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Facultative Frugivory in the Cape Flat Lizard, *Platysaurus capensis* (Sauria: Cordylidae)

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***Platysaurus capensis* is an omnivorous lizard that feeds on Namaqua figs (*Ficus cordata*) when they are available. We studied fig-feeding behavior of male, female, and juvenile lizards at Augrabies Falls National Park, South Africa. Figs were available in three discrete classes depending on their state of hydration/ripeness. Focal sampling and feeding trials were used to quantify fig handling and feeding behavior. Adult *P. capensis* usually ate the entire fig, but handling times were significantly shorter for males than females. Adults frequently used the rock substrate to break figs, whereas juveniles could only eat figs already broken. (Figs were often broken open by birds and other lizards.) Juveniles usually ate only part of each fig, often just the seeds. Juveniles also used a head-shaking behavior rarely seen in adults, to break off manageable pieces of figs. *Platysaurus capensis* recognized figs away from fig trees, indicating a flexible recognition ability. During foraging in debris, lizards stayed close to exposed rock. Interference competition between lizards was strong, resulting in individuals running to areas free of other lizards to avoid harassment during feeding. Adults were more likely to approach feeding lizards than juveniles. Lizards also exhibited a strong sensory bias for moving objects, selecting moving unripe (inedible) figs over stationary ripe figs. Adult lizards chose large ripe figs over two classes of older, more desiccated figs; ripe figs were consumed disproportionately to their availability. Experiments using paint-manipulated ripe and unripe figs showed that, when size is controlled, lizards use color and/or brightness as an initial indicator of fig quality. Visual evaluation was often followed by tongue-flicking or nudging with the snout. This study represents the first detailed examination of feeding behavior in a cordylid lizard.**

LIZARD dietary studies have blossomed in the last 15 years, providing important basic natural history data for many species (e.g., Schoener et al., 1982; Pianka, 1986; Durtsche, 1995). These studies have also provided insights into fundamental ecological issues such as resource partitioning and community ecology (Pianka, 1980; Winemiller and Pianka, 1990; James, 1991); the relationship between foraging mode and morphology, energetics, predation, and reproductive tactics (Anderson and Karasov, 1981, 1988; Huey and Pianka, 1981); as well as prey chemical discrimination and phylogeny (Cooper, 1994, 1995). However, most analyses of lizard foraging and feeding behavior have concentrated on insectivorous lizards. Diets and foraging behavior in many lizards are plastic and may depend on a variety of factors, such as local and seasonal abundance of food resources (Ballinger and Ballinger, 1979; Anderson, 1994; Durtsche, 1995). Dietary plasticity is potentially greatest in omnivorous lizards because resource switching may occur depending on food availability (unpubl. data). Although studies of herbivory (*sensu lato*) in lizards are increasing, few data exist on actual feeding behavior.

Platysaurus capensis is a relatively small (adult snout–vent length [SVL] range: 64–84 mm) cordylid lizard restricted to rocky outcrops in northwest South Africa and southern Namibia (Broadley, 1978; Branch, 1988). Little is known about its ecology although van Wyk and Mouton (1996) recently described the reproductive cycle. Males and females are sexually dimorphic for coloration (Broadley, 1978) and body size (MJW, unpubl.). No published information exists on diet or feeding behavior in this species.

Platysaurus capensis is most abundant along the rocky margins bordering the Orange River. In this rocky terrain, the dominant tree (often the only tree) is the Namaqua fig (*Ficus cordata cordata*), which is relatively sparsely distributed (approximately 2–5 individuals/1000 m^2 in the study area). A thin layer of debris consisting of twigs, leaves, and figs frequently accumulates under trees. Like other fig trees (Berg and Wiebes, 1992), *F. c. cordata* is a sporadic fruiter, resulting in trees that fruit asynchronously of each other but synchronously within a single tree. Our preliminary field observations showed that *P. capensis* is largely insectivorous but feeds on ripe figs when available. Because of the spatial and temporal variability of fruiting *F. c. cordata* trees, figs were an unpredictable resource. The exploitation of *F. c. cordata* figs by *P. capensis* was thus ideal for a study of facultative frugivory. Furthermore, the figs differ from the lizards' normal insect prey in several important ways. At Augrabies, their primary prey are black flies (*Simulium* spp.; pers. obs.), which are small (approximately 2 mm), mobile, and aerial compared with figs, which are much larger, normally stationary, and occur on the ground. Therefore, use of figs as a resource will differ to that of insects. The purpose of this study was to evaluate fig-feeding behavior in *P. capensis*, with regard to the environmental and social contexts of fig-feeding, as well as the selection and handling of figs by different age/sex classes.

MATERIALS AND METHODS

All observations and experiments were conducted during April and May 1996 at Augrabies Falls National Park (28°35'S, 20°20'E; hereafter AFNP), Northern Cape Province, South Africa. AFNP is xeric, but the dryness is ameliorated by the Orange River which not only provides moisture for the lizard's insect prey but also provides a medium in which their primary prey (*Simulium* spp.) breeds. Consequently, lizards often aggregate along the rocky banks of the river to feed on emerging *Simulium* (pers. obs.).

We collected a sample of figs available to lizards on the ground and grouped them into ripe red (RR), shriveled red (SR), and hard brown (HB) categories, which corresponded with moisture content in the order RR > SR > HB. A further fig category, unripe hard white (HW), was sometimes available to lizards when either birds (primarily *Onychognathus nabouroup* and *Pycnonotus nigricans*) or primates (*Papio ursinus* or *Cercopithecus aethiops*) broke them off trees. HW abundance was not measured, but HW figs were used in trials 4 and 7 below. There was no detectable difference in color between RR and SR. In independent tests, both investigators agreed 100% on fig categorization in 30 trials (one fig/trial). We measured the availability of RR, SR, and HB figs under the tree at five sampling points using a 1-m^2 grid. Differences in location and availability among the three classes were examined using a chi-square test.

Fig feeding behavior was characterized for different age/sex classes using 10-min focal sampling (Martin and Bateson, 1993). During focal sampling, we characterized fig handling behavior and behavioral interactions for males, females, and juveniles (juvenile SVL 3–4.5 cm). These behaviors were timed and recorded on microcassette recorders. Focal animals sometimes disappeared from view before 10 min; only animals that were observed for at least 3 min were used in analyses (n = 11 males, 17 females, 17 juveniles). Focal samples had a mean duration of 522.53 ± 18.29 sec (range: 183–600). Of the 45 focal samples, 60% (n = 27) were for the full duration, whereas only 6.7% (n = 3) were for less than five min. There was no evidence that focal samples of less than 10 min affected our results. To reduce the likelihood of nonindependence, focal sampling was carried out in different areas, and on a specific day, only one sex was observed by both investigators. Differences among age/sex classes in the number of figs sampled/min and the number of fig seeds sampled/min were assessed with Mann-Whitney tests using the normal approximation with continuity correction.

To further characterize fig handling between different age and sex groups, handling time and feeding behavior were recorded for lizards fed ripe figs in the field. Prior to trials, a random sample of figs was allocated to each age and sex group, and the long axis of each fig was measured using digital calipers. Differences in handling time between males and females were tested by a Mann-Whitney test using the normal approximation with continuity correction. Significance of differences in the percentage of figs eaten was tested using a chi-square test. Differences in the frequency of specific feeding behaviors among sex and age classes were evaluated using chi-square and Fisher's exact tests. Juvenile handling of broken versus complete figs was also evaluated during feeding trials (n = 19 broken, 18 complete), and differences were assessed using a chi-square test.

Based on field and 10-min focal samples, seven null hypotheses on feeding behavior were erected and tested experimentally. Data from focal sampling were also used to complement hypothesis 7. Null hypotheses that were tested are as follows.

Hypothesis 1.—A fig tree is a necessary context for fig recognition. Ten ripe figs were placed in a group with a circumference of about 30 cm, on the ground away from trees (at least 40 m), and the responses of lizards encountering figs was recorded. The experiment was replicated twice.

Hypothesis 2.—During foraging in debris, lizards are equally likely to forage close to the rock-debris interface and deep (away from rock) in debris. We set up five 1-m^2 grids along the rock-debris interface so that the entire grid was in debris with one side bordering exposed rock and five directly behind so that the grids shared a common side. Grids were then surveyed once for lizards. Differences in lizard abundance were tested using a chi-square test.

Hypothesis 3.—On locating a fig, an individual foraging in the presence of other lizards will pick up the fig and run the same distance as a solitary lizard before feeding. We discreetly rolled figs to lizards in a group ($n = 26$) and to solitary lizards ($n = 20$) and then measured the distance (cm) each lizard ran before feeding. A group was loosely defined as three or more lizards, each with a nearest neighbor distance of at most 1 m. Each lizard was tested only once. Difference in flight distance was assessed for significance by a Mann-Whitney test using the normal approximation with continuity correction. Further information on intraspecific interactions during feeding was obtained from focal sampling. We recorded when a focal animal attempted to take a fig from another lizard or when another lizard attempted to take a fig from a focal animal. A chi-square test was used to assess the significance of differences in the success rate of fig stealing between age and sex classes.

Hypothesis 4.—Lizards respond to a moving fig regardless of color/brightness or ripeness. We threw HW ($n = 21$) and RR ($n = 20$) figs to individual lizards. Difference in response was evaluated using a chi-square test.

Hypothesis 5.—Given a choice between stationary ripe figs on the ground and a moving ripe fig, lizards will select the two equally. Ripe figs were thrown near lizards that already had one or more ripe figs on the ground within about 15 cm in front of them ($n = 25$). Difference in choice was evaluated using a chi-square test.

Hypothesis 6.—Lizards choose figs on the ground randomly, without regard to color or size. Three groups, comprising 15 figs of each category (RR, SR, and HB) were randomly drawn from a bag. The longest axis of each fig was measured using digital calipers. The figs from each group were then mixed in a separate bag, by shaking, and placed in the field in a circle with a diameter of about 30 cm, before the lizard activity period. Once the lizards became active, their behaviors were noted during a 20-min interval. (Twenty minutes allowed an adequate number of lizards to sample figs for statistical resolution.) The remaining figs were scored. Difference in fig consumption among the three categories was tested using a chi-square test. There were no location effects because the groups were only 5 m or 10 m apart, and the three groups were therefore combined for statistical analysis. Fig size differences among color and ripeness categories were assessed for significance using ANOVA. Pairwise comparisons were made using Scheffé F-tests.

Hypothesis 7.—When size is controlled, lizards will select figs randomly with respect to color and/or brightness. We measured HW ($n = 45$) and RR ($n = 45$) figs to ensure that no significant size difference existed ($t_{88} = -1.20$, $P = 0.11$; two-tailed). HW ($n = 15$) were painted red, and RR ($n = 15$) were painted white in a close approximation to natural color, using nontoxic water colors (Pelikan®). A group containing randomly assigned painted figs and unpainted controls was placed in a random group of roughly 20 cm circumference on the ground (15 figs from each of the four groups). We noted which fig type was sampled first by a lizard (tongue-flicked or nudged), as well as the time each fig was eaten. To be conservative, if a lizard picked up and removed a fig without first sampling it, it was not scored as being sampled. Trials lasted 35 min, which allowed a sufficient number of lizards to sample figs for statistical resolution. To determine the expected number of figs sampled under the null hypothesis, we adjusted the probabilities every time a fig was eaten. After a fig was removed, the probability of sampling each fig type at random was calculated, and the overall expected sampling probabilities were then calculated as the mean of these probabilities. A chi-square test was used to assess the effect of paint on choice, whether overall sampling was random, and whether red (painted and unpainted) and white (painted and unpainted) figs were sampled equally.

All data were tested for homogeneity of variance (Bartlett's Test) and normality (rankit method) before application of parametric statistics. Data were analyzed using STATISTIX (Analytical Software, Saint Paul, MN, 1990). Differences were considered significant when alpha was < 0.05. All tests were two-tailed unless otherwise stated. Means are presented ± 1 SE. All statistical procedures follow Sokal and Rohlf (1984).

RESULTS

The three classes of fig were significantly different in size (ANOVA, $F_{2,124} = 72.9$, $P < 0.0001$; Table 1). RR were larger than both SR and HB (Scheffé F = 3.07, $P < 0.05$), which were not significantly different in size ($P > 0.05$). Fig availability differed among sampling points (χ^2_8

Table 1. Descriptive Statistics of Fig Class Measurements (mm).

	n	$\bar{x} \pm$ SE	Range
Red ripe (RR)	45	7.28 (0.07)	6.39–8.33
Hard white (HW)	45	7.41 (0.08)	6.18–9.14
Shriveled red (SR)	42	6.14 (0.07)	4.98–7.16
Hard brown (HB)	40	6.17 (0.09)	4.95–7.31

= 106.38, $P < 0.0001$; Table 2); this was also true when only RR availability was compared ($\chi^2_4 = 73.74$, $P < 0.0001$). Pairwise comparisons of the three classes of naturally available figs (RR, SR, HB) revealed that they were significantly more available in the order SR > HB > RR (χ^2, $P < 0.001$ in each case; Table 2).

Males and females (from focal sampling) did not sample a significantly different number of figs/min (Mann-Whitney $Z = 0.71$, $P = 0.48$; Table 3). Therefore, males and females were combined. Pooled adults sampled more figs/min than juveniles (Mann-Whitney $Z = 3.65$, $P < 0.0003$; Table 3). Juveniles were frequently observed feeding on individual fig seeds from broken figs, as well as fragments of figs. Juveniles sampled significantly more fig seeds/min than did adults (juveniles: n = 17, $\bar{x} = 0.46 \pm 0.1$, 0–1.3; adults: n = 28, $\bar{x} = 0.01 \pm 0.008$, 0–0.2; Mann-Whitney $Z = 4.11$, $P < 0.0001$).

The figs used in handling trials differed significantly in mean size among age/sex classes (ANOVA, $F_{2,106} = 11.35$, $P < 0.001$; Table 4). Figs fed to juveniles were slightly smaller than those fed to adults (Scheffé F = 3.08, $P < 0.05$); there was no size difference between figs fed to males and females ($P > 0.05$).

During handling trials, males and females usually ate the entire fig offered to them (Table 3). No juvenile ate more than 50% of a fig; most picked up and then dropped figs without eating any portion of them. Males and females, when presented with RR figs, ate similar amounts ($\chi^2_1 = 0.15$, $P > 0.15$). Adults ate a significantly higher proportion of each fig than did juveniles ($\chi^2_1 = 46.38$, $P < 0.0001$). Males (n = 26) ate figs in a significantly shorter time than did females (n = 24; Mann-Whitney $Z = 4.0$, $P < 0.0005$, one-tailed; Table 3). Too few juveniles attempted to eat figs to measure handling time.

Male and female lizards used in handling trials exhibited similar feeding behavior (Table 5). Nearly all adults (96%, n = 48 of 50 individuals) used the ground as a frictional surface to break open figs. To split open a fig, a lizard picked up a fig in its mouth, turned its head to one side, and pressed an exposed part of the fig against the ground (hereafter referred to as pressing). A small percentage of adults used head shaking to open figs (14%, n = 7 of 50 individuals), but this was always done in combination with pressing (Table 5). Males used pressing significantly more frequently than head shaking ($\chi^2_1 = 18.62$, $P < 0.001$), as did females ($\chi^2_1 = 8.17$, $P < 0.005$). There was no difference in the frequency of pressing or head shaking among sexes (Fisher's test, $P = 0.18$); but juveniles used head shaking (in combination with pressing) significantly more frequently than pressing alone, when compared with adults (Fisher's test, $P < 0.0001$). Juveniles used head shaking (in combination with pressing) significantly more

Table 2. Mean ($\bar{x}$) Numbers of Figs Available at Five Sampling Points and Their Standard Errors (SE) and Ranges.

	$\bar{x} \pm$ SE	Range
Red ripe (RR)	4.60 (4.12)	0–21
Shriveled red (SR)	102.4 (42.19)	10–241
Hard brown (HB)	48.2 (15.12)	8–90

Table 3. Descriptive Statistics of Mean Number of Figs Sampled/Min, Percent Fig Eaten, and Fig Handling Times (s) for Male, Female, and Juvenile Lizards. The mean number of figs sampled are from focal samples, whereas percentages of fig eaten and handling times are from feeding trials.

	n	$\bar{x} \pm$ SE	Range
Mean # figs sampled/min			
Males	11	0.31 (0.085)	0–0.8
Females	17	0.37 (0.057)	0.02–1.1
Juveniles	17	0.10 (0.029)	0–0.35
Percent fig eaten			
Males	29	89.66 (5.76)	0–100
Females	24	97.08 (2.04)	60–100
Juveniles (entire)	18	5.56 (3.05)	0–50
(broken)	19	38.68 (7.05)	0–100
Handling time			
Males	26	32.46 (4.68)	6–100
Females	24	71.25 (2.04)	60–100

Table 4. Descriptive Statistics of Fig Measurements (mm) Used in Handling Trials.

	n	$\bar{x} \pm$ SE	Range
Males	40	8.21 (0.09)	7.00–9.36
Females	39	8.13 (0.09)	6.89–9.20
Juveniles	30	7.61 (0.10)	6.61–8.54

TABLE 5. FREQUENCY OF SPECIFIC FEEDING BEHAVIORS (PRESSING FIG AGAINST GROUND AND HEAD SHAKING) USED BY LIZARDS DURING FEEDING TRIALS. Numbers in parentheses are individuals; individuals that sampled figs but did not eat them are included. No lizards used only head shaking during feeding.

	Total individuals (=trials)	Pressing (only)	Head shaking and pressing
Males	29	82.8% (24)	6.9% (2)
Females	25	76.0% (19)	20.0% (5)
Juveniles	16	12.5% (2)	87.5% (14)

TABLE 6. NUMBER OF TIMES PAINT-MANIPULATED (RED PAINTED WHITE, RPW; WHITE PAINTED RED, WPR) AND CONTROL FIGS (UNPAINTED RED, RR; UNPAINTED WHITE, HW) WERE SAMPLED TO TEST FIG SELECTION BASED ON COLORATION/BRIGHTNESS, DURING A 35-MIN TRIAL. Only RR figs were eaten; therefore, the expected probability of a sampling event was adjusted each time a RR fig was eaten (for statistical analysis).

RR figs remaining	Number of samplings			
	RR	WPR	HW	RPW
15	0	1	0	0
14	3	0	0	0
13	0	1	0	0
12	1	0	0	1
11	1	2	2	1
10	2	5	0	0
9	1	0	1	0
8	0	2	0	0
7	1	0	0	0
6	0	1	0	0

often than only pressing ($\chi^2_1 = 9.0$, $P < 0.005$) when feeding on broken figs (87.5%, n = 16 total individuals observed). Also, juveniles ate larger portions of individual broken figs than entire figs ($\chi^2_1 = 46.38$, $P < 0.05$; Table 3).

Hypothesis 1.—A fig tree was not a necessary context for fig recognition. In three trials, all figs (n = 30) placed on rock away from trees were eaten by 13 individuals.

Hypothesis 2.—Significantly more lizards were recorded foraging in grids along the rock-debris interface (84.2%, n = 32) than deeper into debris (15.8%, n = 6; $\chi^2_1 = 17.79$, $P < 0.001$).

Hypothesis 3.—When presented with a fig, lizards in a group (most were foraging) ran significantly farther (n = 26; $\bar{x} = 261.53 \pm 30.04$ cm) than solitary lizards (n = 20; $\bar{x} = 8 \pm 3.37$; Mann-Whitney $Z = 5.7$, $P < 0.0001$) before feeding.

During focal sampling, lizards quickly approached conspecifics that were feeding on figs. Of 45 focal animals, 33% (n = 15) attempted to take a fig from a feeding lizard. The best measure of interference competition during feeding was the number of individuals attempting to take a fig from the focal animal. Among focal animals, 31% (n = 14) were approached by a conspecific attempting to steal a fig; focal animals were approached by a mean of 0.84 ± 0.23 lizards (range: 0–5). Of 33 individuals that approached feeding lizards under focal observation, significantly more were adults than juveniles (29 adults, 4 juveniles; $\chi^2_1 = 19.88$, $P < 0.001$); but among adults, there was no relationship to sex (12 males, 17 females; $\chi^2_1 = 1.2$, $P > 0.1$). Of 15 focal individuals that approached feeding lizards, significantly more were adults than juveniles (14 adults, 1 juvenile; $\chi^2_1 = 11.27$, $P < 0.001$); among adults, significantly more were females (3 males, 11 females; $\chi^2_1 = 4.57$, $P < 0.05$). Lizards were generally unsuccessful at taking figs or portions of figs from other lizards (10.26% success rate; n = 39 attempts).

Hypothesis 4.—Lizards responded to moving figs regardless of fig quality. In 20 of 21 trials, lizards seized moving HW figs. In 19 of 20 trials, lizards seized moving RR figs. Three of these trials were repeated when the lizard did not see the fig initially.

Hypothesis 5.—Given a choice between stationary RR figs on the ground and moving RR figs, lizards chose moving figs significantly more often (80%, n = 20 lizards chose moving figs; $\chi^2_1 = 9$, $P < 0.005$).

Hypotthesis 6.—Given a choice between RR, SR, and HB figs, lizards made selections nonrandomly. No HB figs were eaten, and only one SR fig was eaten. Lizards ate 84% (n = 38) of RR figs which was significantly more than SR and HB combined ($\chi^2_2 = 70.04$, $P < 0.001$).

Hypothesis 7.—When fig size was controlled, lizards selected figs based on coloration/brightness. No painted figs (n = 15) or HW figs (n = 15) were eaten by lizards during the experiment, whereas 66.7% (n = 10) unpainted RR had been eaten by lizards. Although lizards did not eat painted figs, painting had no effect on fig sampling by lizards ($\chi^2_1 = 0.14$, $P > 0.5$; comparing painted to unpainted figs; Table 6). Therefore, white figs (painted and unpainted) were compared with red figs (painted and unpainted). Red figs were sampled first by lizards significantly more often than white figs ($\chi^2_2 = 15.61$, $P < 0.001$).

DISCUSSION

Temporal food availability appears to shape the diets of many lizard species, often resulting in tremendous dietary flexibility within a single taxon (e.g., *Leiocephalus*; Schoener et al., 1982). In xeric habitats, food availability is frequently unpredictable (Robinson, 1987; Durtsche, 1995), which may favor dietary generalists, although numerous specialists (e.g., myrmecophagous *Phrynosoma* and *Moloch horridus*) also exist in deserts. *Platysaurus capensis* occurs in xeric habitat, although at AFNP this is ameliorated by the Orange River. At AFNP, fruiting *F. c. cordata* trees represent discrete food resources that are spatially and temporally unpredictable (pers. obs.). Flat lizards that located fig-bearing trees readily fed on fallen figs and frequently occurred at abnormally high densities under these trees (unpubl. data).

Unlike geckos (Whitaker, 1987) and the lacertid *Gallotia galloti* (Valido and Nogales, 1994), which mainly feed on fruit still attached to plants, *P. capensis* fed mostly on fallen figs. However, lizards were seen climbing trees and feeding on both figs and insects when figs approached ripeness but were not available on the ground. Successful ingestion of figs still attached to trees was not evaluated.

Males and females sampled similar numbers and ate similar proportions of individual figs. However, males consumed figs in significantly shorter time than did females. The larger heads of males (MJW, unpubl.) may account for their shorter handling time. Although juveniles sampled significantly fewer figs than did adults, they foraged significantly more on individual fig seeds scattered on the ground. Juveniles also fed readily on fig fragments. Therefore, juveniles were dependent on adult lizards and other animals (usually birds) to break open figs.

In the many lizards that ingest plant material whole, gape size determines the upper limit of the resource. We observed two behaviors to cope with these difficulties. First, juveniles whose gape was too small to swallow entire figs only utilized figs that were already damaged by other vertebrates. Second, they consistently used head shaking to break off manageable pieces of fig. Conversely, adults consumed entire figs, often using the rock as a friction surface to break open figs. Therefore, morphological functional constraints were overcome behaviorally by the mechanical breaking of figs on rock.

Successful facultative exploitation of plant material depends not only on the lizard's ability to ingest and digest plant material (Ostrom, 1963; Sokol, 1967) but also on location and recognition of edible plant material (Dearing and Schall, 1992). Exploitation of food plants may require a very different search strategy and recognition template (Cooper, 1994). Flat lizards exhibited a plastic recognition ability, such that lizards ambushing moving insects away from fig trees inspected and ate stationary figs placed on nearby rocks. Similarly, lizards feeding on figs underneath fig trees frequently chased flying insects and bird feathers that blew overhead. Therefore, *F. c. cordata* trees were not a necessary context for fig recognition by *P. capensis*.

Valido and Nogales (1994) found that *Gallotia galloti* foraged in areas that were well protected from predators. *Platysaurus capensis* usually avoided foraging deep in debris, but when they did, they immediately ran out onto open rock after picking up a fig (pers. obs.). This preference may result from their better locomotory performance on rock, which reduces predation risk and/or social interference (see below). Another explanation may be a higher availability of figs along the rock-debris interface. Although we did not specifically measure fig availability in debris near rock versus away from rock, we saw no evidence that fig availability was higher along the interface.

Interference competition between lizards was strong and was more prevalent among adults than juveniles. Consequently, when lizards located edible figs, they frequently ran to unoccupied areas to feed. The low success of pursuers attempting to steal figs raises questions about the potential energetic benefits of chasing. Because lizards chased conspecifics with figs even in areas of high fig availability, the behavior may be more consistent with the lizard's strong sensory bias for movement than with energetic consequences.

The cordylids have been characterized as ambushers (Cooper et al., 1997). Feeding behavior characteristic of ambushers consists of short dashes to capture passing insects, and *P. capensis* has acute ability to detect moving insects (pers. obs.; Cooper et al., 1997). *Platysaurus capensis* exhibited a strong sensory bias for moving objects that overrode opportunities to feed on available figs in front of them. This behavior was seen repeatedly in several different contexts (e.g., chasing moving bird feathers) and may be related to their predominantly insectivorous diet. In the experiment in which lizards had a choice between ripe figs on the ground and a moving fig, it is possible that some lizards may have decided not to eat the stationary fig before they were offered the moving fig. However, during foraging for figs, most lizards were continually moving, and we generally performed trials as lizards approached stationary figs.

Although frugivory is facultative, *P. capensis* displayed complex exploitation behaviors relating to the utilization of figs. Figs were selected nonrandomly and disproportionately to their availability, using a combination of visual and chemical/tactile information. Our data support the notion that visual information is used at a distance and that chemical/tactile information is used at close range. White, unripe figs, when painted red (size controlled), were approached ahead of controls, demonstrating that lizards were initially making a selection using visual (color/brightness) information. Rand (1978 and citations therein) showed that lizards are often attracted by red, and this stimulus may be another sensory bias, or it may be learned. However, the lizard's preference for ripe-red as opposed to shriveled-red figs suggest that size may also be an important determinant of food choice.

During experiments and focal sampling, lizards frequently used either tongue-flicking or nudging prior to selecting a fig. It is believed that after secondarily adopting ambushing, the Cordylidae lost their ability to discriminate prey chemicals from other chemical cues (Cooper, 1994; Cooper and van Wyk, 1994). This was recently demonstrated for *Cordylus cordylus* (Cooper and van Wyk, 1994) but has not been demonstrated for any *Platysaurus*. We could not determine whether lizards were using tongue-flicking to assess figs chemically or some other quality such as hydration (possibly based on fig texture). Painted figs were visually attractive to lizards, but after physical contact of the fig by the lizard, no painted figs were consumed.

The number of documented cases of herbivory in small lizards is growing, and Pough's (1973) finding that herbivorous lizards are generally >100 g has been challenged (Greene, 1982; Dearing, 1993). *Platysaurus capensis* at AFNP is a facultative frugivore, but this may be because Namaqua figs are an unpredictable resource that are only sporadically available. We observed large numbers of lizards returning to fruiting trees daily until ripe figs were no longer available. Feeding on figs is therefore opportunistic but raises a number of questions relating to food choice, energetics of herbivory in a small lizard, and possible adaptations of the alimentary canal to processing plant material.

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