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FORAGING-MODE PLASTICITY IN THE LIZARD *PLATYSAURUS BROADLEYI*

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ABSTRACT: Lizards are not widely regarded as able to alter their foraging mode substantially in relation to the specific food source utilized. Rather, their foraging mode determines the food type that they utilize. We studied *Platysaurus broadleyi*, a lizard that utilizes food resources differing in several fundamental characteristics. We found that they maintain this broad feeding niche by altering their foraging behavior. Adult lizards ambushed mobile insects but searched actively when feeding on stationary figs beneath trees. This flexibility in foraging behavior allowed *P. broadleyi* to utilize figs, a high energy but ephemeral resource. Lizards did not vary their foraging mode in response to insect-prey density, but attack distances were further at the site with lower insect density, as predicted by optimal foraging theory. Juveniles adopted an intermediate foraging mode irrespective of the resource utilized.

Key words: Foraging mode; Plasticity; Cordylidae; Herbivory; Ambush foraging; *Ficus*

HISTORICALLY, insectivorous lizards are divided into active (or wide) and ambush (or sit-and-wait) foragers (Perry and Pianka, 1997). Typical active foragers move through their habitat in search of stationary and often hidden prey, whereas ambush foragers wait motionlessly and catch passing prey (Huey and Pianka, 1981). Perry (1999) found that this division is artificial and that there is a continuum of modes between extreme ambush and active foraging modes. However, because adaptations for efficiency in catching and consuming one food type represent trade offs against efficiency of utilizing alternative prey resources, a lizard's morphology and physiology should constrain it to a specific foraging mode. This results in an evolutionarily inflexibility which is reflected in some entire families of lizard utilizing a single mode (Cooper, 1995; Cooper et al., 1997; Perry 1999). There is some evidence that foraging mode is associated with a host of coevolved traits (Huey and Pianka, 1981; McLaughlin, 1989); more actively foraging lizards tend to have more slender morphologies (Losos, 1990; Vitt and Congdon, 1978), higher metabolic rates (Anderson and Karasov, 1981; Belliure et al., 1996; Vitt and Morato de Carvalho, 1995), and their clutch masses are relatively lower (Magnusson et al., 1985; Vitt and Congdon, 1978) than most ambush foragers. Typical active foragers rely on chemoreception as well as visual cues to locate prey, whereas typical ambush foragers use visual cues only (Cooper, 1995, 1997; Cooper and van Wyk, 1994; Evans, 1961). Also, active foragers tend to escape predators by fleeing, whereas ambush foragers rely on crypsis (Cooper et al., 1990; Vitt and Price, 1982). Similar associations between life history traits and foraging mode can be found in other taxa (flat worms: Calow and Woollhead, 1977; frogs: Toft, 1980).

Unlike insectivorous species, little attention has been given to the exact mode of foraging in herbivores. Durtsche (1992) and Rand (1978) argued that herbivores should employ ambush-like strategies. However, because plant material is by nature immobile and clumped in space, a strategy more akin to active foraging should be most apt for plants (Cooper and Alberts, 1990). A few studies have indeed found herbivores to employ very active forging behaviors (Brown, 1991; Cooper and Alberts, 1990; Krekorian, 1989), and Cooper (1994) defined it as a herbivorous foraging mode.

In a few species, foraging mode varied so much that it touched both extremes (Auffenburg, 1978, 1981; Cooper and Whiting, in press; Lister and Garcia Aguayo, 1992; Robinson, 1978; personal communication from M. D. Robinson; Schluter, 1984; Taylor, 1986). Given the apparent stability of foraging modes in lizards, it is intriguing to ask what factors lead to facultative alterations in the foraging mode. One possible important proximal factor that would facilitate foraging mode alterations is when a variety of food items are utilized opportunistically. The Augrabies flat lizard, *Platysaurus broadleyi* [formerly *Platysaurus capensis* (Branch and Whiting, 1997)] typically feeds on winged insects (Cooper et al., 1997) but also eats the fallen figs of *Ficus cordata cordata* (Whiting and Greeff, 1997) and is thus a suitable subject for a study of variation in foraging mode.

Platysaurus broadleyi is in a lineage (Cordylidae) that has most likely adopted an ambush type foraging mode secondarily (Cooper et al., 1997). Cooper et al. (1997) found a large degree of variation in foraging mode between individuals of *Platysaurus broadleyi.* Although a large mass of fruit accumulates underneath fruiting trees, lizards utilize only freshly fallen ripe figs, rejecting hard desiccated ones (Whiting and Greeff, 1997). Hence, because figs are clumped in space and stationary, they are more akin to food resources utilized by active foragers (Huey and Bennett, 1986; Huey and Pianka, 1981; Johnson and Crowley, 1980).

We investigated whether adults and juveniles of *P. broadleyi* alter their foraging behavior to accommodate the broad spectrum of food types that they utilize. Because lizards have been found to increase their foraging velocity as prey density increases (Huey and Pianka, 1981; Lister and Garcia Aguayo, 1992; Pietruszka, 1986), we also investigated the effect of insect density on foraging behavior. We address these issues by quantifying lizard foraging behavior in three microhabitats with different prey densities and characteristics: fruit, high insect availability, and low insect availability. We predicted that lizards should forage most actively when feeding on figs and be the most ambush-like when foraging at the insect sites.

MATERIALS AND METHODS

Study Area

Field work was conducted at Augrabies Falls National Park (28° 35′ S, 20° 20′ E), Northern Cape Province, South Africa, during April 1996. Lizards are not reproductively active during this period and therefore sexual interactions do not affect the foraging behavior (personal observations). The area is arid and warm and the habitat consists of continuous granite sheets and boulders flanking the Orange river (Branch and Whiting, 1997). Dotted along the rocky banks of the river are Namaqua fig trees (*Ficus cordata cordata*). Apart from the fig trees, the rocky banks are largely devoid of other vegetation. The lizards inhabit crevices close to the river, where they feed mainly on recently emerged flying black flies (Branch and Whiting, 1997). A more detailed description of the general study area can be found in Branch and Whiting (1997) and Whiting and Greeff (1997). We observed the lizards at three sites: an insect rich site, an insect poor site, and underneath a fig tree. Briefly, the insect poor site (hereafter Poor Site) was a rocky area adjacent to the Orange River gorge (>100 m from the river, vertical distance). There were a few fig trees nearby, but none in fruit. The insect rich site (hereafter Rich Site) had no fig trees in the immediate area and consisted largely of exposed granite forming the western bank of the Orange River. Boulders and crevices allowed lizards to seek shade and conceal themselves from predators. The third site was on granite slabs underneath and around a fruiting fig tree (hereafter Fig Site). Apart from searching for figs on the slabs, the lizards also entered a small layer of debris beneath the tree. The fig and rich sites were >100 m apart, while the poor site was >1 km from the fig site, the nearer of the two easterly sites.

Foraging Mode

To quantify foraging mode, 10-min focal observations were performed on males, females, and juveniles (<50 mm SVL). Lizards sometimes disappeared from view before 10 min; we only used focal samples exceeding 3 min. Focal samples had a mean duration of 543.6 s (±8.98, 1 SE). Of the 148 focal samples, 63.5% ($n = 94$) were for the full duration, whereas only 4.7% ($n = 7$) were for <5 min. Insect densities were not quantified, but at the rich site, black flies occurred in plumes that allowed lizards to catch them continuously, whereas singular passing insects were preyed upon at the poor site. Few juveniles were present at the rich site, and we did not collect data on them. Observations were made during peak activity (prior to 1100 h). To avoid sampling the same lizard twice, observations were made on the same day for each age group, and in different areas. All prey capture attempts, successful prey captures, and movements >10 cm were noted. Because we could not always distinguish prey captures from prey capture attempts, we used the latter for statistical purposes. Observations were recorded on a dictaphone and transcribed later. From the data, we extracted the number of prey capture attempts per minute, number of moves per minute (MPM), the percentage time spent moving (PTM), and the distances of attack at the rich and poor sites. Time spent on social interactions and thermoregulation was excluded from analysis.

Data Analyses

We used Mann-Whitney *U*-tests (two-tailed) to test for differences in prey capture attempt rates. The assumptions of homogenous variances and normal distributions in MPM and PTM data could not be met despite transformations. Therefore, we analyzed the data for males, females, and juveniles separately using Kruskall-Wallis tests. When significant differences were detected, we made post-hoc comparisons using SATISTIX (Analytical Software, 1996).

RESULTS

The rate of prey capture attempts did not differ between the sexes at the two insect-feeding sites (Poor Site: Mann-Whitney $U_{22,15} = 151$, $P = 0.62$; Rich Site 2: $U_{21,20} = 164$, $P = 0.23$). Therefore, the sexes were combined. Adult lizards at the Rich Site attempted to capture insects more often than at the Poor Site (Mann-Whitney $U_{37,41} = 70$, $P < 0.001$: Table 1). At the Fig Site, adults ($n = 28$) specialized in fig feeding: only five caught some insects whereas 22 ate figs (Table 1). Juveniles differed from adults in that half the Fig Site animals consumed some insects. Further, juveniles ate many ants and also individual fig seeds. Adults were not observed to eat either of these. When only considering the attempted captures of insects, juveniles made more prey capture attempts at the Poor Site than at the Fig Site (Mann-Whitney $U_{23,16} = 64$, $P = 0.0006$). However, when fig items consumed were added to the attempted captures of insects, Fig Site juveniles obtained more food items (Mann-Whitney $U_{23,16} = 68.5$, $P = 0.001$).

TABLE 1.—Number of prey capture attempts per minute directed at insects, and the average number of figs or fig parts consumed per minute at the Fig Site.

Locality	Age class	n	Mean (±1 SE)
Poor Site	Males	22	0.07 (0.02)
	Females	15	0.09 (0.04)
	Juveniles	23	0.034 (0.07)
Rich Site	Males	21	3.53 (0.12)
	Females	20	2.44 (0.42)
Fig Site			
figs:	Males	12	0.12 (0.04)
	Females	16	0.30 (0.06)
	Juveniles	16	0.66 (0.11)
insects:	Males	12	0.05 (0.02)
	Females	16	0.02 (0.02)
	Juveniles	16	0.10 (0.03)

Descriptive statistics for MPM and PTM are given in Table 2. Kruskall-Wallis tests showed that there were significant differences in MPM and PTM at the different sites in males and females, but not in juveniles (Table 3). Post-hoc multiple comparisons showed that males and females at the Fig Site were significantly different from the insect sites ($P < 0.05$). Unlike adults, juveniles did not differ significantly between the feeding sites. Regardless of the feeding site, juveniles adopted

TABLE 2.—Sample sizes (*n*) and means (±1 SE) for PTM and MPM at the three localities for adult males and females, and for juveniles.

Locality	Sex/age	*n*	MPM	PTM
Poor Site	Male	22	0.72 (0.02)	4.87 (1.08)
	Female	15	0.78 (0.26)	2.48 (0.67)
	Juvenile	23	1.54 (0.18)	9.55 (1.43)
Rich Site	Male	21	0.74 (0.12)	4.42 (0.62)
	Female	20	0.91 (0.09)	5.14 (0.54)
Fig Site	Male	12	1.49 (0.19)	13.26 (2.58)
	Female	16	2.21 (0.18)	17.20 (2.07)
	Juvenile	16	1.62 (0.15)	9.88 (1.85)

a more active foraging behavior than that of a typical ambusher.

Males and females attacked prey over significantly longer distances at the Poor Site than at the Rich Site (respectively: Mann-Whitney test: $U_{22,21} = 23.0$, $P < 0.0001$; $U_{15,20} = 24$, $P < 0.001$; Table 4)

DISCUSSION

Adults of *Platysaurus broadleyi* adjusted their foraging behavior to the type of resource utilized. Males and females feeding on figs moved more frequently and spent more time moving than insect-feeding lizards, regardless of the insect density. In other words, lizards adopted a more active foraging mode and moved through the habitat to locate edible fruits. Observations that adults made significantly more prey capture attempts at the Rich Site than at the Poor Site, despite using the same foraging strategy, support our classification of the two areas as being insect-rich and insect-poor sites.

To emphasize the marked changes in foraging parameters between fig and insect-feeding, it is useful to pin the data to the traditional bimodal framework. When feeding on insects, adult lizards used a typical ambush strategy. When feeding on figs, their MPM was as high as that of some lizards considered active foragers. PTM was, despite the approximately fourfold increase, still below figures for most active foragers (Cooper and Whiting, in press). This difference in PTM and MPM is in agreement with Cooper et al. (1997) who found that *P. broadleyi* makes many short movements of low duration.

TABLE 3.—A comparison of MPM and PTM for the three sites (two sites in juveniles) using Kruskal-Wallis tests.

	MPM		PTM	
Group	*H*	*P*	*H*	*P*
Males	11.21	0.0037	10.52	0.0052
Females	25.88	<0.0001	27.43	<0.0001
Juveniles	0.059	0.808	0.007	0.932

The difference in attack distances at the two insect feeding sites can have two possible explanations. First, prey may have been so abundant at the high-density site that no movement was required from adults. Second, and more interesting, lizards at the high-density site may be more satiated and hence have a lower motivation to attack prey that are further away (Shafir and Roughgarden, 1998).

The foraging plasticity of *P. broadleyi* is further evidence against the long-standing emphasis on two discrete foraging modes. Does this plasticity bring into doubt the arguments for a close fit between foraging behavior and other life history parameters? More phylogenetic information is required to answer this question. However, the switch to eating figs does not require many novel behavioral patterns. Typical of ambush-like foragers, the lizards use sight to locate ripe fruits (Whiting and Greeff, 1997) rather than employing chemoreception.

Unlike adults, juvenile feeding behavior did not differ between the fig and poor sites. This may be because they are more opportunistic feeders than adults, as is reflected by their frequent consumption of insects at the Fig Site. This may result from selection of small prey items such as ants, which are relatively abundant, but are not eaten by adults.

TABLE 4.—Attack distances (in cm) of males and females at site 1 and 2. Means were calculated as the average of the mean attack distance of *n* lizards.

Sex	Locality	*n*	Mean (±1 SE)
Males	Poor Site	8	65.6 (26.6)
	Rich Site	22	6.1 (1.1)
Females	Poor Site	7	21.3 (10.1)
	Rich Site	19	7.4 (2.4)

Differences in foraging behavior between the three sites may be due to factors other than prey type and availability. The following factors may affect lizard foraging behavior: (1) thermal environment, (2) physical environment (habitat structure), and (3) risk of predation. We can discount differences in the thermal environment because all sites had ample shade, precluding any thermal stress that may influence foraging behavior at a particular site. Although an obvious structural difference between the three sites is the presence of a large fig tree at the Fig Site, the sites shared many habitat features. All sites were characterized by granite bedrock and a general lack of vegetation. Also, there were fig trees near the poor site, but these were not in fruit. The influence of predation risk on foraging behavior is more difficult to evaluate. Crevices and boulders offered similar opportunities for escape from predation at all three sites. Predation risk for a lizard under a fig tree may differ from that of a lizard foraging on exposed rock, but we did not detect any obvious behavioral differences that may be related to predation risk. Because the work was performed when the lizards were not sexually active, we feel that differences between males and females in time allocation budgets (Perry, 1996; Parmelee and Guyer, 1995) did not confound our results either.

The foraging plasticity displayed by individuals of *P. broadleyi* allows them to use a wide range of resources efficiently by matching their foraging behavior to the resource. The high rate at which lizards were able to locate and consume ripe figs (Whiting and Greeff, 1997), combined with the high energy (Greeff and Whiting, 1999) and water (Compton et al., 1996) content of figs, suggest a substantial benefit to lizards in this dry desert terrain.

Platysaurus broadleyi not only alter its foraging mode to utilize figs but also uses birds as heterospecific cues to locate fruiting fig trees (Whiting and Greeff, 1999). We therefore concur with Shafir and Roughgarden (1998) that lizards are adept at solving foraging problems, and are excellent models for testing optimal foraging theory.

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