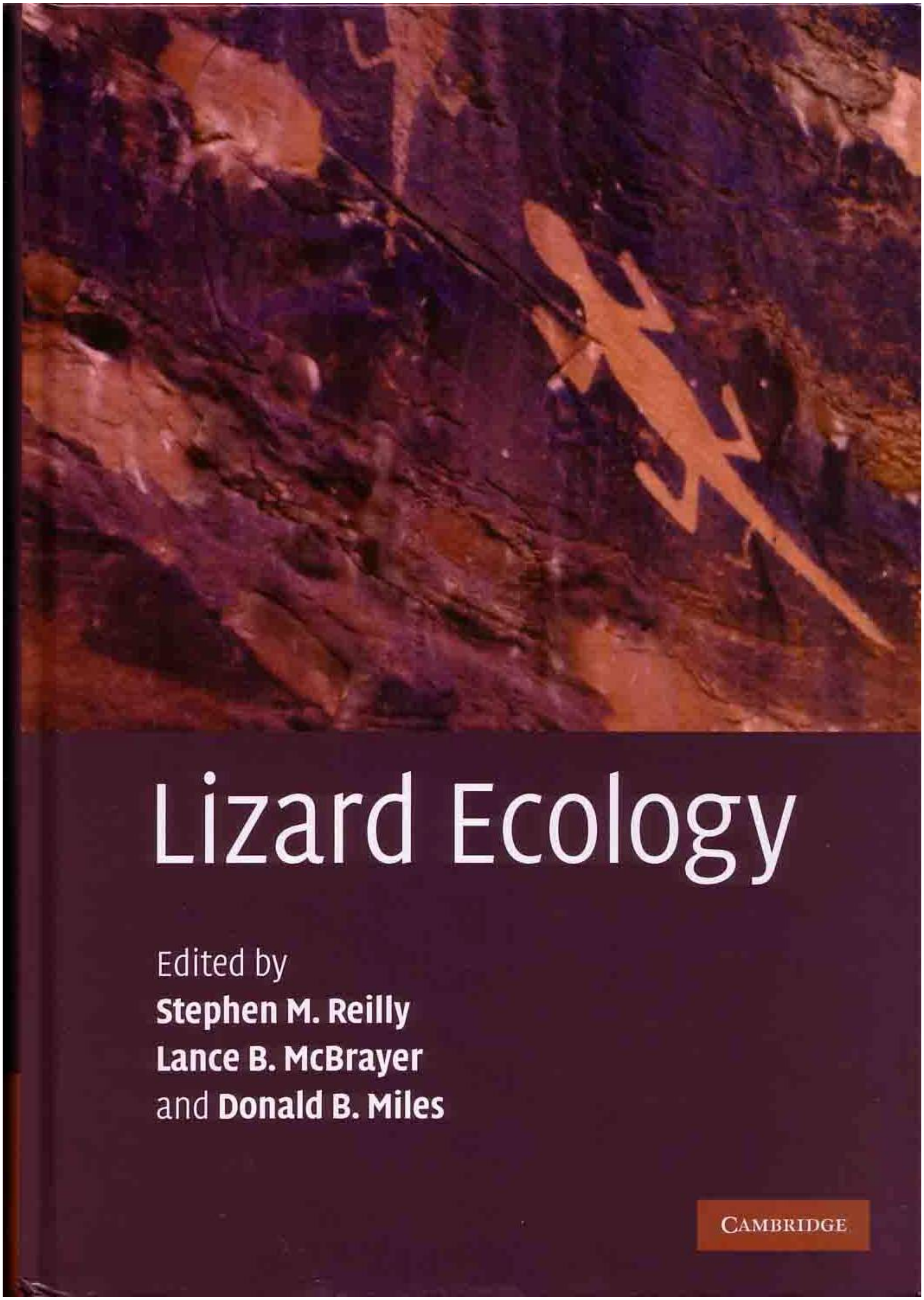

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Foraging mode in the African cordylids and plasticity of foraging behavior in *Platysaurus broadleyi*

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Introduction

Understanding the evolution of key life history traits frequently involves searching for broad-scale patterns among diverse organisms (see, for example, Vitt *et al.*, 2003). When consistent patterns emerge, particularly among members of multiple clades, our understanding of how suites of traits co-evolve is improved. In the process, new hypotheses are generated, allowing further testing of patterns and the mechanisms that generate them. The simplified goal of this book is to disentangle the evolution of foraging mode within a major vertebrate lineage: lizards. In particular, we wish to understand the relationship between foraging mode and a suite of co-evolved characters. Fundamental to lizard foraging theory is the tenet that foraging mode has greatly constrained (or shaped) the evolution of certain traits, including aspects of morphology and physiology. For example, ambush foragers are often tank-like and have a high relative clutch mass, relatively slow sprint speed and lower metabolic rate than active foragers, which are slender, relatively fast, and with lower relative clutch mass (Huey and Pianka, 1981; see references in Greeff and Whiting, 2000). More recently, there is accumulating evidence that although foraging mode has had a profound influence on aspects of lizard biology, foraging mode is deeply rooted in history (phylogeny) and only one of many traits explaining current lizard diversity (Perry, 1999; Vitt *et al.*, 2003). Lizard foraging mode is also remarkably stable within entire clades (e.g. families) of lizards (Cooper, 1994, 1995). Just as identifying broad-scale patterns is important for understanding the evolution of foraging mode in lizards, identifying deviations from these patterns may be equally, if not more, informative. What factors allow an organism to alter its foraging mode and foraging behavior to exploit another resource, and when is it beneficial to do this? I tackle this question by reviewing foraging mode for one clade of

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lizards, the African Cordylidae. Specifically, I focus most of my review on one particular species (*Platysaurus broadleyi*) that exhibits remarkable foraging behavior and plasticity of foraging mode within a clade that exhibits relatively inflexible foraging mode.

Systematic placement of Cordylidae within the Cordyliformes

The Cordyliformes are a monophyletic clade of scincomorph lizards consisting of the Old World families Cordylidae (Africa) and Gerrhosauridae (Africa and Madagascar) (Odierna *et al.*, 2002). There is some disagreement on whether cordylids and gerrhosaurids are separate families, or subfamilies, within the Cordylidae (Lang, 1991; Mouton and Van Wyk, 1997; Zug *et al.*, 2001). However, there is little dispute that as a clade the Cordyliformes are monophyletic (see Odierna *et al.*, 2002). I follow Lang (1991) and Odierna *et al.* (2002) in considering gerrhosaurids as a separate family, and focus this review on Cordylidae *sensu stricto*. Furthermore, until recently, the Cordylidae consisted of the genera *Cordylus*, *Pseudocordylus*, *Chamaesaura*, and *Platysaurus*. A recent molecular phylogeny for all four genera demonstrated a monophyletic grouping of *Cordylus* + *Pseudocordylus* + *Chamaesaura*, placing them within *Cordylus* with *Platysaurus* as the sister taxon (Frost *et al.*, 2001). Since Frost *et al.* (2001), some papers have followed this convention. However, the use of *Cordylus sensu lato* has created nomenclatural instability; additional systematic work on the Cordylidae may result in further name change at the level of genus (P. Mouton, pers. comm.). For this reason, and because the majority of published work on cordylid foraging behavior follows the original convention, my review will focus on the traditional four genera within Cordylidae (*Cordylus*, *Pseudocordylus*, *Chamaesaura*, and *Platysaurus*) (Fig. 13.1).

Natural history of cordylids

Cordylus (girdled lizards; Fig. 13.1A) currently consists of 31 species (Frost *et al.*, 2001) and ranges from the southern Cape coast of South Africa as far north as southern Ethiopia (Odierna *et al.*, 2002). The primary radiation appears to have been in southern Africa, where the majority of species occur. Most taxa are rupicolous and occur either on rocky mountains or small rock outcrops (Mouton and Van Wyk, 1997). One species (*C. giganteus*) is colonial and lives in self-excavated burrows in Highveld grasslands (Van Wyk, 2000). Several other species are also terrestrial (e.g. *C. macropholis*, *C. tasmani*) or semi-arboreal, using dead trees or logs (e.g. *C. tropidosternum*). Most species are colonial and all are primarily insectivorous, although some taxa will eat

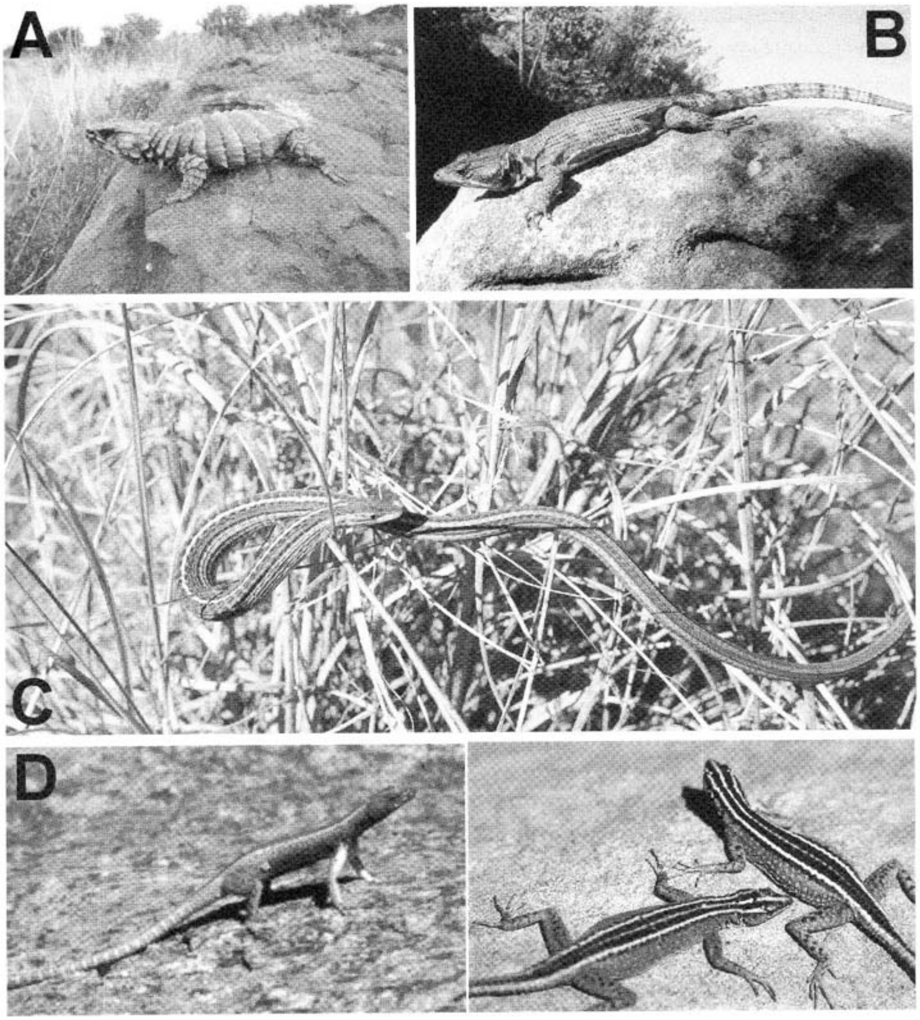

Figure 13.1. Representative cordylids. (A) *Cordylus cataphractus*; (B) *Pseudocordylus microlepidotus*; (C) *Chamaesaura anguina*; (D) *Platysaurus broadleyi* (male left, female right). (A–C) ©le Fras Mouton, (D) ©Martin Whiting.

small quantities of plant material (see, for example, Mouton *et al.*, 2000). *Cordylus* have osteoderms, which are thought to provide a degree of armament useful against predatory attack (Mouton and Van Wyk, 1997). Interestingly, *Cordylus* vary in their degree of armature such that more heavily armoured species have short legs, slow sprint speed, and are more likely to seek refuge in a crevice (Losos *et al.*, 2002).

Pseudocordylus (crag lizards; Fig. 13.1B) currently consists of seven species, all of which are found in several mountain ranges in the southern African subregion (Branch, 1998). All *Pseudocordylus* are rupicolous and insectivorous. Unlike most *Cordylus*, *Pseudocordylus* males are often conspicuously colored. Compared with *Cordylus*, *Pseudocordylus* are also less heavily spined (an index of armature), have longer hindlimbs, and sprint faster (Losos *et al.*, 2002).

Chamaesaura (grass lizards; Fig. 13.1C) currently consists of three species distributed from the coastal Cape of South Africa as far north as East Africa (Rwanda, Burundi, S. Kenya) (Lang, 1991). Among cordylids, *Chamaesaura* are unique because of their vestigial limbs and serpentiform morphology and locomotion. Furthermore, unlike other cordylids, which are largely rupicolous, *Chamaesaura* occur in grasslands, generally on mountain slopes and plateaus. *Chamaesaura* are insectivorous and possess long tails, which can be autotomized (Branch, 1998).

Platysaurus (flat lizards; Fig. 13.1D) currently consists of 24 taxa (15 species + subspecies) distributed from South Africa to southern Tanzania. They are so named because of their extreme dorso-ventral flattening, enabling them to fit into tight crevices (Scott *et al.*, 2004). All *Platysaurus* are rupicolous and largely insectivorous, although they will eat plant matter (small fruits, seeds, flower petals, young leaves) when available (Broadley, 1978; Whiting and Greeff, 1997). Currently, only the Augrabies flat lizard (*P. broadleyi*; formerly *P. capensis*) from a single population (Augrabies Falls National Park; hereafter Augrabies) has been studied in any detail in the field. *Platysaurus broadleyi* occurs predominantly along the granite banks of the Orange River beginning just east of the southern border between Namibia and South Africa and extending for a distance of several hundred kilometres to the west of Augrabies (Branch and Whiting, 1997; Scott *et al.*, 2004). The greatest densities occur at Augrabies. Male *P. broadleyi* are elaborately colored (Fig. 13.1D; Whiting *et al.*, 2003) while females are drab and retain the stripes they have as juveniles. Males are also larger than females, are aggressive and territorial, and may adopt alternative reproductive tactics (Whiting, 1999; Whiting *et al.*, 2003; Whiting *et al.*, 2006).

Foraging mode in Cordylidae

The current approach to determining lizard foraging mode is to quantify movement related to foraging behavior and the percent time spent moving while foraging (Pianka, 1966; Huey and Pianka, 1981; Perry, 1999; Chapter 1). Lizards that spend less than 10% of their time moving are considered ambush or sit-and-wait foragers; those that move for greater than 10% of their active time are considered active foragers. Although these criteria are arbitrary, this convention has been useful for categorising foraging mode and allowing broad-scale comparative analyses for a number of species (see, for example, Cooper, 1995; Perry, 1999). The problem arises when species do not fall neatly into either of the two modes. As such, foraging modes are no longer accepted as bimodal and are now thought to represent a continuum (see, for example, Pietruszka, 1986; Perry, 1999). Alternatively, more than one mode may exist (Cooper, 2005). For example, saltatory foraging has been suggested for when an animal makes many short moves punctuated by long pauses (pause–travel; Cooper, 2005). Alternatively, other authors consider saltatory foraging to consist of infrequent, but long, movements (Eifler and Eifler, 1999). Nevertheless, Cooper (2005) suggests that clusters of foraging mode still remain useful for seeking correlates with other variables. Given that many of the cordylids studied to date fall neatly into a traditional sit-and-wait mode of foraging (Cooper *et al.*, 1997; Mouton *et al.*, 2000; du Toit *et al.*, 2002), I use the 10% cut-off as a criterion for identifying foraging mode, for the purposes of this review.

Foraging mode has been quantified for nine cordylids (five *Cordylus*, two *Pseudocordylus*, one *Chamaesaura*, and one *Platysaurus*). Data therefore currently exist for the entire family. *Cordylus* is the best studied genus; reasonable data exist for four of the five taxa presented here (Fig. 13.2A, B). (*Cordylus imkae* foraging mode is unfortunately preliminary, being inferred from only a single data point (Cooper *et al.*, 1997) during which the lizard remained immobile.) *Cordylus* studied to date use elevated rock platforms, from where they make short foraging trips to capture insects (Cooper *et al.*, 1997). Data on movement rate (moves per minute) and activity (percent time moving) for the remaining four *Cordylus* strongly suggests that members of this genus are extreme ambush foragers (MPM range 0–0.23; PTM range 0–2.2; Fig. 13.2A, B).

The two species of *Pseudocordylus* that have been studied conform to an ambush foraging mode (Fig. 13.2A, B), but interestingly, during foraging bouts *P. capensis* may make longer movements (sometimes > 20 s) than is typical of ambush foragers (Cooper *et al.*, 1997). More data are needed on *Pseudocordylus* to properly evaluate its foraging mode and any degree of foraging mode plasticity.

It was originally believed that *Chamaesaura*, in part because of its serpentiform morphology (Fig. 13.1C) and speed, might be an active forager (Branch, 1998). However, foraging mode was quantified for *Chamaesaura anguina* in seminatural outdoor enclosures, where they behaved like typical ambushers (du Toit *et al.*, 2002) (Fig. 13.2).

In summary, the paradigm of a dichotomous foraging mode works well for the cordylids. When feeding on insects, all species adequately meet the criteria of a sit-and-wait foraging mode.

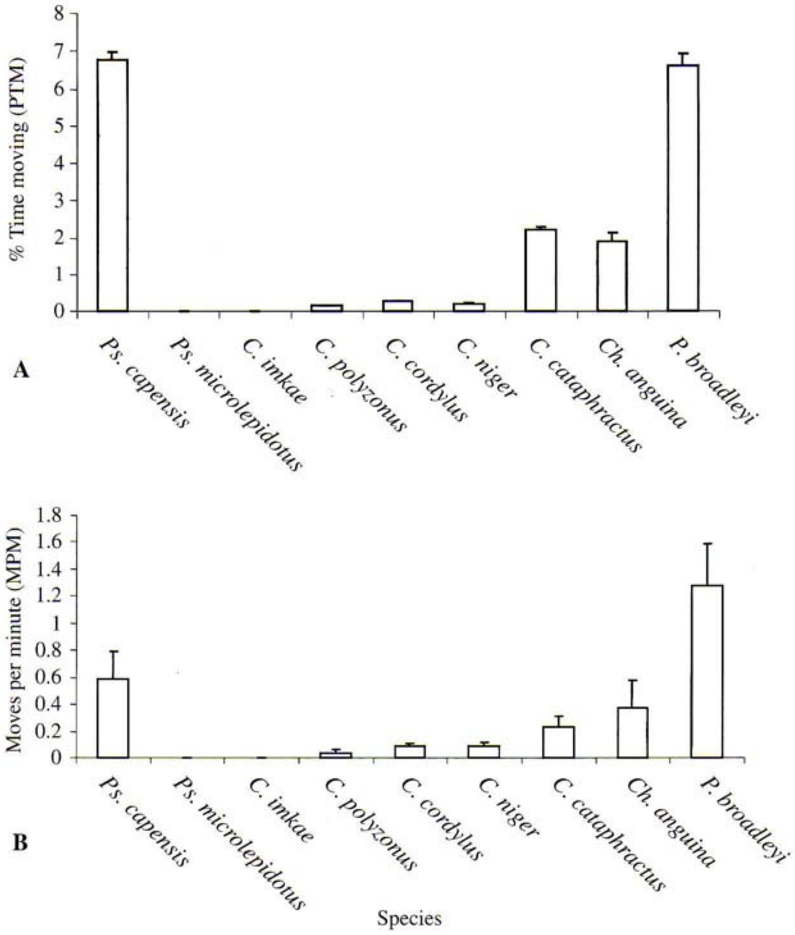

Figure 13.2. (A) Foraging mode of cordylid lizards quantified by using percent time moving (PTM). (B) Foraging mode of cordylid lizards quantified by using moves per minute (MPM). Data are from Cooper *et al.* (1997), Mouton *et al.* (2000), and du Toit *et al.*, (2002). *Cordylus* are all classical ambush foragers; *Pseudocordylus capensis* and *Platysaurus broadleyi* (Cooper *et al.*, 1997) had higher values, but were still within the range for ambush foraging.

The special case of *Platysaurus broadleyi*: plasticity of foraging mode

To find a fig: use of heterospecific cues

Platysaurus broadleyi is a facultative omnivore that feeds on Namaqua figs when they are available. Namaqua fig trees are pollinated by fig wasps and fruit asynchronously as a result (Berg and Wiebes, 1992). As such, figs are unpredictable in time and space. Ripe figs are energetically rich and constitute a valuable resource (Greeff and Whiting, 1999). Therefore, fruiting fig trees represent a high pay-off if discovered by lizards. Because of the unpredictable timing of fruiting, systematically or randomly searching for figs by travelling to trees that are dispersed in the landscape would be too energetically costly for lizards. In addition, lizards may be more vulnerable to predation. Instead, *P. broadleyi* use heterospecific cues to locate fruiting trees. When figs are ripe, large aggregations of birds are attracted to fig trees to feed on the fruit. During foraging, birds constantly move about the tree, flying short distances to locate new figs. This makes for almost continuous movement in the tree. *Platysaurus broadleyi* has a 'sensory bias' for movement and is attracted to fluttering birds. This was demonstrated by Whiting and Greeff (1997) experimentally, by showing that lizards are attracted to the movement of caged birds on bare rock, away from the context of the fig tree. More importantly, *P. broadleyi* were more likely to approach a non-fruiting fig tree containing caged birds than a fig tree with an empty cage. As such, lizards take advantage of high bird activity in fruiting trees as a cue to locate ripe figs, presumably as a result of this sensory bias for movement (Whiting and Greeff, 1997, 1999). Whether lizards make a cognitive connection between high bird activity and a fruiting fig tree is debatable but also immaterial: the pay-off is the same. Once fruiting trees are discovered, lizards return daily to feed on figs until this resource is spent.

Facultative frugivory: how to deal with a fig, fig stealing, and influence on foraging mode

Platysaurus broadleyi will either feed on fallen figs or climb into trees and remove ripe figs still attached to the tree (pers. obs.). During this time, lizard aggregations under these trees can number in the hundreds (pers. obs.; Greeff and Whiting, 1999). Lizards are in competition for this relatively limited resource with birds, rock hyraxes, and monkeys (Greeff and Whiting, 1999). Intraspecific competition for figs is also intense. Lizards attempt fig stealing (33% of individuals) if a nearby conspecific discovers a fig; up to five individuals have been recorded to approach a focal individual in possession of a fig (Whiting and Greeff, 1997). This behavior is largely unsuccessful (10.3% success rate), but forces lizards to move away from the source of competition before consuming any figs they may find. Furthermore, the distance lizards move to consume figs is a function of their perceived risk of interference competition: the presence of more conspecifics results in lizards moving further away (Whiting and Greeff, 1997). The biggest perpetrators of interference competition through fig stealing were adult females, although adult males also attempted this behavior (Whiting and Greeff, 1997).

Table 13.1 *Summarized foraging data on moves per minute (MPM) and percent time moving (PTM) for* Platysaurus broadleyi *from Augrabies Falls National Park by sex and cohort*

Data are expanded from Greeff and Whiting (2000) for lizards observed at an insect-rich site, an insect-poor site, and a fig site. Included for comparison are data from Cooper *et al.* (1997). Mean values are reported ± 1 SE.

Site	Sex/age	N	MPM	SE	Range	PTM	SE	Range
Insect-poor	males	21	0.75	0.14	0–2.7	5.1	1.11	0–17.67
	females	16	0.87	0.25	0–3.85	2.54	0.63	0–7.86
	adults	37	0.8	0.13	0–3.85	3.99	0.71	0–17.67
	juveniles	24	1.54	0.18	0.1–3.46	9.55	1.43	0.17–24.31
	all lizards	61	1.09	0.12	0–3.85	6.18	0.78	0–24.31
Insect-rich[a]	males	22	0.72	0.11	0–1.95	4.35	0.6	0.01–11.58
	females	20	1.76	0.49	0.3–9	5.14	0.54	0.5–9.9
	adults	42	1.22	0.25	0–9	4.73	0.4	0.01–11.58
All insects	males	43	0.74	0.09	0–2.7	4.72	0.62	0–17.67
	females	36	1.36	0.3	0–9	3.98	0.46	0–9.9
	adults	79	1.02	0.15	0–9	4.38	0.4	0–17.67
	all lizards	103	1.14	0.12	0–9	5.59	0.5	0–24.31
Fig site	males	13	1.51	0.18	0.4–2.4	13.6	2.33	1–30.13
	females	19	2.08	0.16	0.6–3.59	19.2	2.15	7–42.0
	adults	32	1.85	0.13	0.4–3.59	16.93	1.64	1–42.0
	juveniles	17	1.61	0.15	0.7–3	9.93	1.77	2.5–28.8
	all lizards	49	1.77	0.1	0.4–3.59	14.5	1.32	1–42.0
Cooper *et al.*, (1997)	adults	22	1.27	0.32	0–6.82	6.62	1.58	0–24.17

[a] Insufficient data for juveniles.

The very nature of a fig requires a different foraging behavior for a normally insectivorous lizard. Compared with their primary prey, which is aerial (black flies, *Simulium* spp.), figs are stationary and dispersed in a localized area in or under the tree, often in a substrate containing debris. Lizards therefore adjust their foraging behavior to suit this resource. *Platysaurus broadleyi* shift to a more active foraging mode, during which time they make more movements and cover more ground while actively searching for ripe figs (Fig. 13.3). Adult lizards performed significantly more moves per minute and spent longer moving while foraging for figs compared to foraging for insects (Greeff and Whiting, 2000) (Table 13.1; Figs. 13.3 and 13.4). Juvenile lizards, on the other hand, did not shift their foraging mode significantly in the context of fig compared with insect foraging (Fig. 13.3). Values for mean PTM during foraging for figs were in the range of those reported for some active foragers (see, for example, Perry, 1999) (Fig. 13.3A). Similarly, *P. broadleyi* made frequent movements in search of figs (Fig. 13.3B). Female lizards had the highest mean PTM (19.2%); one individual

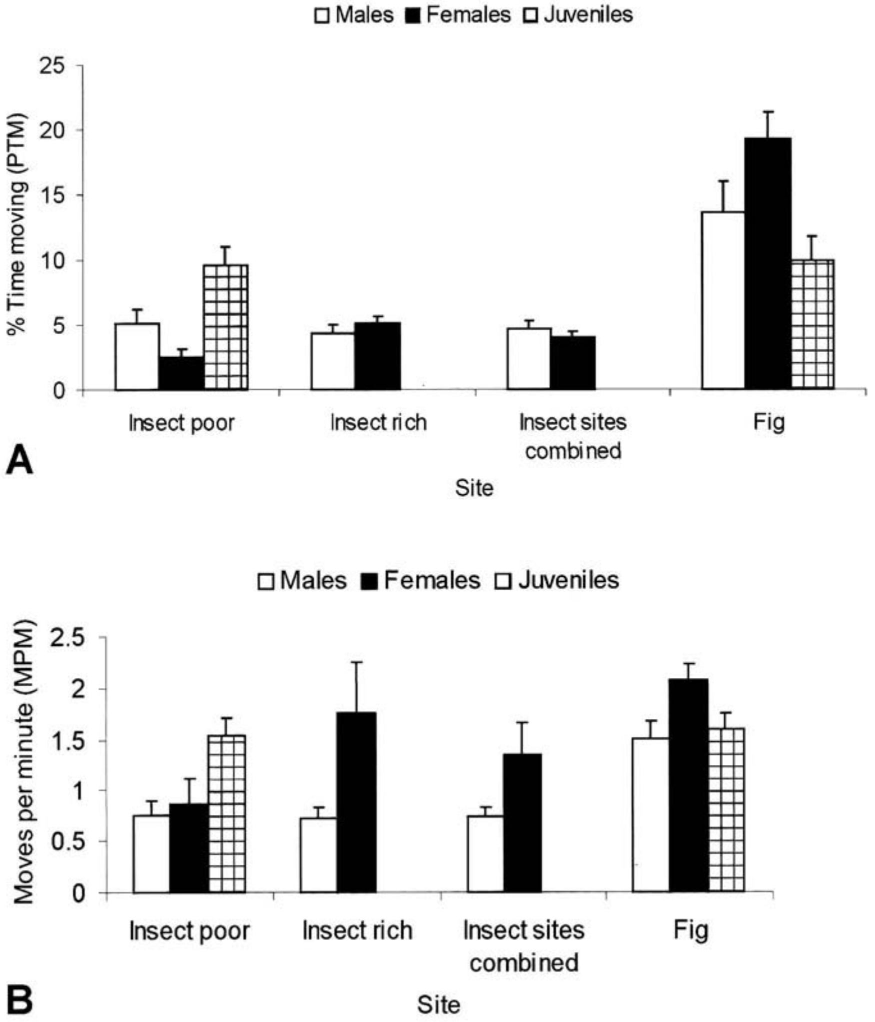

Figure 13.3. Foraging mode of *Platysaurus broadleyi*, quantified by using (A) percent time moving (PTM) and (B) moves per minute (MPM) for two insect sites of variable density and a fig site. Adults of both sexes switched to active foraging when searching for figs, but ambushed insects in similar ways at both insect sites. Juveniles had similar values for PTM and MPM at both the insect-poor site and the fig site (there were insufficient data for the insect rich site); these values bordered on active foraging.

spent 42% of observation time actively foraging for figs (Table 13.1). Evaluating the range of values for PTM, in addition to simply using mean PTM, was informative. These data show a number of individuals with high values of PTM: 65% ($n = 32/49$) were above the 10% cut-off for active foragers (Fig. 13.4).

While foraging for figs, lizards tongue-flicked the substrate (pers. obs.) and either nudged or tongue-flicked figs before eating them (Whiting and Greeff,

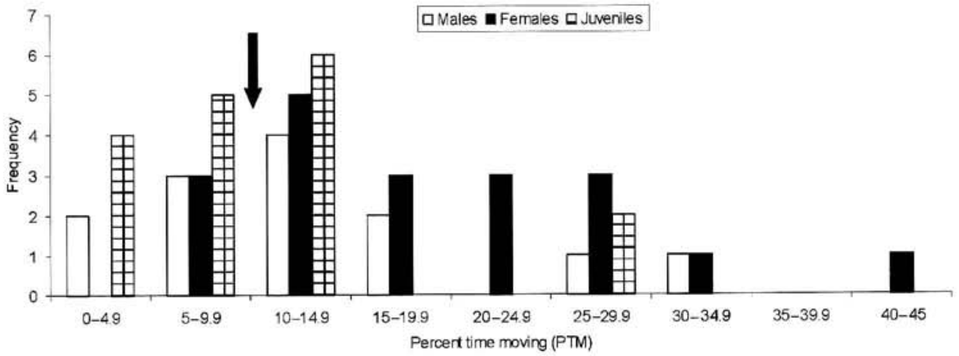

Figure 13.4. Frequency of male, female and juvenile *Platysaurus broadleyi* foraging for figs according to intervals of percent time moving (PTM). The arrow indicates the traditional cut-off (10%) separating ambush and active foragers (Perry, 1999). Most individuals (65%) are above that cut-off.

1997). This is contrary to expectation for an ambush forager. For a sit-and-wait predator, crypsis is essential for the element of surprise and may be disrupted by tongue flicking. Therefore, lizards that ambush prey do not tongue-flick; in addition, lizards that belong to lineages that have shifted from active to ambush foraging typically lose their ability to detect prey chemicals and cease tongue flicking potential food (Chapter 8). Why, then, do *P. broadleyi* tongue-flick figs?

At Augrabies Falls National Park, blackflies (*Simulium* spp.) breed in the shallow, fast-flowing sections of the Orange River, where large plumes of male flies await the emergence of females, which soon disperse in search of a blood meal. Lizards travel defined routes from crevices away from the river to feed on these fly plumes (pers. obs.). While foraging for insects, *P. broadleyi* are typical ambushers. A feature of ambush foragers is an absence of tongue flicking and a dependence on visual cues for prey location and capture (see Chapter 8). *Platysaurus broadleyi* locate prey visually and lunge forward to capture them in the air, sometimes performing a complete 360° aerial flip (pers. obs.). No tongue flicking is used during insect foraging. In contrast, *P. broadleyi* readily sample figs by using tongue flicking. While visual cues are used for initial assessment of fig quality, *P. broadleyi* tongue-flick or nudge figs prior to consumption (Whiting and Greeff, 1997). These observations suggest that *P. broadleyi* uses tongue flicking either to evaluate fig quality (possibly hydration) or to detect fig chemicals through vomerolfaction.

Food chemical discrimination

Whiting and Cooper (2003) tested the hypothesis that *P. broadleyi* can discriminate fig chemicals. Free-ranging *Platysaurus broadleyi* were presented with fig and fly extract on laminated cardboard tiles; the number of tongue-flicks directed at these stimuli, and the time spent at these stimuli, were compared with an odorless control. Lizards directed more tongue-flicks at the fig-labeled stimulus, spent more time at the fig-labeled tile, and attempted to eat this tile significantly more often than the insect or control stimulus. These results are surprising because previously tested omnivores within scleroglossan lizards have the ability to discriminate both insect and plant chemicals (Chapter 8). However, one alternative explanation is that *P. broadleyi* respond to fig cues by using gustation, rather than vomerolfaction (Whiting and Cooper, 2003). *Platysaurus broadleyi* were also observed licking the fig-labeled tile, a behavior seen in other lizards capable of gustation (Eifler, 1995; Cooper *et al.*, 2002). Furthermore, lizards will lick discarded soft fruit, such as over-ripe banana, that would not normally occur in their environment. Nevertheless, this behavior may be an adaptive response that allows *P. broadleyi* to assess the suitability of figs for consumption.

Age-specific foraging behavior

Like adults, juvenile *P. broadleyi* at Augrabies also feed predominantly on blackflies (Greeff and Whiting, 2000). Unlike adults, juvenile *P. broadleyi* do not eat entire figs, but tend to eat fig seeds and fragments of figs, presumably because of their smaller gape size (Whiting and Greeff, 1997). When feeding on fig fragments, juveniles used head shaking and 'pressing' (using the substrate as leverage) to obtain manageable pieces for ingestion (Whiting and Greeff, 1997). Adults of both sexes also engaged in head shaking and 'pressing' during fig handling, and always used head shaking in combination with 'pressing', but not *vice versa*. Adult males had the shortest fig handling time and both males and females ate entire figs, but unlike juveniles, they never ate fig seeds. When foraging for figs, adults generally ignored insects, whereas juveniles were equally likely to attempt insect prey captures. In addition to blackflies, juveniles were also observed eating small ants, something adults never did (Greeff and Whiting, 2000). While adults shifted foraging mode in response to resource type, juveniles did not, and had similar values for PTM and MPM for insect and fig foraging (Table 13.1). However, juveniles spent more time moving while foraging for insects than adults, and hovered around the 10% cut-off for an active foraging mode (Table 13.1) (Greeff and Whiting, 2000).

Thus, *P. broadleyi* show age-specific differences in foraging behavior partly explained by differences in morphology (body and gape size). Optimal foraging theory predicts that animals ignore lower-quality prey items if the pay-off does not warrant the time and effort expended in capture and prey handling

(Shafir and Roughgarden, 1998). Given the energetic rewards of a ripe fig, the expectation is that lizards would focus their efforts on finding figs when in the presence of a fruiting tree. Why *P. broadleyi* ignore insects while foraging for figs as adults, but not as juveniles, is an intriguing question that may be related to different energetic pay-offs for different lizard–prey body size ratios. It may be that for juvenile lizards there is less of a difference between an insect and a fragment of fruit. Alternatively, age-specific differences in foraging behavior may be explained by learning and/or copying of foraging behavior. We tend to think of lizard foraging behavior as very 'hard wired' and often ignore cognitive processes that may influence a lizard's foraging decisions (but see Day *et al.*, 1999). *Platysaurus broadleyi* appear to be acutely aware of conspecific behavior during foraging. In lizard species that aggregate, copying and learning could be very important processes shaping foraging behavior and even foraging mode. The influence of cognition on foraging behavior and foraging mode, could be a very rewarding, but challenging, future avenue of research.

Risk-sensitive foraging

While searching for figs in debris, lizards appear to engage in risk-sensitive foraging by concentrating their effort along the rock–debris interface. Figs were no more abundant in this area than closer to the tree base. However, *P. broadleyi* are rock specialists and only occasionally cross sandy areas between rock. By staying close to rock, they presumably reduce the risk of predation on a suboptimal substrate.

Influence of insect prey density on foraging mode

The spatial availability, density, and type of prey can influence predator space use and activity in several ways. For example, male lions either hunt for large prey (buffalo) in male coalitions in savanna woodlands where buffalo are more abundant, or associate with females (and scavenge more) in open savanna, during which time they feed on smaller prey (e.g. zebra and wildebeest) (Funston *et al.*, 1998). In lizards, these patterns are less dramatic, but may nevertheless result in a shift of the core activity area of a home range and greater spatial overlap among neighbors (Eifler, 1996). What is less well understood is how lizards alter their foraging behavior and foraging mode under variable food availability. The only cordylid to be studied under variable insect prey availability is *P. broadleyi.* Extreme concentrations of blackflies occur in fast-flowing sections of the Orange River at Augrabies and quickly

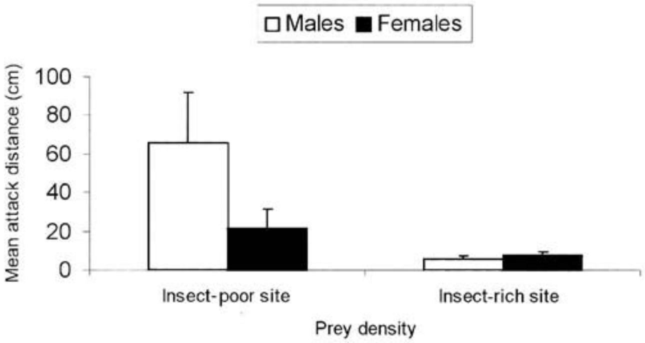

Figure 13.5. Mean (±1 SE) attack distance for adult *Platysaurus broadleyi* at an insect-rich and an insect-poor site. Attack distance was significantly greater for adults attempting to capture blackflies at the insect poor site.

taper off as a function of distance from the river. The highest aggregations of these lizards occur in the region of these plumes (pers. obs.). If insects are abundant, optimal foraging theory predicts that lizards should be able to expend less energy foraging by only selecting insects in close range if food quality is uniform (see, for example, Shafir and Roughgarden, 1998). If insects are abundant, optimal foraging theory predicts that lizards should be more selective and focus on profitable prey (see, for example, Stephens and Krebs, 1986; Shafir and Roughgarden, 1998). Alternatively, if prey quality is uniform, lizards can expend less energy foraging by only selecting insects in close range. This scenario is easily tested in *P. broadleyi* because blackflies are relatively invariant in size. Greeff and Whiting (2000) tested this hypothesis by measuring attack distance in an area of high and low insect density. *Platysaurus broadleyi* had shorter mean attack distances at the insect-rich area (Fig. 13.5). However, *P. broadleyi* did not adjust its foraging mode in any significant way in response to insect density. Lizards performed similar numbers of movements and spent similar amounts of time moving (Table 13.1; Fig. 13.3). What sets *P. broadleyi* apart from other cordylids and many other ambush foragers of insect prey is their high frequency of short movements (Cooper *et al.*, 1997; Greeff and Whiting, 2000). These movements are at least partly dictated by their insect prey. To catch enough small flies to meet their energy budget, *P. broadleyi* are expected to make many, short foraging movements.

Cooper *et al.* (1997) quantified foraging mode in *P. broadleyi* (*Platysaurus capensis* in their paper) at Augrabies. Mean PTM was comfortably within the range of typical ambush foragers (6.6%) (Fig. 13.2A), but they noted that *P. broadleyi* moved frequently during foraging (mean MPM: 1.27) (Fig. 13.2B). However, these movements were brief, resulting in relatively low PTM. They also found wide variation among individuals in both PTM (range: 0–24.17) and

MPM (range 0–6.82), with some individuals exhibiting values comfortably in the range of active foraging (e.g. maximum PTM = 24.2%). Greeff and Whiting (2000) reported measures of foraging mode for males, females, and juveniles from the same population, but under high and low prey availability. I have re-examined this data and present a slight expansion here (Table 13.1). I constructed frequency histograms to graphically capture variation in PTM at the insect sites and to allow visual comparison with the fig site. Frequency distribution of PTM values depicts classic ambush foraging in lizards that were feeding on insects, but active foraging in lizards that were feeding on figs (Fig. 13.6A). I also plotted the frequency distribution for MPM for adults at the two insect

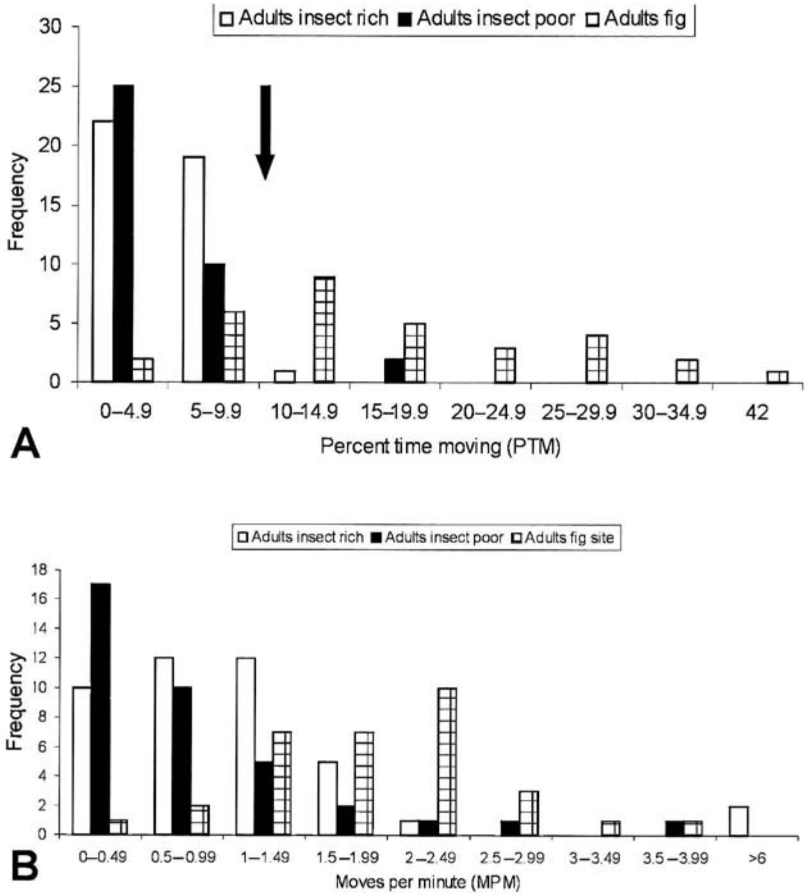

Figure 13.6. Frequency of adult male and female *Platysaurus broadleyi* by (A) intervals of percent time moving (PTM) and (B) intervals of moves per minute (MPM) for the insect-rich site, the insect-poor site, and the fig site. Values for the insect sites cluster around those predicted for an ambush forager; values for the fig site conform to active foraging and are extreme in some cases (e.g. 42% PTM).

sites for comparison with the fig site. Again, MPM values were similar for the two insect sites but significantly lower than for lizards foraging for figs (see Greeff and Whiting (2000) for statistical analysis) (Fig. 13.6B).

How do these patterns relate to phylogeny?

Scincidae (skinks) are basal to the Cordyliformes and considered their sister group (Lang, 1991; Odierna *et al.*, 2002) (Fig. 13.7). As a clade, active foraging in skinks is stable, with only a few exceptions (see, for example, Cooper and Whiting, 2000). Furthermore, gerrhosaurids (the sister group to Cordylidae), based on data for two taxa and parsimony, are considered active foragers (Cooper *et al.*, 1997). Therefore, the most parsimonious scenario for the evolution of foraging mode in Cordylidae is that active foraging was the ancestral state and that an ambush foraging mode has evolved once, independently, within Cordylidae (Cooper, 1995; Cooper *et al.*, 1997). Interestingly, among squamates this is a rare case of foraging mode reversal from active to ambushing within a clade. Ambush foraging is basal among squamates, characterizing the major clades Iguania and Gekkota (with some exceptions), which are basal to the Autarchoglossa, where active foraging first appears (Cooper, 1994). Among cordylids, all genera are clear-cut ambush foragers (Cooper *et al.*, 1997; Mouton

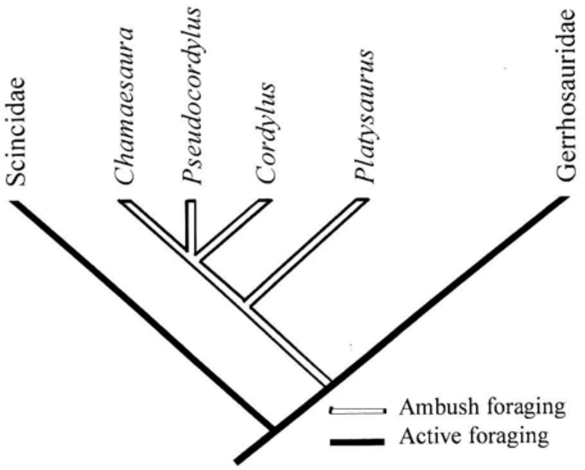

Figure 13.7. Hypothesis for the evolution of foraging mode in the Cordylidae and sister taxa (skinks + gerrhosaurids) following Cooper *et al.* (1997) and more recent data (e.g. du Toit *et al.*, 2002). Phylogenetic information follows Frost *et al.* (2001) and Odierna *et al.* (2002). Data on foraging mode in Gerrhosauridae are limited. Preliminary observations and parsimony suggest that gerrhosaurids are active foragers and therefore that the ancestor of the Cordylidae was an active forager. Branch lengths are not to scale.

et al., 2000; du Toit *et al.*, 2002) and therefore exhibit strong foraging mode stability within their clade. Of the *Platysaurus* species, *P. broadleyi* is the only member of the genus for which foraging mode has been quantified and ambushes insects (albeit with high variation among individuals) but actively searches for figs. So why does *P. broadleyi* exhibit plasticity of foraging mode and how is *P. broadleyi* different from other cordylids?

Covariation of morphology, antipredator behavior, and foraging mode in cordylids

Cordylus are typically tank-like and have short legs; several species are heavily armoured (Mouton and Van Wyk, 1997; Branch, 1998; Losos *et al.*, 2002). Morphology for 24 species, mostly of *Cordylus*, but also several of *Pseudocordylus* and *Platysaurus*, were examined by Losos *et al.* (2002). A subset of these were quantified for sprint speed and antipredator (escape) behavior. Losos *et al.* (2002) were specifically interested in quantifying the trade-off between sprint speed and degree of armature. Degree of armature was inversely related to distance fled from an approaching predator, such that more heavily armoured species took refuge following a short flight distance relative to less armoured species that sometimes did not take refuge. Heavily armoured species are all extreme ambush foragers (Cooper *et al.*, 1997; Mouton *et al.*, 2000), typifying the previously documented link between co-evolved traits such as morphology and foraging mode (Chapter 11, this volume; Vitt and Congdon, 1978; Losos, 1990).

The gerrhosaurids, the sister taxon to the cordylids, contain an interesting mix of dorsoventrally flattened, elongated, and 'cylindrical' forms. They are putatively considered to be active foragers (Cooper *et al.*, 1997). *Gerrhosaurus validus* is a large (max. SVL 285 mm), dorsoventrally flattened lizard that, like *P. broadleyi*, is omnivorous and takes refuge in rock crevices. *Gerrhosaurus flavigularis* and *G. nigrolineatus* are elongate, slender-bodied lizards that are terrestrial and insectivorous (Branch, 1998). The genus also contains the highly specialized *G. skoogi* (formerly *Angolosaurus skoogi*) (Lamb *et al.*, 2003) from the Namib Desert, which is cylindrical, psammophilous and largely herbivorous. Unlike most other lizard herbivores, *G. skoogi* feeds mostly on grasses and seeds (Pietruszka *et al.*, 1986). Considering the variation in habitat use (savannah, rock, sand), morphology (flattened, elongate, cylindrical) and diet (seeds and grasses, insects, fruits and leaves), gerrhosaurids offer enormous potential to test the foraging mode 'paradigm' and to test for additional plasticity of both foraging mode and feeding behavior. Rather than adding taxa that fit neatly into either extreme of foraging mode, we need to search for exceptions to the 'paradigm,' particularly among closely related taxa exhibiting divergent traits and which have divergent diets.

Cordylus and *Pseudocordylus* meet all the expectations of an organism with a specialized morphology and concordant evolution of associated traits linked to foraging mode, but what of *Chamaesaura* and *Platysaurus*? *Chamaesaura* are slender, and serpentiform; they have vestigial limbs that may be used for balance while stationary (Branch, 1998) but not in any significant way during locomotion. Given their slender morphology and adept locomotion in thick grass (features of an active forager) and phylogeny (predicting ambushing), their foraging mode was equivocal (Cooper *et al.*, 1997), until recently determined as sit-and-wait (du Toit *et al.*, 2002). Phylogeny has therefore played a major role in maintaining a relatively invariant foraging mode among the cordylid clade, even in a taxon (*Chamaesaura*) experiencing major morphological specialization.

Platysaurus are a separate clade within Cordylidae (Fig. 13.7) which lack protective spines and armour (Losos *et al.*, 2002); although they use rock crevices, they often only seek refuge as a last resort (*P. broadleyi*) (Whiting, 2002). Furthermore, females (and juveniles) of all species of *Platysaurus*, except one, have dorsal stripes (Broadley, 1978) that during flight may help create an optical illusion to a visual predator (Brodie, 1992) and are therefore probably adaptive. Many actively foraging lizards, for example African *Trachylepis* (formerly *Mabuya*) and many of the African lacertids, also have stripes (Branch, 1998). *Platysaurus broadleyi* have relatively high sprint speed (unpubl. data), tend to use flight to evade predators, and make many short movements during foraging. (Typical ambush foragers use crypsis to avoid detection by predators.) In comparison with *Cordylus*, they have relatively long hindlimbs (Losos *et al.*, 2002), which may facilitate more movement. As such, they do not have the suite of traits characteristic of ambush foragers. Furthermore, *Platysaurus* have extreme dorsoventral flattening, which facilitates the use of vertical rock surfaces (Losos *et al.*, 2002). That *Platysaurus* have stripes, are unconstrained by armature (cf. *Cordylus*), have relatively long hindlimbs, are relatively fast, and stay in the open, are all traits that are likely to promote active foraging.

That *P. broadleyi* is not a typical ambush forager is therefore not surprising. However, disentangling the relative effects of phylogeny and ecology, and the interplay of associated morphological and behavioral traits on foraging mode, is a challenge. *Platysaurus broadleyi* exhibits flexible foraging behavior by ambushing insects and by actively searching for figs. Furthermore, there appears to be an ontogenetic shift towards less active insect foraging as an adult, and adults exhibit high variation in foraging mode with some individuals showing values of PTM and MPM typical of active foragers. Spatial variability in insect prey is by itself insufficient to shift foraging mode, although *P. broadleyi* are more selective foragers when flies are abundant. Therefore, phylogeny has to some degree constrained *P. broadleyi* in its mode of prey capture. However, *P. broadleyi* is flexible enough to exploit another food resource (figs), which is variable in time and space, and thereby switch foraging mode to maximize intake of this resource. Broadley (1978) reported stomach contents for 13 other species of *Platysaurus*. Ten of these contained plant material, suggesting that herbivory/frugivory is widespread in the genus and deserves further attention. It may be that plasticity of foraging mode is more widespread than previously believed, particularly for species that exploit resources that are spatially and temporally variable (see, for example, Eifler and Eifler, 1999).

Conclusions and future directions

Platysaurus broadleyi is a member of a clade of lizards that are sit-and-wait foragers (Cooper, 1994, 1995). However, *P. broadleyi* vary greatly in foraging behavior depending on age, sex, or resource type. As juveniles, they spend almost 10% of their time moving during foraging for insects: right at the ambush – active foraging interface (Perry, 1999). They also make frequent movements. As adults, they spend less time moving while foraging, but still make many short movements. If figs are available, they switch to active or 'herbivorous' foraging (*sensu* Cooper, 1994) to increase the probability of finding an immobile, discrete resource. This is true of all age and sex classes of *P. broadleyi* (Whiting and Greeff, 1997).

The fitness benefits of resource switching are very difficult to measure and are unknown in *P. broadleyi*. If lizards are able to take advantage of a high-quality resource, presumably this will speed growth and fat deposition, all of which should have positive fecundity/fitness spin-offs. But whether lizards trade off the amount of time they spend foraging against reproductive behavior (courtship and territory defense), or simply maximize energy intake, is an intriguing question that would require careful study.

Biologists are always interested in exceptions to the rule, and what these mean for mechanisms explaining diversity in traits and species. With respect to cordylids, all taxa except *Platysaurus* fit into the extreme end of the sit-and-wait category of foraging mode. The *Platysaurus* system suggests two promising areas of research: (1) how widespread is foraging mode plasticity and what is the influence of a high-energy resource that is variable in time and space on foraging mode? and (2) what does having a combination of traits common to ambush and active foragers mean for foraging mode (see above)? A number of lizard species from multiple clades show omnivory and/or ontogenetic or seasonal shifts in diet (see, for example, Durtsche, 2004). We need to explicitly measure foraging mode for these species, from a range of clades. It is unlikely that shifts in foraging mode in response to prey type are rare. For example, Eifler and Eifler (1999) manipulated insect prey spatial availability (but not fruits) for the omnivorous grand skink (*Oligosoma grande*). As a result, females (but not males) switched to making fewer moves of longer duration to feed on larger insects, and ate less fruit. Plasticity of foraging mode has also been documented in non-lizard taxa such as birds and fish. For example, American robins adopt a sit-and-wait foraging mode to capture foliage insects, but actively search for terrestrial insects and fruit (although some variables measured for fruit were intermediate). Foraging mode for American robins was therefore a function of food type and distribution, in addition to habitat structure (Paszkowski, 1982). Brook charr (a fish) show divergent foraging modes in the same population because of intraspecific competition that could ultimately result in a resource polymorphism. Some individuals ambush crustaceans from the lower water column while others actively forage for insects in the upper water column. Furthermore, aggressive individuals adopted either sit-and-wait or active foraging modes, whereas non-aggressive fish had intermediate foraging modes (McLaughlin *et al.*, 1999). More studies experimentally manipulating food availability and food type are needed to test the 'paradigm' and to further explore plasticity of foraging mode as a function of a host of social and environmental variables.

The Gerrhosauridae also beg further study. The incredible range of body shapes, diets, and habitats suggest that foraging mode could be variable. A relatively invariant foraging mode within this clade would strongly support a phylogenetic influence. However, gerrhosaurids are on a continuum from insectivory to almost complete herbivory. Do they actively forage irrespective of food type, as phylogeny would suggest, or is there plasticity of foraging mode?

Finally, we need a better understanding of foraging-related cognitive processes (cognitive ecology *sensu* Dukas, 1998) that may influence foraging mode and how lizards exploit temporally and spatially variable resources (Regal, 1978). *Platysaurus broadleyi* may be a suitable candidate for such studies because they take advantage of heterospecific cues to find fruiting fig trees and have variable foraging modes. They also live in a very simple landscape, occur in large aggregations, and appear to cue in on conspecific behaviors during foraging (e.g. fig stealing) (Whiting and Greeff, 1997). Copying of conspecific behavior and cultural transmission during foraging may be more prevalent in lizards that aggregate than we have previously believed. Furthermore, the ability of animals to track changes in food availability in their environment and to respond by selecting the most economic foraging mode is poorly understood; lizards may be suitable candidates. Investigating the cognitive ecology of foraging in *P. broadleyi* and other lizards promises to be highly rewarding.

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