Copeia, 2000(1), pp. 112–118

Ambush and Active Foraging Modes Both Occur in the Scincid Genus *Mabuya*

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Foraging methods of insectivorous lizards fall into two major modes, ambush foraging, in which the lizard waits immobile to detect prey, and active foraging, in which the lizard moves through its habitat while searching for prey. Both modes exhibit remarkable phylogenetic stability. Ambush foraging is the sole mode of all iguanians examined to date, and active foraging is the only known mode in large scleroglossan clades such as Teiidae and Varanoidea. We present quantitative data on foraging behavior demonstrating the existence of intrageneric variation in foraging mode in the scincid genus *Mabuya* in southern Africa. Like the large majority of skinks, *Mabuya striata sparsa*, *M. sulcata*, and *M. variegata* are active foragers that have high values of number of movements per minute (MPM), proportion of time spent moving (PTM), and mean speed (average speed including time spent immobile) but relatively low speed while moving. In contrast, *M. acutilabris* and *M. spilogaster* are ambush foragers having significantly lower MPM, PTM, and mean speed but higher average speed while moving than the other species. The importance of these findings is twofold. First, intrafamilial variation in foraging mode in Scincidae and intrageneric variation are verified for *Mabuya.* Second, because intrageneric variation in foraging mode was previously known from quantitative data only in the lacertid genera *Acanthodactylus* and *Pedioplanis* (and atypically in *Meroles*), an excellent opportunity is provided to test hypotheses about foraging mode without confounding interfamilial phylogenetic differences.

SUCCESSFUL foraging is a *sine qua non* for survival and reproduction in a wide range of taxa; and differences in habitat features, prey abundance and distribution, competitors, predators, and phylogeny presumably jointly determine the most effective foraging style for a given population. Among insectivorous lizards, two major foraging modes are recognized, active (wide) foraging and ambush (sit-and-wait) foraging (e.g., Pianka, 1966; Huey and Pianka, 1981). Active foragers move through the environment while searching for prey visually and by tongue-flicking to locate chemical cues (Evans, 1961; Cooper, 1995, 1997a). In contrast, ambush foragers wait motionless at ambush posts where they search visually (Huey and Pianka, 1981; Cooper, 1995, 1997a).

Foraging mode may profoundly affect several aspects of life history and behavior (e.g., Stamps, 1976; Huey and Pianka, 1981; Cooper, 1997a). Active foragers expend far more energy than ambushers to obtain food because of their prolonged movement but have higher capture rates (Anderson and Karasov, 1981, 1988) in part because of ability to encounter temporary patches of high prey abundance (Huey and Pianka, 1981; Huey and Bennett, 1986). Active foragers often have greater stamina than ambushers but lower sprint speeds (Huey, 1982; Nagy et al., 1984). Active foragers are more vulnerable than ambush foragers to ambush predators (Huey and Pianka, 1981) and use speed as the primary defense, but ambushers employ crypsis through immobility and fleeing when crypsis fails (Vitt, 1983). Because of the high cost of carrying a large egg mass while searching for food, active foragers have lower relative clutch mass than active foragers (Vitt and Congdon, 1978; Huey and Pianka, 1981; Vitt and Price, 1982). Active foragers use the lingual-vomeronasal system to locate prey, but ambush foragers do not (Cooper, 1994a, 1995, 1997a), and this is reflected in differences in chemosensory morphology (Cooper, 1996a, 1996b; 1997b).

Despite differences in degree of active foraging among taxa, the two basic foraging modes are quite stable in diverse lizard taxa. Only a single mode occurs in most families of insectivorous lizards, and some higher taxa appear to exhibit only one mode, for example, ambush in iguanians, active foraging in Varanoidea (Cooper, 1994b, 1997a; Cooper et al., 1997). However, both foraging modes occur in a few families, notably Lacertidae (Huey and Pianka, 1981; Perry et al., 1990; Cooper and Whiting, in press), Gekkonidae (Arnold, 1990; Perry, 1995), Pygopodidae (Webb and Shine, 1994), and Scincidae (e.g., Castanzo and Bauer, 1993; Cooper, 1994b).

When most of the ideas about life-history consequences of foraging mode were being developed, comparative methods that take phylogeny into account were unavailable to ecologists. Because of the absence of variation in foraging mode among close relatives, most of the tentative conclusions drawn in the literature regarding hypotheses about relationships between foraging mode and other life-history and behavioral traits have been based on comparisons between species belonging to distantly related families, each having a different, fixed foraging mode. They suffer from the possibility that the observed differences might be attributable to phylogenetic differences among families unrelated to foraging behavior. There are only two major exceptions, comparative studies of evolutionary correlation between foraging mode and chemosensory detection of prey (Cooper, 1995, 1997a) and studies of correlates of foraging mode in lacertids from southern Africa (e.g., Huey and Pianka, 1981; Nagy et al., 1984).

Huey's studies remain cogent because hypotheses were tested in closely related lacertid species differing in foraging mode, but they provide only fragments of the information needed to test the broad evolutionary hypotheses using the comparative method. Data on members of various families in which both foraging modes occur can be useful in comparative studies, but the number of transitions in foraging mode at the familial level limits the usefulness of this approach. Intrafamilial and intrageneric variation in foraging mode can provide additional datapoints for comparative analyses that are more convincing due to the greater recency of common ancestry.

A first step toward quantitative comparative hypothesis testing is measurement of foraging mode. We present the first quantitative data on several measures of the foraging behavior of several lygosomine scincid lizards of the genus *Mabuya* from southern Africa, all but one of them syntopic, and show that they differ in foraging mode. We examine several behavioral variables used to determine foraging mode, characterize the foraging modes of the species, and briefly discuss their foraging behavior and its bearing on hypotheses about other life-history and behavioral variables. Finally, we recommend these species of *Mabuya* as excellent subjects for study of the consequences of foraging mode. Although the precise relationships among species of *Mabuya* are unknown, their closer relationship to each other reduces the phylogenetic difference from which many previous studies suffered. However, the genus seems to be paraphyletic (Greer, 1977), and it is not known whether southern African species are monophyletic.

MATERIALS AND METHODS

Data on foraging behavior were collected in Namibia and South Africa. *Mabuya acutilabris, M. spilogaster, M. sulcata*, and *M. variegata* were observed at Farm Bergvellei in the Outjo District of northwestern Namibia (19°37′S, 14°40′E, 20 km west of Kamanjab). All data at Farm Bergvellei except for *M. sulcata* were collected 7–13 October 1994. Additional data on *M. sulcata* were collected at Farm Bergvellei on 19–22 February 1996 and at Ybeep in Namaqualand, South Africa (29°58′S, 17°59′E) on 27 March 1993 (single observation). *Mabuya striata sparsa* was observed on Farm Arabi, Keetmanshoop District in southeastern Namibia (26°25′S, 18°45′E) on 20–21 October 1994.

We conducted focal observations only on sunny days when lizards were active. We slowly walked through the habitat using binoculars and unaided vision to locate lizards. Upon detecting a lizard, the observer stopped moving to minimize any disturbance to the lizard. We recorded data on microcassette tapes, excluding data on individuals that appeared to have been disturbed. We observed focal animals continuously for 10 min if possible, but sometimes less if the lizard moved out of sight behind rocks, in vegetation, or into holes or crevices. All focal observations lasted at least 1.5 min. Of the focal observations, 51 lasted the full 10 min, 11 more lasted at least 5 min, and 14 lasted less than 5 min. We sampled the same area only once to ensure that datapoints were independent.

For each focal observation we recorded the species, locality, date, time, and behavior. The foraging behaviors noted were times spent moving and stationary, distance moved, and feeding attempts. We also noted whether feeding attempts were initiated by lizards that detected prey while the lizards were immobile or by lizards that located prey by active search. Postural adjustments that did not involve translation to a new location, such as tail movements and turning in place, were not recorded. Immobility was recorded whenever a lizard paused for two or more consecutive seconds. Use of shorter intervals might have been inaccurate because of the difficulty of simultaneously observing lizards, reading time on a stopwatch, and recording times at which transitions between movement and immobility occurred.

The foraging measure most directly related to food acquisition is the percentage of attacks on prey or captures initiated by lizards that discov-

TABLE 1. SAMPLE SIZES (n), MOVEMENTS PER MINUTE (MPM), PROPORTION OF TIME SPENT MOVING (PTM), AND TOTAL TIME (min) IN FIVE SOUTHERN AFRICAN *Mabuya*.

Taxon	n	MPM			PTM			Total time (min)
		$\bar{x}$	SE	range	$\bar{x}$	SE	range	
Mabuya acutilabris	27	0.366	0.067	0.000–1.300	0.014	0.003	0.000–0.042	269.47
M. spilogaster	11	0.305	0.109	0.000–1.000	0.029	0.060	0.000–0.199	105.10
M. striata sparsa	2	1.667	0.471	1.200–2.143	0.414	0.012	0.403–0.424	7.31
M. sulcata	20	1.354	0.189	0.060–4.600	0.492	0.060	0.083–0.887	118.50
M. variegata	16	1.187	0.220	0.000–3.000	0.288	0.064	0.000–0.726	115.80

ered prey as a result of mobile searching (PAM percent attacks while moving), but this measure has been ignored because it would often prolong observation sufficiently to impede comparative studies. Our recorded data on attacks were useful only to corroborate other measures of foraging activity.

Degree of foraging activity is usually measured in several other ways believed to be tightly correlated with PAM, the most common measures of lizard foraging activity being the proportion of the time spent moving (PTM) and the number of movements per minute (MPM; e.g., Huey and Pianka, 1981; Perry, 1995, Cooper et al., 1997). Active foragers typically have much higher PTM and MPM than ambush foragers. Because some variation exists within modes, there has been minor disagreement about cutoff values to distinguish modes (Huey and Pianka,1981; Perry, 1995), but differences in PTM and MPM are usually clear-cut. From each lizard's movement data, we calculated MPM and PTM.

Data on other correlates of foraging mode are much rarer. Ambush foragers are expected to show greater speed while moving (primarily attacking prey or moving to new ambush posts) and slower average speed (because they are largely immobile) than active foragers, which often move slowly, tongue-flicking to locate chemical prey cues and visually searching complex litter and plant surfaces in prey patches (Huey and Pianka, 1981; Anderson, 1993). We calculated moving speed as the distance moved divided by the time spent moving (i.e., the average speed while moving). Mean speed was total distance moved divided by the duration of the entire observation interval including time spent motionless (i.e., the average speed over the entire interval including any time not moving). Data for all these variables are reported as $\bar{x} \pm 1.0$ SE. Two difficulties with activity data are that it is sometimes difficult to distinguish between immobile ambush foraging and basking for warming or to enhance digestion. To avoid these difficulties, data were recorded only at times of day when lizards had had the opportunity to reach preferred body temperature and lizards were active.

Statistical tests of differences in the foraging variables among species were conducted for the four *Mabuya* species from Farm Bergvellei. *Mabuya striata sparsa* was excluded because of insufficient sample size. Because of heterogeneity of variance and nonnormality of MPM, parametric analysis of variance could not be used. Differences among species in MPM were analyzed using a Kruskal-Wallis one-way analysis of variance followed by multiple comparisons (Zar, 1996). All but one of the significance tests were two-tailed. A single one-tailed test of difference in speed while moving between *M. variegata* and *M. acutilabris* was justified by higher predicted moving speed for an ambush forager. Alpha was 0.05. Because of expected variation in speed with interspecific differences in body size, we conducted two Mann-Whitney *U*-tests of differences in size-adjusted mean speed. Although the ratios of maximum body length of *M. acutilabris* and *M. spilogaster* to *M. sulcata* are 0.74 and 0.83 (Branch, 1988), mean speed of *M. sulcata* was reduced by 50% for these tests. Although the alpha level required for significance in these tests was adjusted downward by a sequential Bonferroni procedure (Wright, 1992) as if all six possible paired comparisons had been made, the pattern of significance was not affected.

RESULTS

Two distinct patterns of foraging movements were observed in *Mabuya* (Tables 1–2). Three species, *M. sulcata, M. striata sparsa*, and *M. variegata* had high MPM and PTM values typical of active foragers and had low speed while moving but high average speed. The remaining species, *M. acutilabris* and *M. spilogaster*, had much lower MPM and PTM values typical of ambush forag-

TABLE 2. AVERAGE SPEED WHILE MOVING (m/s), AVERAGE SPEED DURING THE ENTIRE OBSERVATION INTERVAL (m/s), AND THEIR SAMPLE SIZES (n) FOR FIVE SOUTHERN AFRICAN *Mabuya*.

	Moving speed				Mean speed			
Species	n	$\bar{x}$	SE	range	n	$\bar{x}$	SE	range
Mabuya acutilabris	23	0.188	0.039	0.034–0.883	27	0.002	0.001	0.000–0.010
M. spilogaster	7	0.210	0.088	0.012–0.610	11	0.003	0.002	0.000–0.020
M. striata sparsa	2	0.040	0.021	0.019–0.061	2	0.016	0.008	0.008–0.025
M. sulcata	20	0.079	0.018	0.024–0.387	20	0.035	0.008	0.005–0.155
M. variegata	15	0.080	0.013	0.006–0.180	16	0.013	0.003	0.000–0.039

ers combined with higher moving speed and lower average speed.

In a test excluding *M. striata sparsa* because of insufficient sample size, MPM varied significantly among species ($\chi^2 = 38.08$, df = 3, $P < 0.001$). *Mabuya acutilabris* and *M. spilogaster* each had significantly lower MPM than each of the other two species ($P < 0.001$ each) but did not differ significantly from each other ($P > 0.10$). MPM did not differ significantly between *M. variegata* and *M. sulcata* ($P > 0.10$).

PTM differed significantly among *Mabuya* species (*M. striata sparsa* not tested; $\chi^2 = 47.53$, df = 3, $P < 0.001$). *Mabuya acutilabris* and *M. spilogaster* each had significantly lower PTM than the each of the other two species ($P < 0.001$ each except 0.005 for the difference between *M. spilogaster* and *M. variegata*) but did not differ significantly from each other ($P > 0.10$). PTM did not differ significantly between *M. variegata* and *M. sulcata* ($P > 0.10$).

Mean speed varied significantly among species ($\chi^2 = 43.45$, df = 3, $P < 0.001$). *Mabuya acutilabris* and *M. spilogaster* had much lower mean speeds than the other two species (Table 2), and these differences were significant ($P < 0.01$ each for the differences with *M. variegata* and $P < 0.001$ each for differences with *M. sulcata*). The differences between *M. acutilabris* and *M. spilogaster* and between *M. variegata* and *M. sulcata* were not significant ($P > 0.10$ each). In the tests involving reduced mean speeds of *M. sulcata* to eliminate effects of body size differences, *M. sulcata* still had significantly higher mean speed than either *M. acutilabris* ($U = 29$; n = 20, 27; $z = -5.18$; $P < 0.001$) or *M. spilogaster* ($U = 20$; n = 11, 20; $P < 0.001$).

Moving speed also varied significantly among species, but in a reversed pattern ($\chi^2 = 12.50$, df = 3, $P < 0.015$). *Mabuya acutilabris* and *M. spilogaster* both had higher moving speeds than did the other two species (Table 2), but these differences were significant only for *M. acutilabris* ($P < 0.035$, one-tailed for the differences with *M. variegata* and $P < 0.01$ for that with *M. sulcata*). None of the other differences was significant ($P > 0.10$ each).

Few feeding attempts were recorded, but both attempts by *M. spilogaster* were from ambush, and the single attempt by *M. variegata* was on an insect discovered by active search. *Mabuya acutilabris* and *M. spilogaster* rarely tongue-flicked during the observations, but the other three species tongue-flicked frequently while moving (qualitative observations).

DISCUSSION

Foraging modes.—All available data indicate that *M. acutilabris* and *M. spilogaster* are ambush foragers and that *M. striata sparsa, M. sulcata,* and *M. variegata* are active foragers. Among the four species that could be examined statistically, the former two species both had the much lower MPM and PTM values traditionally used to identify ambush foragers and differed significantly from each of the other two species, which had MPM and PTM values typical of active foragers (Perry, 1995). Based on only two focal observations, *M. striata sparsa* appears to be an active forager. However, the maximum PTM was substantially higher for *M. spilogaster* than for *M. acutilabris* despite the smaller sample size, suggesting that the former may not be as extreme an ambush forager. Further data are needed for *M. spilogaster*, especially considering that only three individuals were observed in the morning, when the greatest foraging activity is likely to occur.

Another important feature of active foraging is search of a wider area per unit time as a result of greater mean speed than in ambush foraging, resulting in greater intake (Schoener, 1971; Anderson and Karasov, 1981). As expected, the active foragers as shown by high MPM and PTM also had greater mean speed than the ambush foragers. Although we lack data on body lengths of the individuals observed and on the precise relationship between body length and speed, this finding is robust. The mean speed of *M.*

variegata was greater than that of the similarly sized *M. acutilabris.* Although the greater mean speed of *M. sulcata* than of the two ambush foragers might have been the result of greater body size, the same pattern of significant differences was found when mean speed of *M. sulcata* was decreased by an amount that more than compensated for body size differences. These findings suggest that the greater mean speeds of the active foragers were a result of differences in foraging behavior, not merely differences in body size.

As predicted, moving speed was greater in the ambush forager *M. acutilabris* than in the active foragers, *M. sulcata* and *M. variegata.* Foraging mode rather than body size differences likely accounts for differences in speed because *M. sulcata* is the largest of these species and the other two are of similar size (Branch, 1988). Moving speed is measured less frequently than MPM and PTM due to effects of differences in body size among species and the greater difficulty of measuring distance traveled while recording time spent moving and numbers of movements. Despite similar trends, the differences between *M. spilogaster* and its actively foraging congeners were not significant, probably because of the very small sample size (n = 7) for the former.

Present findings support the predictions of associations between lower MPM, PTM, and mean speed and greater moving speed in ambush foragers and higher MPM, PTM, and mean speed and lower moving speed in active foragers. The few observations of feeding attempts were related as predicted to foraging mode, as were the more extensive observations of tongue-flicking. Because active foraging is plesiomorphic in Scincidae and ambush foraging in this family is known only in *Mabuya,* the results indicate at least one origin of ambushing in *Mabuya* (or its common ancestor), and possibly two depending on the unknown phylogenetic relationship between *M. acutilabris* and *M. spilogaster.* Marked differences in movement patterns and rates in *Mabuya* likely have evolved in two distinct suites specifically for differences in foraging style, but the possibility that phylogenetic differences in locomotory capacities unrelated to foraging are responsible for these differences cannot be excluded. Similar findings from previous studies of taxa differing simultaneously in foraging mode and family, which are more likely to have been misleading because of morphological and physiological differences among families, are strongly supported within a single genus.

TABLE 3. FORAGING MODES OF *Mabuya.*

Species	Mode	Sources
Mabuya acutilabris	ambush	1, 2
M. frenata	mixed	3
M. heathi	active	4
M. nigropunctata	active	5
M. quinquetaeniata	active	6
M. sloanii	active	7
M. spilogaster	ambush	1
M. striata sparsa	active	1
M. sulcata	active	1
M. unimarginata	active	7
M. variegata	active	1

1 = this paper; 2 = Castanzo and Bauer, 1993; 3 = Vitt, 1991; Vrcibradic and Rocha, 1998; 4 = Vitt, 1995; 5 = Vitt and Zani, 1996; Vitt et al., 1997; 6 = Attum, 1998; 7 = Perry, 1995.

Variation in foraging mode and its consequences in Mabuya.—Our quantitative foraging data confirm and extend previous qualitative reports that both ambush foraging and active foraging occur in the genus *Mabuya* (Table 3). In southern Africa and Latin America, both foraging modes occur in congeners, and one species, *M. frenata,* has been described as exhibiting a mixed foraging mode in which both tactics are used with some frequency (Vitt, 1991). Our data show substantially higher PTM for the three active foragers than for previously studied active foragers from Latin America (Perry, 1995; Vitt et al., 1997). Because phylogenetic relationships within *Mabuya* are unknown, intrageneric evolutionary changes in foraging mode cannot be traced to assess whether independent changes in foraging mode have occurred in Africa and Latin America. Because of its multiple representatives of each foraging mode, *Mabuya* is an excellent genus for comparative study of consequences of foraging mode (Huey and Pianka, 1981; Huey and Bennett, 1986; Cooper, 1995) and will be more so when a phylogeny becomes available.

Some preliminary information regarding consequences of foraging mode in *Mabuya* is available for sprint speed, diet, use of chemical senses during foraging, and antipredatory behavior. The ambushing *Mabuya acutilabris* has longer limbs than the actively foraging *M. sulcata* and *M. variegata* relative to body size (Castanzo and Bauer, in press), which suggests that the former species may have the predicted greater sprint speed (Garland, 1985; Losos et al., 1989; Losos, 1990). Huey and Pianka (1981) found that actively foraging lacertids included higher proportions of patchily distributed prey in their diets than did ambushers but no such major difference in *M. acutilabris, M. sulcata,* and *M. variegata*, although the former ate slightly more termites (Castanzo and Bauer, in press). Because the three species of *Mabuya* forage in distinct microhabitats, the hypothesis is not contradicted. The prediction that active foragers, but not ambushers, use chemical cues to detect prey is supported by the absence of prey chemical discrimination in *M. acutilabris* and its presence in *M. striata sparsa* (WEC, unpubl. data).

No quantitative data are available on interspecific differences in antipredatory behavior in *Mabuya*, but we frequently observed the actively foraging species from a distance as a result of their movement, whereas *M. acutilabris* were more difficult to locate because of immobility and crypsis. These observations support the hypothesis that ambushers employ crypsis maintained by immobility as the primary defense to avoid detection, whereas active foragers must rely more on speed or other means of escape after having been detected (Vitt and Price, 1982).

Ambush foragers have clutches with greater mass relative to total body mass than do active foragers (Vitt and Congdon, 1978). In preserved females from the collection of the Transvaal Museum, the mean clutch mass divided by the sum of clutch mass and clutch-free female mass for the oviparous *M. acutilabris* was 0.157 (n = 19, SE = 0.01), which is in the low end of the range typical for scleroglossan ambushers and greater than reported for active foragers (Vitt and Congdon, 1978). Direct comparisons with oviparous congeners are desirable.

ACKNOWLEDGMENTS

This study was partially supported by grants to WEC from Indiana University's Research Support Fund and International Projects and Activities Program and by a fellowship to WEC from the Ellerman Foundation through the John Ellerman Museum of Natural History at the University of Stellenbosch. We thank the Transvaal Museum for use of field vehicles in 1994 and 1996. We are grateful to our hosts in Namibia, J. and A. Steyn and A. and L. Hoffman, who kindly allowed us to conduct field studies on their property and provided generous hospitality and friendship. K. Komen graciously dissected gravid *Mabuya* on our behalf.

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