (=FPT, time required for an animal to cross a circle of a given radius). Three prey types were used: termites, flies, and rice (control). FPTs were longer following termite encounters than following fly or control encounters. Control treatments produced no change in FPT, while lizards searching for termites showed the greatest change. The use by *Pedioplanis namaquensis* of ARS was most pronounced for the typically aggregated prey type.

**Keywords** Area-restricted search · First passage time · Foraging · Lizard · Prey distribution

## Introduction

Locating prey is sometimes the most difficult aspect of foraging; there can be strong incentives for adopting strategies that increase prey encounter rates. Foragers can attempt to increase prey encounter rates by adjusting their search behavior (O'Brien et al. 1990) or by biasing their search effort toward areas of higher prey density (Kareiva and Odell 1987; Farnsworth and Beecham 1999). Information concerning prey distributions can be used to increase prey encounter rates.

If predators combine information about prey distribution with recent foraging experience to refine foraging efforts, they can make informed decisions about whether continued searching in the immediate area is merited or likely to be counterproductive (Iwasa et al. 1981). Many animals engage in localized searching after encounters with food (=area-restricted searching or ARS; Wiens et al. 1997; Frair et al. 2005; Johnston et al. 2005; Dias et al. 2009). The advantage and use of ARS should be dependent on prey characteristics; ARS is most clearly warranted when prey are typically aggregated.

We tested for a relationship between prey distribution and predator searching in the lizard *Pedioplanis namaquensis* (Namaqua sand lizard). *Pedioplanis namaquensis* spends the majority of its foraging time actively searching for prey (Huey and Pianka 1981; Cooper and Whiting 1999), which is predominantly termites (Huey and Pianka 1981), a typically aggregated prey. We experimentally determined whether *P. namaquensis* engages in ARS in response to encounters with prey and whether prey characteristics (i.e., aggregated or solitary) influenced the use of ARS.

## Materials and methods

We studied area-restricted searching in *P. namaquensis* from 8 to 16 December 2009 on Masetlhaneng Pan

D. A. Eifler · K. Baipidi · L. Nguluka
Department of Biological Sciences, University of Botswana,
4775 Notwane Rd., Gaborone, Botswana

D. A. Eifler (✉) · M. A. Eifler
Erell Institute, 2808 Meadow Drive, Lawrence, KS 66047, USA
e-mail: deifler@erellinstitute.org

D. Dittmer
Department of Fisheries and Wildlife Sciences,
Texas A&M University, College Station, TX, USA

(23°41′20″S, 20°52′19″E), Kgalagadi District, Botswana. We prompted feeding events among active, free-ranging *P. namaquensis* by propelling prey items through a straw into their immediate vicinity, and documented the intensity of their search effort both before and after feeding events. We characterized localized search effort using the first-passage times (FPT) of active lizards. First-passage time is the time required for an animal to cross a circle of a given radius (Fauchald and Tveraa 2003); FPT can be used to study the location and scale of ARS (Pinaud and Weimerskirch 2005; Pinaud 2008; Hamer et al. 2009). Surface active foragers from a single *Hodotermes mossambicus* termite hole (our aggregated prey treatment) do not typically range further than 1 m (personal observation); we used a circle with a 1 m radius for determining FPT.

Trials were conducted on active lizards from 0900 to 1130 hours and from 1630 to 1800 hours. When we sighted a lizard, we waited at least 60 s before commencing data collection. We obtained a series of three FPTs (=pre-treatment), where the time required to leave a circle of 1 m radius centered on the lizard's initial position was recorded; we waited 60 s after each pre-treatment FPT before beginning the next. After the third pre-treatment FPT was obtained, we waited 60 s and then introduced either a termite worker (*Hodotermes mossambicus* = aggregated prey), a fly (Diptera spp. = solitary prey), or a grain of rice (control) by propelling it through a straw into the immediate vicinity of the lizard (typically <30 cm; =trial type). Once the lizard found and consumed the prey item, we determined an additional FPT (=post-treatment). On occasion, the lizard moved out of the vicinity of the prey without discovering it and we retrieved the prey and reintroduced it. For control trials, we started measuring FPT when the rice landed. After each trial was completed, we captured the lizard, then measured (snout-to-vent length, SVL), sexed, and individually marked it using a non-toxic paint pen before returning it to the site of capture. Each lizard was used only once and was randomly assigned to an experimental trial type. The two prey types used in trials were selected because they were similar-sized but different in aggregation tendencies, allowing us to assess whether lizard use of ARS depended on prey distribution. *Hodotermes mossambicus* is a social insect that forages during the day on the surface. Workers emerge from holes to forage, bringing vegetation back to their nest via the same hole. Small groups of workers are typically active in a local area, and finding one worker typically means that other foragers are nearby (Coaton 1963; Wilson and Clark 1977). The flies were chosen as a second prey type because, prior to our study, we observed that lizards were attentive to fly activity, but flies seemed to be neither abundant nor spatially clumped. When collecting flies for trials, we never observed flies close together, as we did termites. Thus, they represent a comparable reward to termites, without the expectation that additional prey should be nearby. The live prey used for presentations were freshly caught on the study site each day. The flies used in trials had their wings trimmed so that they were mobile but unable to use flight to escape the lizards.

The three pre-treatment FPTs for each lizard were averaged to produce a single pre-treatment FPT value. Comparisons among trial types were done using pre-treatment values, post-treatment values, and the change in FPT, which was calculated for each lizard as the difference between their post- and mean pre-treatment FPT value. Unless otherwise stated, we used one-tailed tests based on the prediction that post-treatment FPTs would rank control < fly < termite, and that only fly and termite trials might be associated with ARS. This ranking and the use of one-tailed tests was appropriate because (1) ARS would only be expected for prey items (control < prey), (2) we predicted more extreme ARS for more aggregated prey (fly < termite, see prey descriptions above), and (3) casual observations, outside the study, suggested that *P. namaquensis* searched intensively upon finding areas of termite activity, but its interactions with flies were primarily characterized as simple lunges. All statistical analyses were performed using Minitab 13 (College Park, PA, USA) with a significance level of $P \leq 0.05$. We initially examined the effect of trial type, body size, and gender on FPT with a General Linear Model, and then assessed the effect of trial type on FPT with Kruskall–Wallis tests; we used Dunn's test to determine whether significant changes in FPT occurred within treatment.

## Results

Sixty-nine lizards were observed during the course of the study (26 control, 17 fly, and 26 termite). During pre-treatment trials, there were no significant effects of trial type, SVL, or gender on FPT (General Linear Model: $F_{2,60} = 1.12$, $P = 0.333$; $F_{1,61} = 0.46$, $P = 0.391$; and $F_{1,61} = 0.75$, $P = 0.391$, respectively), nor were there any differences among the trial types in average pre-treatment FPT values (Kruskal–Wallis: $H = 3.56$, $df = 2$, $P = 0.168$; Table 1). During post-treatment trials, trial type significantly influenced FPTs (General Linear Model: $F_{2,60} = 4.80$, $P = 0.012$), but SVL did not ($F_{1,61} = 1.29$, $P = 0.26$), and gender had a slight effect, with females having slightly longer FPTs than males ($F_{1,61} = 4.33$, $P = 0.042$). There was significant variation among trial types in the post-treatment FPT (Kruskal–Wallis: $H = 10.36$, $df = 2$, $P = 0.006$; Table 1), with no significant difference in the FPT for control versus fly but with termite FPT significantly longer than either control or fly FPTs.

**Table 1** First-passage times (s) for 1-m radius areas prior to (pre) and after (post) presentation of experimental prey or control to the lizard *Pedioplanis namaquensis*

| Measure | Trial type | | |
| --- | --- | --- | --- |
| | Control | Fly | Termite |
| Pre-treatment | 11.5 (6.0–99.6) | 8.6 (2.6–39.3) | 11.0 (3.3–65.6) |
| Post-treatment | 13.5 a (3.0–50.0) | 19.0 a (5.0–19.0) | 34.0 b (5.0–221) |
| Change (post–pre) | 2.5 a (−63.6 to 40.6) | 10.3 b (−13.6 to 83.0) | 18.8 c (−44.6 to 204.0) |

Change values represent the difference in first-passage times between post- and pre-treatment. Values are presented as median (range). Pre-treatment values represent the average of each individual's 3 pre-treatment first-passage times. Different letters within a row indicate significant differences

The change in FPT from pre- to post-treatment was significantly different among trial types with each trial type being significantly different from the other two ($H = 11.47$, $df = 2$, $P = 0.003$; Table 1); the largest change in FPT was for lizards searching for termites. The change in FPT for controls was not significantly different from zero (Wilcoxon 2-tailed: $W = 199.5$, $n = 26$, $P = 0.551$), but both the fly and termite trials showed a significant increase in FPT (fly: $W = 127.0$, $n = 17$, $P = 0.009$; termite: $W = 313.0$, $n = 26$, $P < 0.001$).

## Discussion

*Pedioplanis namaquensis* uses ARS while foraging, and the use of ARS was most pronounced for the prey type that was typically aggregated. Lizards have longer FPT after feeding on a termite than when encountering either flies or controls. In terms of changes in FPT, capturing food leads to an increase in FPT and capturing a termite leads to the greatest increase in FPT. Using ARS is consistent with using prey dispersion patterns to guide foraging decisions. Lizards looking for termites should remain close to where one was found, and, in fact, lizards finding termites display FPT approximately three times longer than pre-treatment FPT. By contrast, the flies that we used for feeding trials are not abundant, and finding one does not necessarily result in encountering another nearby (personal observation); FPTs were still more than twice as long after encountering a fly as FPTs before prey encounters, even though from the observer's perspective ARS was less justified for flies. Prey encounters do not always lead to ARS (Weimerskirch et al. 2007; Hamer et al. 2009); nonetheless, finding one prey item means that a forager is in the right microhabitat for that prey type and some additional searching may be warranted. A variety of factors could influence a forager's response to different prey types (Perry and Pianka 1997); most of these, such as predation risk or habitat structure, were beyond the scope of our brief study. Our observed differences in response between termite and fly trials are consistent with expectations based on the distribution patterns associated with the two prey types. Thus, the capture of prey elicits ARS in *P. namaquensis*, but the extent of the restricted searching depends on the nature of the prey. In a laboratory study, the ant *Palto-thyreus tarsatus*, which naturally hunts extensively for termites, will use ARS after encounters with a single termite while comparable interactions with similar-sized beetle larvae do not lead to ARS (Déjean et al. 1993). More generally, our results are consistent with laboratory studies where foragers learn the distribution of food and adjust ARS based on food characteristics (Zach and Falls 1977; Haskell 1997; Hill et al. 2002). The extent to which free-ranging foragers rely on information about prey characteristics to adjust search behavior needs broader investigation.

Among the predicted mechanisms leading to ARS are reduced search speeds and increased turning to keep foragers in areas of prey abundance (Kareiva and Odell 1987). Our general impression was that movements subsequent to feeding included more "zig-zag" paths; however, this needs to be subjected to more focused study. Likewise, changes to foraging behavior may also take place on larger scales (Pinaud and Weimerskirch 2005; Hamer et al. 2009). One meter is a reasonable distance for determining FPT since the workers associated with a single *H. mossambicus* foraging hole rarely travel further than 1 m (personal observation). However, colonies may be spread over hundreds of square meters underground (Coaton 1963; Wilson and Clark 1977) and, just as encountering a single worker may indicate something about the location of other workers, a single foraging hole may be indicative of other foraging holes active nearby. Further work using multiple scales of response is needed to evaluate whether foragers use information at multiple levels when assessing prey distribution.

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