Foraging modes in lacertid lizards from southern Africa

William E. Cooper, Jr.[1], Martin J. Whiting[2]

[1] Department of Biology, Indiana University-Purdue University, Fort Wayne, Indiana 46805, USA
e-mail: cooperw@ipfw.edu
[2] Department of Herpetology, Transvaal Museum, Paul Kruger Str., P.O. Box 413, Pretoria 0001, South Africa

Abstract. Most lacertids are active foragers, but intrafamilial variation in foraging mode is greater than in most lizard families. We collected data on eight species of African lacertids to assess this variation. Both active and ambush foraging occurred within *Pedioplanis* and *Meroles*. *Meroles ctenodactylus* had a proportion of time moving and proportion of attacked prey detected while moving intermediate to those for actively foraging and ambushing *Pedioplanis*, but its number of movements per minute was exceptionally high. This species has a unique mixed foraging mode. Like active foragers, it seeks food by tongue-flicking while moving and spends a high percentage of the time moving. Like ambush foragers, it searches visually for prey during pauses between movements. Our findings confirm published data on four Kalahari lacertids. We discuss the history of foraging modes in advanced lacertids.

Introduction

Effective foraging behavior is a prerequisite for survival and reproduction of desert lizards, but no single foraging style is most effective for all species. Insectivorous lizards exhibit two major foraging modes: active (wide) foraging and ambush (sit-and-wait) foraging (MacArthur and Pianka, 1966; Huey and Pianka, 1981). Active foragers move through the habitat searching for prey by sight and by frequent tongue-flicking to collect chemical samples (Evans, 1961; Huey and Pianka, 1981), whereas ambushers adopt ambush posts where they remain immobile while scanning visually for approaching prey (Huey and Pianka, 1981; Cooper, 1995, 1997). These foraging modes are highly stable, some entire families of lizards and even higher taxa being restricted to a single mode (Cooper, 1994, 1995, 1997; Cooper et al., 1997). However, in a few families some species are ambushers and others are active foragers (e.g., Huey and Pianka, 1981; Arnold, 1990; Cooper, 1994; Webb and Shine, 1994). Within the two major foraging modes, substantial variation occurs in the degrees and patterns of movements (Perry, 1995).

Differences in foraging behavior among lizards strongly influence important aspects of lizard life history. Foraging modes are correlated with energy budgets (Anderson and Karasov, 1981, 1988), relative clutch mass during reproductive intervals (Vitt and Congdon, 1978; Huey and Pianka, 1981; Vitt and Price, 1982), defense against predators (Huey and Pianka, 1981; Vitt, 1983), and the evolution of the tongue-vomeronasal system and the associated reliance on chemosensory detection of prey (Cooper, 1994a,b, 1995, 1996a,b, 1997a,b). Despite its great importance and numerous studies of ecological and behavioral correlates of foraging mode (Huey and Pianka, 1981; Huey and Bennett, 1986; Cooper, 1994b, 1995a, 1997a), little is known about the ultimate factors that determine which foraging mode is used by a particular species.

Early studies of lizards emphasized the discrete nature of the two foraging modes, but a number of authors later suggested that foraging activity may vary along some portion of a continuum from complete inactivity to continual activity rather than being restricted to two separate ends of the continuum (Magnusson et al., 1985; Pietruszka, 1986; Perry et al., 1990). There is still some disagreement, but the two foraging modes are widely recognized as distinct. McLaughlin (1989) presented evidence that lizard foraging activity does show some continuous variation within each mode, but that the range of activity does not overlap between modes.

Lizard foraging activity is usually determined by measuring either or both of two variables, the proportion of the time spent moving (PTM) and number of movements per minute (MPM) (e.g., Huey and Pianka, 1981; Perry, 1995; Cooper et al., 1997). In a review of all published quantitative data on lizard foraging modes, Perry (1995) chose PTM < 0.100 as the criterion for ambush foraging. Huey and Pianka (1981) considered lizards having PTM as high as 0.143 to be ambush foragers. In addition to PTM and MPM, some investigators have measured mean speeds over the entire period of observation and during movement.

In the Lacertidae, a large family of small lizards ranging throughout much of Europe, Asia, and Africa (Arnold, 1989, 1993), a large majority of species are active foragers. Among 65 species in 13 genera reviewed by Cooper (1994), only two species in two genera had been characterized as ambush foragers. Active foraging is believed to be plesiomorphic in the Lacertidae (Cooper, 1994, 1995), the relatively primitive European taxa all having been characterized as active foragers (Arnold, 1993). Ambush foraging is known only in a few species in the advanced lineage of Africa and Eurasia (Arnold and Burton, 1978; Arnold, 1990, 1993). Even in the advanced lineage, a large majority of species are active foragers. Both foraging modes are believed to exist within the subsaharan genera *Pedioplanis* and *Meroles* (Huey and Pianka, 1981; Arnold, 1990), but quantitative data are available for only six species of Kalahari lacertids, including two species of *Pedioplanis* differing in foraging behavior (Huey and Pianka, 1981).

Here we present quantitative data on the foraging modes of eight species of lacertids representing four genera found in arid zones of South Africa and Namibia. In addition to MPM and PTM, we present information on foraging speeds and frequency of attacks on prey initiated by lizards while moving and still. We compare foraging behaviors of species differing in mode in two genera, describe a mixed foraging mode in *Meroles ctenodactylus*, and discuss the evolution of foraging modes in advanced lacertids and possible reasons for intrageneric variation.

Methods

Foraging data were collected at several sites, all in South Africa except as noted. Observations were conducted on *Meroles ctenodactylus* on 29 February and 1 March 1996 at Hondeklipbaai (30° 18′S, 17° 16′E); *M. knoxii* on 29 February and 1 March 1996 at Hondeklipbaai and on 3 March 1996 at Papendorp (31° 41′S, 18° 13′E); *M. reticulatus* on 25 February 1996 at the foot of Dune 7 (22° 58′30″S, 14° 40′24″E) in Namibia near Walvis Bay; *Pedioplanis lineoocellata* in the Kalahari on 24 March at Koegechop (28° 15′S, 21° 5′E) and 26 March 1993 at Loerkop (28° 14′S, 20° 55′E); *P. namaquensis* in Namaqualand at Ybeep (29° 58′S, 17° 59′E) on 27 and 28 March 1993 and Wolfhoek (30° 22′S, 18° 12′E) on 29 March 1993, with single observations on 24 March at Koegechop and 26 March 1993 at Loerkop; *P. undata* on 11 to 14 October 1994 and 20 and 21 February 1996 at Farm Bergvellei in Namibia (19° 37′S, 14° 40′E, 20 km west of Kamanjab); *Heliobolus lugubris* on 24 March 1993 at Loerkop in the Kalahari and 20-21 February 1996 at Farm Bergvellei. Data were collected for a single *Nucras tessellata* on 28 March 1993 at Ybeep.

Observations were made only on sunny days when lizards were active. We located lizards with binoculars and unaided vision while walking slowly through an area. Upon detecting a lizard, the observer stopped moving to reduce possible disturbance to the lizard. Data were recorded on microcassette tapes only for individuals that did not appear to have been disturbed. Focal animals were observed continuously for 10 min if possible, but often less if the lizard moved out of sight. Minimum acceptable observation time was 1.5 min. To ensure that data were collected only once per individual, we avoided repeated sampling in the same area.

For each lizard we recorded species, locality, date, and foraging behaviors, including time moving and stationary, distance moved (within ca. 2 cm for very short movements, but ca. 0.5 m for the longest movements of $\geqslant 10$ m), and feeding attempts. Postural adjustments not involving translation (e.g., turning, tail movements) were not recorded. Immobility was recorded whenever a lizard paused for one or more seconds. Shorter intervals would have been inaccurate due to competing demands of reading time, observing lizard movements, and recording both.

From the movement data we calculated PTM, MPM, and two measures of foraging speed (Huey and Pianka, 1981). Moving speed was average speed while moving, i.e., distance moved divided by time spent moving. Mean speed was calculated over the entire observation interval, including time not moving. The measurements of mean speed and movement speed are rather crude due to limitations in measures of distances moved, but are more than adequate to show differences among species. We pooled data for juveniles and adults after ascertaining that there were no significant age differences in MPM or PTM (Mann-Whitney *U* tests).

All of the movement measures reflect activity levels, which are sensitive to factors such as body temperature and digestion. If care is not taken to record data only for lizards that are warm enough to forage normally and have not become so full as to stop foraging, activity data may give a distorted view of foraging. Although we could not completely control effects of differing environmental temperatures, we minimized effects of temperature by collecting data only at times of day when lizards normally forage and in light and temperature conditions affording them the opportunity to maintain body temperatures at preferred levels through thermoregulation.

In addition to activity, the two foraging modes have another basic difference: Ambushers initiate attacks on prey while immobile, whereas active foragers initiate attack after finding the prey while moving. We recorded feeding attempts, noting whether attacks were initiated by lizards that detected (often moving) prey while immobile or by lizards that were moving when they detected the prey. The proportion of attacks initiated while moving (PAM) provides an independent measure of foraging mode that is much less subject than the activity measures to influence by variation in factors such as temperature and satiation. PAM must be very low in ambush foragers and is expected to increase with degree of active foraging.

Differences among species in proportions of moves of various durations were analyzed using chi square tests. For such tests to be completely valid, movement duration must be independent of individuals, but we recorded numerous movements per individual, possibly violating the assumption of independence. Interspecific differences in duration could be tested using average duration for each individual, but the tests would not permit examination of the distribution of movement durations. Short of collecting data on one movement each for a very large sample of individuals, the tests employed provide a reasonable way to approximate significance of differences in duration distributions. Two-tailed tests were conducted with a basic $\alpha = 0.05$, which was adjusted downward for number of tests conducted by a sequential Bonferroni procedure (Wright, 1992). The pattern of significance was not affected by adjustment.

The evolution of foraging mode on the phylogeny of advanced lacertids was traced using MacClade 3.01 (Maddison and Maddison, 1992). Figure 1 depicts a partial lacertid phylogeny (Arnold, 1989, 1993) showing relationships for the advanced lacertid genera most closely related to *Meroles* and *Pedioplanis*.

Results

Two of the three species of *Pedioplanis* had similar high values of PTM, both ten times that for *P. lineoocellata* (table 1). Of these two, *P. namaquensis* appears to have had a

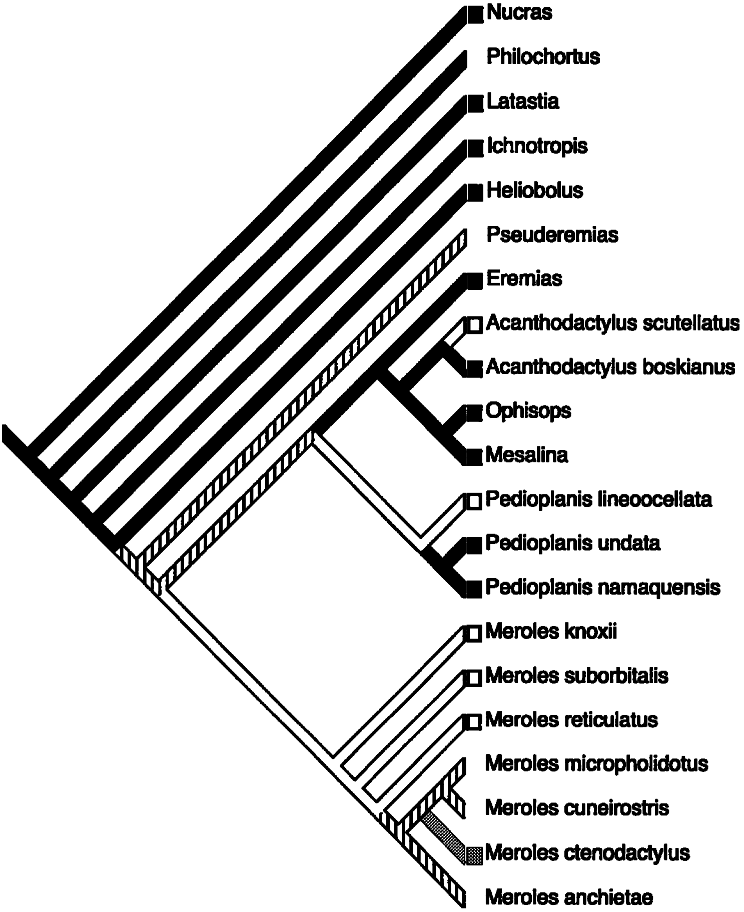

Figure 1. Reconstruction of the evolution of foraging mode in lacertid genera most closely related to *Meroles*, all members of the advanced African and Middle Eastern clade. Active foraging is indicated by solid black branches, ambush foraging by empty branches, and mixed foraging mode by a gray branch. Equivocal foraging mode is indicated by hatched branches. The absence of small boxes between branch tips and taxonomic names indicates that data are lacking for those taxa. Thus, the active foraging mode indicated for Philochortus is inferred by parsimony, but there are no data to confirm this expectation.

slightly higher MPM (table 1). *Pedioplanis lineoocellata* had low values of moving speed and mean speed, both several times lower than the corresponding values for the other two species (table 2). The only feeding attempt observed by *P. lineoocellata* was an ambush (table 2). Completing the contrast, the other species initiated a large majority of attacks after finding prey while moving (table 2).

Very high values of PTM and PAM indicate that *Heliobolus lugubris* is an active forager. Due to its relatively low speed while foraging and high PTM, the difference between moving and mean speeds was much lower than in some other species (table 2). Foraging

Table 1. Proportion of time moving (PTM), movements per minute (MPM), and total time observed for eight species of lacertids from southern Africa.

Species	PTM			MPM			n	Time
	x	s_x	Range	x	s_x	Range		(min)
Pedioplanis undata	0.50	0.05	0.15-0.81	1.39	0.17	0.60-3.28	16	119.4
P. namaquensis	0.54	0.04	0.15-0.88	1.87	0.15	0.60-3.75	26	237.4
P. lineoocellata	0.05	0.04	0.00-0.17	0.49	0.39	0.00-0.20	4	40.5
Meroles ctenodactylus	0.29	0.06	0.20-0.50	3.24	0.60	1.30-4.40	5	50.0
M. knoxii	0.07	0.02	0.00-0.34	0.61	0.11	0.00-1.71	27	235.3
M. reticulatus	0.00	0.00	0.00-0.00	0.05	0.05	0.00-0.20	4	34.9
Heliobolus lugubris	0.64	0.05	0.24-1.00	1.49	0.18	0.50-2.60	14	89.6
Nucras tessellata	0.90			0.70			1	10.0

Table 2. Average lizard speeds, given as mean (standard error), both while moving and during the entire observation interval, and the proportion of feeding attempts initiated by lizards that detected their prey by active search (PAM). *Meroles reticulatus* is omitted due to lack of data.

Species	Speed (km/h)				PAM	n
	Moving	n	Mean	n		
Pedioplanis undata	0.482 (0.058)	1	0.212 (0.029)	16	1.00	4
P. namaquensis	0.421 (0.047)	19	0.209 (0.029)	19	0.95	58
P. lineoocellata	0.104 (0.065)	2	0.004 (0.004)	3	0.00	1
Meroles ctenodactylus	0.356 (0.047)	5	0.104 (0.025)	5	0.33	6
M. knoxii	0.572 (0.090)	21	0.025 (0.007)	26	0.00	6
Heliobolus lugubris	0.241 (0.068)	13	0.144 (0.040)	13	1.00	45
N. tessellata	0.108	1	0.097	1	1.00	1

speeds were low at least in part because 10 of the 14 lizards observed were juveniles having body lengths no more than half that of adults. MPM was similar to that of the actively foraging species of *Pedioplanis*. The single *Nucras tessellata* had very high PTM, but relatively low MPM because it spent most of its time foraging intensively beneath two large bushes, where it moved very slowly, probing holes and litter with its snout. It located a prey by tongue-flicking and unearthed it by digging.

Meroles knoxii and *M. reticulatus* had low PTM and MPM values typical of ambush foragers (table 1). The low PAM and mean speed of *M. knoxii* (table 2) agree with the other variables in indicating ambush foragering. We usually observed the lizards under or just outside the edges of bushes. A lizard would rush out to catch prey, then return to the bush. *Meroles ctenodactylus* spent a much greater proportion of the time moving than its congeners (table 1), and had higher mean speed than *M. knoxii* (table 2). PAM was higher

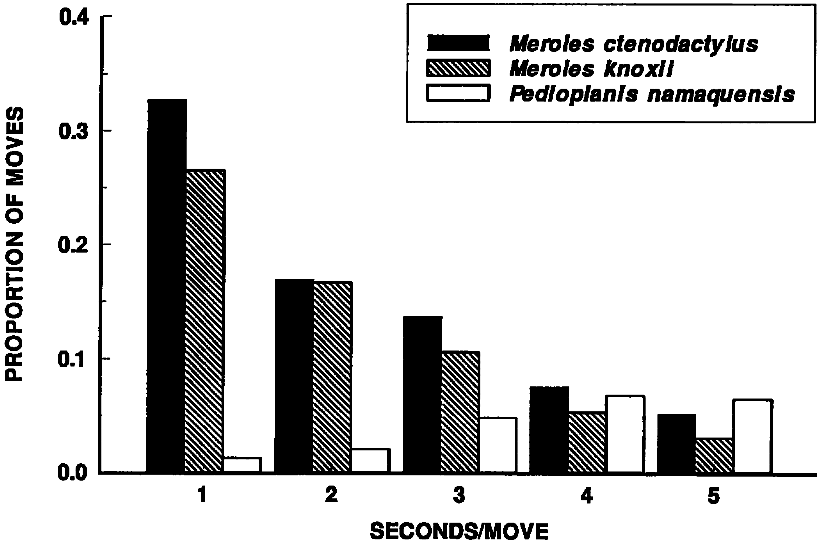

Figure 2. The proportional distribution of movements lasting five seconds or less in a typical active forager, *Pedioplanis namaquensis*, a typical ambush forager, *Meroles knoxii*, and a lizard having a mixed foraging mode, *Meroles ctenodactylus*.

in *M. ctenodactylus* than in any of the ambush foragers, but lower than in the active foragers (table 2).

The frequency distributions of movement durations were very similar in *M. ctenodactylus* and *M. knoxii* (fig. 2). When tested in categories of 1-5, 6-10, and > 10 seconds (Table 3), the distributions did not quite differ significantly (X^2 = 7.14, df = 2, $P < 0.063$), with *M. ctenodactylus* having a slightly higher proportion of moves lasting five or fewer seconds and a slightly lower proportion thereafter. When analyzed separately for durations of each second up to five seconds (fig. 3), the proportions of movements lasting five seconds or less did not differ between the two species (X^2 = 1.00, df = 4, $P > 0.10$). The greater PTM of *M. ctenodactylus* is attained by a higher frequency of movements of all durations, as revealed by the very high MPM.

Rather than exhibiting long intervals of nearly continuous movement as do active foragers, *Meroles spp.* made many brief moves. Compared with the typical active forager *P. namaquensis*, *M. ctenodactylus* and *M. knoxii* had much higher proportions of brief moves and lower proportions of movements lasting more than five seconds (figs. 2, 3). For movements of all durations, the distribution of durations differed markedly among species (X^2 = 173.90, df = 4, $P < 0.001$). *Pedioplanis namaquensis* differed from *M. ctenodactylus* (X^2 = 146.40, df = 2, $P < 0.001$) and *M. knoxii* (X^2 = 79.99, df = 2, $P < 0.001$) in having a much lower proportion of moves lasting 5 or fewer seconds and a higher proportion of longer-lasting moves (fig. 2). Movements of longer duration accounted for a much greater proportion of PTM in *P. namaquensis*. The difference is most

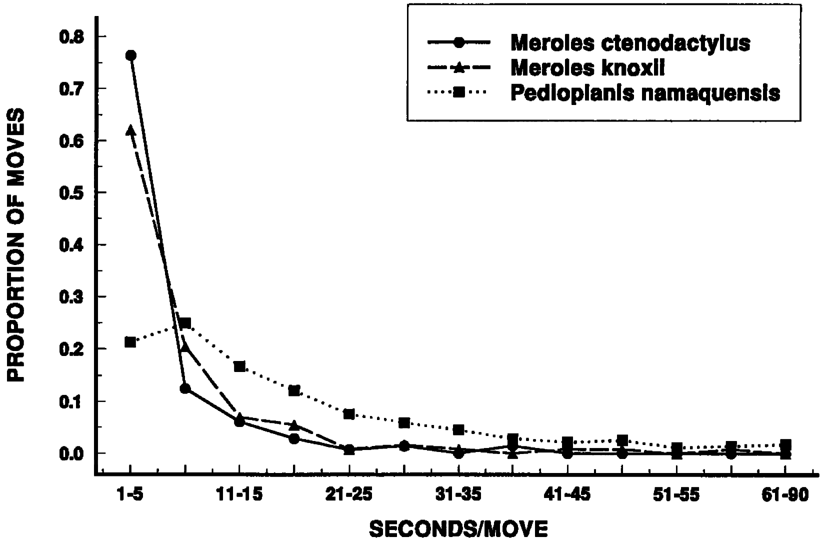

Figure 3. The proportional distribution of movement duration in a typical active forager, *Pedioplanis namaquensis*, a typical ambush forager, *Meroles knoxii*, and a lizard having a mixed foraging mode, *Meroles ctenodactylus*.

pronounced for movements of 1-5 seconds (fig. 3). Considering only movements lasting up to 5 seconds, the distribution of movements differs strongly among species ($X^2 = 78.64$, df = 8, $P \ll 0.001$), with each species of *Meroles* having substantially higher proportions than *P. namaquensis* for moves lasting 1-3 seconds ($X^2 = 58.14$, df = 4, $P \ll 0.001$ for *M. ctenodactylus*; $X^2 = 57.99$, df = 4, $P \ll 0.001$ for *M. knoxii*).

The history of foraging in advanced lacertids is depicted in figure 1. Active foraging has been retained in at least the five upmost genera of figure 1, but there is considerable uncertainty about the advent of ambush foraging. Below *Pseuderemias* are two equally parsimonious pathways. Ambush foraging could have been present in the common ancestor of *Meroles* and the taxa below *Pseuderemias*, having evolved in the common ancestor or earlier. In that case, active foraging would have reevolved in the common ancestor of the *Eremias-Acanthodactylus-Ophisops-Mesalina* clade. Ambush foraging also might have evolved separately in the common ancestors of *Pedioplanis* and *Meroles*. Either way, the common ancestor of *Meroles* was an ambusher and the mixed foraging of *M. ctenodactylus* is derived.

Discussion

Foraging modes in Pedioplanis, Heliobolus, Nucras, *and* Meroles

Our data confirm the existence of both foraging modes in *Pedioplanis*, in agreement with earlier assessments (Huey and Pianka, 1981; Arnold, 1990): *P. namaquensis* and *P. undata* are highly active foragers, and our limited data strongly suggest that *P. lineoocellata* is an ambusher. Our PTM values for *P. namaquensis* are nearly identical with those Huey and Pianka (1981), and the speeds are quite similar. The only notable difference is lower MPM in the present study. The strong similarity for the sole species having a reasonably large sample size in both studies suggests that the methods used are reliable between investigators. Minor differences in PTM, MPM, and speeds for *P. lineoocellata* between our study and that of Huey and Pianka (1981) may reflect sampling error or differences in variables such as habitat, diet, season, and temperature.

Our PTM and MPM data on *Heliobolus lugubris* agree with those of Huey and Pianka (1981) in indicating highly active foraging. That our values of MPM and speed were substantially lower than those reported by Huey and Pianka (1981) may be attributable to differences in ecological conditions or between populations. Our single observation of *Nucras tessellata* (tables 1, 2) confirms the active foraging mode of this species (Huey and Pianka, 1981).

Meroles knoxii and *M. reticulatus* are ambushers, as is *M. suborbitalis* (Huey and Pianka, 1981). The mean speed of *M. knoxii* (table 2) is somewhat lower than those of the two lacertid ambushers studied by Huey and Pianka (1981). In contrast, *M. ctenodactylus* had a PTM typical of an active forager. Its MPM was much higher than for the other lacertids in this study (table 1) and is the second highest reported for a lacertid (Pianka et al., 1979). Moving speed was somewhat greater in *M. knoxii* than in *M. ctenodactylus* (table 2), and both values were in the range reported by Huey and Pianka (1981) for other lacertids, bracketing the value for *M. suborbitalis*. Moving speed was not related to foraging mode in the lacertids studied.

Arnold (1990) suggested that advanced species of *Meroles* occupy more open habitats and forage less actively than the basal *M. knoxii*. Branch (1988) characterized *M. knoxii* as active lizards often seen dashing between bushes. Surprisingly, our data show *M. knoxii* to be an ambusher. At both sites, the lizards spent most of the time immobile under cover of bushes or in the open at the edges of bushes. Although they spent little time in the open away from bushes, their presence was obvious during movements from one bush to another, giving the misleading impression of high activity. Foraging appears to be conducted primarily by ambush under bushes and shortly beyond them. The rapid movements between bushes presumably minimize exposure to predators and high temperatures and maximize time in profitable foraging patches.

Using Arnold's (1990) well-corroborated phylogeny, the high PTM and MPM of *M. ctenodactylus* are derived within *Meroles* (fig. 1). A recent review of quantitative data on lizard foraging revealed no gap in PTM between modes at an arbitrary cutoff point of 0.10 (Perry, 1995). Had Perry selected a slightly higher value, a substantial gap would have been apparent, no species having PTM ca. 0.15-0.20. The value for *M. ctenodactylus* places it among active foragers, but its MPM is exceptionally high and its mean speed is low for active foragers of similar size. Unlike its two congeners, *M. ctenodactylus* spent the a large majority of the time observed in the open on sand between bushes, in agreement with Arnold's (1990) characterization.

Although it forages more actively than less derived congeners, *M. ctenodactylus* has not simply reevolved active foraging as conducted by ancestral lacertids. Its foraging behavior fits neither conventional foraging mode. It spends a much higher percentage of time moving than ambush foragers, but makes frequent moves of short duration rather than exhibiting substantial intervals of nearly continuous movement as do typical active foragers (figs. 2, 3). Compared with the active forager *P. namaquensis*, both *M. ctenodactylus* and *M. knoxii* had much higher proportions of brief and lower proportions of longer-lasting movements (figs. 2, 3), reflecting the retention by *M. ctenodactylus* of the foraging repertoire of ambushing ancestors within *Meroles*.

Meroles ctenodactylus also exhibits atypical tongue-flicking and patch selection. Ambushers tongue-flick at ambush posts almost exclusively immediately after arrival and just before moving to another location (Cooper et al., 1994), but wide or intensive foragers tongue-flick while moving to investigate sites where prey may be hidden (Evans, 1961; Anderson, 1993; Cooper, 1994). *Meroles ctenodactylus* often tongue-flicked when immobile immediately after arriving at a new spot and just before moving, but also often while moving. One individual located hidden prey by tongue-flicking, a behavior typical of active, but not ambush, foragers.

Another behavior distinguishing *M. ctenodactylus* from typical active foragers is that each time it stops, it stands with forelegs fully extended and head elevated until it moves again. Although it might promote detection of predators or reduce thermal stress, this posture also may permit more effective scanning for prey during periods of immobility. A similar posture adopted by *Podarcis sicula* has temporal dynamics similar to scanning by *Podarcis muralis* (Avery, 1991; Avery et al., 1993). In saltatory foraging, a rapid stop-and-go pattern studied primarily in fish (O'Brien et al., 1990), frequent moves bring the forager to new sites to be scanned, as in *M. ctenodactylus*. However, in comparison with typical saltatory foragers, *M. ctenodactylus* has longer scan durations relative to brief movements and more variable movement durations.

Ambushing lizards have long scan intervals while immobile and brief interscan intervals during movements. Active foragers have long scan intervals while moving and, at least for chemosensory investigation, interscan intervals while immobile. The most remarkable aspect of the foraging behavior of *M. ctenodactylus* is scanning (prey search) during both movement and while still. These lizards search for prey by tongue-flicking while moving and scan for prey visually using a specific posture while immobile. In addition to longer movements accompanied by tongue-flicking, *M. ctenodactylus* frequently make brief movements without tongue-flicking and adopt the scanning posture between movements. By scanning while moving and immobile, these lizards gain advantages of both foraging modes. While immobile, they may detect prey moving on the surface, the fare of ambushers (Huey and Pianka, 1981). While active they can locate hidden prey (Huey and Pianka, 1981). *Meroles ctenodactylus* thus has a mixed foraging mode containing elements of ambush and active foraging. Possible benefits of a mixed mode are access to greater diversity of prey, the potential for nearly continuous foraging, and flexible adjustment of foraging to currently available prey types.

Evolution of foraging in advanced lacertids

There have been at least two, and possibly three independent origins of ambush foraging, one origin of mixed foraging, and a possible reversal from ambushing to active foraging in advanced lacertids (fig. 1). Among the advanced genera only active foraging is known in *Nucras*, *Heliobolus*, *Eremias*, *Latastia*, *Mesalina*, *Ophisops* and *Ichnotropis* (this paper, Pianka et al., 1979; Huey and Pianka, 1981; Bowker, 1984; Perry et al., 1990; Cooper, 1994; Perry, 1995). No data are available for *Philochortus*, which is only inferred to forage actively, or for *Pseuderemias*. In *Pedioplanis* the most basal species are believed to be ambush foragers, as in *Meroles*, but at least one species is a confirmed ambush forager (Arnold, 1990; this paper). At least one species of *Acanthodactylus* is also an ambush forager (Perry et al., 1990, fig. 1).

Given that the three basal species of *Meroles* for which foraging data are available are ambush foragers (Arnold, 1991, fig. 1), the mixed foraging mode of *M. ctenodactylus* appears to have arisen in the common ancestor of the four lowest species in figure 1, the common ancestor of *M. ctenodactylus* and its pair of sister species, or in *M. ctenodactylus* itself. Foraging modes of the sister species *M. cuneirostris* and *M. micropholdotus* are unknown, but very flexible foraging occurs in *M.* (*Aporosaura*) *anchietae*, which sit and wait for seeds while the wind is blowing, but forage actively for insects when it is not (Robinson and Cunningham, 1978).

That both active and ambush foraging coexist in *Pedioplanis* and *Acanthodactylus* and ambush and a mixed foraging mode occurs in *Meroles* reveals a strong potential for evolutionary plasticity in basic aspects of foraging behavior in the advanced lacertid clade (Huey and Pianka, 1981; Perry et al., 1990; this paper). Because all species in most lizard families are restricted to the same foraging mode (Cooper, 1994a,b), this is unusual among lizards.

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