Movement- and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa

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Abstract. Two lizard foraging modes, ambush and active foraging, are usually quantified by the variables MPM (movements per minute) and PTM (proportion of time spent moving), but both variables may be affected by behaviors other than foraging. We introduce PAM, the proportion of attacks on prey discovered while lizards are moving (in relation to total attacks). PAM focuses exclusively on foraging behavior. Preliminary data reveal a very high, significant rank correlation between PAM and PTM, and a fairly high, but nonsignificant correlation between PAM and MPM. Collection of PAM data can be very time-consuming. In the absence of PAM, PTM appears to be a superior index of foraging activity to MPM, but all three indices provide valuable information on different aspects of foraging. We additionally present data for four agamine and five gekkonid species from southern Africa. The first quantitative data for agamines (all for *Agama*) agree with previous qualitative assessments that members of several agamine genera are ambush foragers. All the gekkonids, including three species of *Rhotropus* and one each of *Pachydactylus* and *Phyllodactylus*, are ambush foragers, like most geckos studied to date.

Introduction

Two discrete foraging modes have long been recognized in lizards (e.g., Evans, 1961; Pianka, 1966). In ambush foraging, also called sit-and-wait foraging, lizards remain still until prey are detected, then rush to the attack. In active foraging, also called wide foraging, the lizards search for food while moving through the habitat. These two modes have many important ecological and behavioral correlates, suggesting that foraging mode may play a central role in lizard life histories (Cooper, 1994a, b, 1995, 1997; Evans, 1961; Huey and Bennett, 1986; Huey and Pianka, 1981). Although Huey and Bennett (1986) presented evidence supporting several predictions about the ecological consequences of foraging mode, a lack of quantitative data on foraging movements has hampered use

of the comparative method to demonstrate any effects of foraging mode independent of phylogeny.

Based on their qualitative definitions, a major difference between ambush and active foraging is the relative amount of time spent in motion while foraging. The original qualitative definitions had to be modified when it became apparent that foraging activity can vary within each mode along some portion of a continuum from immobility to perpetual activity (Magnusson et al., 1985; Perry et al., 1990; Pietruszka, 1986). In the absence of quantitative data on a sufficient number of species, it is not yet clear whether there is any region of the activity continuum that is unrepresented. Nevertheless, although there is continuous variation within each foraging mode, McLaughlin (1986) found that the ranges of activity did not overlap between modes in the data then available. Although overlap between modes may be detected in future studies, recognition of the polar extremes of the continuum as ambush and active foraging will continue to be a useful shorthand for large differences in behavior. Any intermediate cases can readily be incorporated into comparative tests based on quantitative measures.

Despite the importance of foraging modes to lizard ecology, there are conceptual problems with the traditional measurements of foraging activity and large gaps remain in our knowledge of foraging mode in many lizard taxa. The two foraging modes sometimes appear to be defined on conflicting bases. Ambush foraging is defined by the nature of the attack, while active foraging is defined by the lizard's movement pattern. We believe this conflict to be more apparent that real. If one uses the term sit-and-wait foraging, the terms for both modes stress movement or its absence.

Unfortunately, the usual measurements of foraging activity suffer from the difficulty of recognizing when lizards are engaged in activities other than foraging, such as thermoregulation or search for conspecifics. Although the traditional measures of lizard foraging mode have the advantage of emphasizing search behavior, they do not directly reveal responses to prey. Because the most important factor for foraging success is the contribution of the moving and nonmoving tactics to the diet, we propose a new measure of foraging mode that directly reflects the capture rates by immobile and mobile lizards. Because movement or its absence can be observed at any time, whereas attacks and captures are more rarely observed, movement data have been used nearly exclusively in studies of lizard foraging mode. It is thus important to establish whether the commonly used movement indices of foraging mode are correlated with frequencies of attack launched by moving and immobile lizards.

Here we present foraging data on several southern African species representing two large taxa, the chamaeleonid subfamily Agaminae (Frost and Etheridge, 1989) and the family Gekkonidae. Data adequate for the new foraging index were obtained only for one agamine and one gekkonid species. By comparing data for these two species with preexisting data for lacertid species, we investigated relationships among the traditional foraging indices and the percent of attacks while moving. We present preliminary evidence

that the proportion of time spent moving is a good index of foraging mode in that it is highly correlated with percent of attacks while moving.

The data also permit the first quantitative characterization of foraging in the taxa studied. Insectivorous agamines are widely believed to be ambush foragers, and a number of them have been so characterized on the basis of qualitative observations (Cooper, 1994b; Al-Johany, 1995), but there are no published quantitative measurements of foraging activity for any agamine. Most gekkonids studied have been characterized as ambush foragers, but active or mixed foraging has been described qualitatively in six genera (Cooper, 1994b). Quantitative data are available for far fewer gekkonids. Of these, eight species in four genera are ambushers, whereas a single species is an active forager (Perry, 1995). We present such movement data for four species of the genus *Agama* and five gekkonid species in three previously unstudied genera, *Pachydactylus*, *Phyllodactylus*, and *Rhotropus*.

Methods

Taxa and numbers of individuals observed are presented in table 1. Observations were made of *Agama aculeata* on 7 October 1994 and 19 February1996 at Farm Bergvellei in northwestern Namibia (19°37′S, 14°40′E, 20 km west of Kamanjab); *A. anchietae* on 29 February 1996 at the western edge of the Namib Naukluft Park in Namibia (23°33′S, 15°50′E); *A. atra* in South Africa primarily in Namaqualand at Ybeep (29°58′S, 17°59′E; $n = 4$) on 27 and 28 March 1993, Wolfhoek (30°22′S, 18°12′E; $n = 15$) on 28 and 29 March 1993, at 29°54′S, 17°49′E ($n = 1$) on 1 March 1996, and in the Western Cape Province at Jonaskop (33°58′S, 19°31′E; $n = 4$); *A. planiceps* at Farm Bergvellei on 8-11 October, 1994; *Pachydactylus turneri* at Farm Bergvellei on 20-22 February 1996; *Phyllodactylus porphyreus* in the Western Cape Province at Stellenbosch (33°57′S,

Table 1. Sample sizes (n = number of individuals), movements per minute (MPM), proportion of time spent moving (PTM), and total time (minutes) observed for representatives of two southern African families of lizards. Each individual was observed for ten minutes when possible.

Species	n	MPM			PTM			Total
		$\bar{x}$	$s_{\bar{x}}$	range	$\bar{x}$	$s_{\bar{x}}$	range	time
Chamaeleonidae								
Agama aculeata	3	0.20	0.15	0.00-0.50	0.00	0.00	0.00-0.00	30.00
A. anchietae	1	0.00			0.00			10.00
A. atra	24	0.27	0.08	0.00-1.59	0.01	0.00	0.00-0.04	232.12
A. planiceps	27	0.56	0.13	0.00-2.43	0.02	0.00	0.00-0.07	239.85
Gekkonidae								
Pachydactylus turneri	11	0.16	0.07	0.00-0.60	0.00	0.00	0.00-0.01	110.00
Phyllodactylus porphyreus	5	0.04	0.04	0.00-0.20	0.01	0.01	0.00-0.06	43.88
Rhotropus afer	3	0.00	0.00	0.00-0.00	0.00	0.00	0.00-0.00	25.00
R. barnardi	23	0.28	0.08	0.00-1.40	0.01	0.00	0.00-0.05	208.43
R. boultoni	24	0.29	0.07	0.00-1.20	0.01	0.00	0.00-0.04	232.50

18°53′E) on 27 October 1994; *Rhotropus afer* in Namibia east of Swakopmund (22°41′S, 14°35′E) on 25-26 February 1996; *R. barnardi* at Farm Bergvellei on 9-13 October 1994 and 19-21 February 1996; and *R. boultoni* at Farm Bergvellei on 8-13 October 1994.

We conducted focal observations only on sunny days when lizards were active. We walked slowly through an area searching for lizards with binoculars and unaided vision, and stopped moving as soon as a lizard was detected to minimize any disturbance. The distance between observer and lizard was greater than 5 m, often greater than 30 m for the larger agamines. We observed focal animals for 10 min when possible, but sometimes less (minimum 1.5 min) if the lizard disappeared from view. Data were recorded on microcassette tapes for individuals that did not appear to have been disturbed. Each area was sampled only once to ensure that data points were independent.

Data we recorded were species, locality, date, time, and behaviors. The raw behaviors noted were time spent moving, time stationary, total distance moved, feeding attempts, and whether lizards initiated feeding attempts after detecting prey while immobile or after detecting prey by actively searching. No distinction was made between successful and unsuccessful feeding attempts. Lizards were recorded as being still when making postural changes and movements of specific body parts that did not involve translations to a new location.

From the raw data we calculated three measures of foraging activity. The first two were the traditional indices of lizard foraging mode, the proportion of time spent moving (PTM) and number of movements per minute (MPM) (e.g., Cooper et al., 1997; Huey and Pianka, 1981; Perry, 1995). Ambush foragers typically have much lower PTM and MPM than active foragers. Values of PTM less than 0.10 have been considered to indicate ambush foraging (Perry, 1995), but no corresponding criterion seems possible for MPM because some ambushers move relatively frequently (e.g., *Platysaurus broadleyi*, Cooper et al., 1997) and some foragers may stop so infrequently that they have low MPM (*Cnemidophorus tigris*, Anderson, 1993). Our third foraging measure was the percentage of total attacks on prey or captures by lizards that discovered prey as a result of mobile searching (PAM = proportion of attacks on prey discovered while lizards were moving in relation to total attacks). Because movements by ambushers to attack prey detected while the lizards were immobile are considered part of the attack, they do not contribute to PAM. Although this variable is tied more closely to food acquisition than PTM and MPM, it is absent from the literature presumably because low feeding rates often make it very time-consuming to measure. Inclusion of PAM data partially addresses the difficulty that most studies of foraging mode focus exclusively on movement data, obscuring other aspects of food acquisition (Anderson, 1993). Only for *R. barnardi* and *A. atra* were we able to obtain data that could be used to corroborate the other measures presumed to be highly correlated with PAM.

We tested the hypothesis that *R. afer* moves less frequently than either of its congeners (Odendaal, 1978) using Fisher exact tests (Zar, 1996) of the frequencies of lizards that moved at least once and those that were immobile throughout observation. We also

examined relationships between PAM, MPM, and PTM using Spearman rank correlation tests corrected for ties. Data points were assumed to be independent because we were interested in relationships among different measures of the same activity, not in correlated evolution between variables. Tests of significance were one-tailed with $\alpha = 0.05$.

Results and discussion

MPM, PTM, PAM and foraging

For two species of ambushers from this study, a lacertid ambush forager, and four lacertid active foragers (Cooper and Whiting, 1999) for which all three measures are available (table 2), PTM is very highly correlated with PAM ($r_S = 0.95$, $n = 7$, $P < 0.005$), but MPM and PAM are fairly highly, but not significantly, correlated ($r_S = 0.63$, $n = 7$, $0.05 < P < 0.10$). Due to the small number of species and small sample sizes for some of them, these correlations must be considered preliminary. Further investigation is needed because the correlations have important implications.

If PTM and MPM are to be used as valid indices of foraging mode defined by the nature of the attacks on prey, they must increase as PAM increases. Ambush foraging clearly requires attacks to be launched by lizards that have waited immobile and then attacked prey upon detecting them. Similarly, active foragers must attack prey found during the course of mobile search. Because all lizards move and are still at times, both types of attacks are to be expected occasionally even in extreme ambush and active foragers. However, the greater the proportion of time spent moving, the greater the opportunity for attacks on prey detected while moving, leading to the high correlation between PTM and PAM.

The number of movements is expected to increase with the proportion of time spent moving in most lizards, but some species with relatively low PTM may make frequent

Table 2. Foraging data for seven species used to study relationships among the foraging variables MPM (movements per minute), PTM (percent time moving), and PAM (percent of attacks initiated after discovering prey while moving). The leftmost figure is the sample size for MPM and PTM. Numbers of attacks are in parentheses following PAM.

Species	*n*	MPM	PTM	PAM	(*n*)
Chamaeleonidae					
Agama atra	24	0.27	0.01	0.00	(9)
Gekkonidae					
Rhotropus barnardi	23	0.28	0.01	0.00	(4)
Lacertidae					
Heliobolus lugubris	14	1.49	0.64	1.00	(45)
Meroles ctenodactylus	5	3.24	0.29	0.33	(6)
M. knoxii	27	0.61	0.07	0.00	(6)
Pedioplanis namaquensis	26	1.87	0.54	0.95	(58)
P. undata	16	1.39	0.50	1.00	(4)

moves of short duration, and others with very high PTM may have low MPM because they stop infrequently (data in Perry, 1995; Cooper and Whiting, 1999). The former species have a short time available to detect prey while moving, and may not even scan for prey except while immobile (Fleishman, 1986). The existence of such species must lower the correlations between MPM and PAM. Therefore, although MPM provides valuable information in its own right, PTM is to be preferred as the best single movement index of foraging mode when PAM is unavailable. Nevertheless, we fully expect that MPM and PTM will be shown to be significantly correlated when more data are available.

One of the major problems with using MPM or PTM data as indices of foraging mode is that either moving or immobile lizards may be engaging in activities other than foraging. Thus, MPM and PTM are correlates of foraging activity rather than direct measurements. MPM and PTM can be improved by excluding time engaged in social behavior, antipredatory behavior, or other nonforaging activities, but such exclusion does not address the problem of simultaneous activities. PAM has the distinct advantage of focusing exclusively on foraging behavior, but does not reveal the extent of search activity. Whereas MPM and PTM provide information on the duration and frequency of movements used to locate prey, PAM gives complementary information on the importance of immobility versus mobility to the immediate discovery of prey. Use of all three indices potentially can provide a more comprehensive view of foraging, including search and its consequential attacks.

Agaminae

The data for agamas all show relatively low MPM and very low PTM (table 1). Sample sizes are adequate to be confident that these figures reflect foraging behavior reasonably well only for *A. atra* and *A. planiceps*. However, additional unrecorded qualitative observations (Cooper, personal observations) indicate that *A. aculeata* and *A. anchietae* also have low MPM and PTM values as suggested by the limited data from focal observations. In both *A. atra* and *A. planiceps* numerous individuals did not move at all during the 10 min observation interval, but a few individuals moved much more frequently. All movements were brief and translations were rapid, unaccompanied by tongue-flicking or other obvious investigation of substrates during movement. Nine feeding attempts by *A. atra* were observed, only four by focal animals included in table 1. All attacks were made by individuals that were immobile when they detected the prey visually and then ran to capture prey, yielding a PAM = 0.00.

The MPM and PTM data for all four species of *Agama* and the limited observations in which all attacks were launched by immobile lizards agree with published qualitative assessments for other species of *Agama* (*A. agama*, Dunham et al., 1988; *A. sanguinolenta*, Shenbrot et al., 1991; *A. yemenensis*, Al-Johany, 1995) and for agamines representing numerous species in five other genera (Al-Johany, 1995; Arnold, 1984; Dunham et al., 1988; Heatwole, 1970; Shenbrot et al., 1991; Vitt and Price, 1982). Oddly, the present

data are the first quantitative measurements of foraging mode for any agamines. Although sample sizes were adequate for confidence only for *A. atra* and *A. planiceps*, they confirm the widely held belief that agamas are ambush foragers. The PAM value of 0.0 for *A. atra* provides strong evidence for ambush foraging by that species.

Gekkonidae

All five gekkonid species had low very MPM and PTM. The standard errors differed little among species for both MPM and PTM in the three species having the largest sample sizes, suggesting a strong similarity in movement patterns. Some individuals of all species, including numerous *Rhotropus spp.* and *P. turneri*, were motionless throughout the observation interval. A few *Rhotropus spp.* moved as often as once per minute. Movements by all species were typically very brief. Feeding attempts were recorded only for *R. barnardi*; all four attacks on prey were initiated from a standstill (PAM = 0.00).

Numbers of lizards that did not move even once during focal observations were 3 of 3 for *R. afer*, 8 of 24 for *R. boultoni*, and 10 of 23 for *R. barnardi*. Despite the very small sample size for R. afer, that species had a proportion of immobile individuals almost significantly greater than *R. boultoni* ($P = 0.056$, Fisher exact test) and there was a pronounced trend in the same direction for the comparison with *R. barnardi* ($P = 0.110$, Fisher exact test). Mean time per observation was slightly lower for *R. afer*, but not enough to produce such differences.

As indicated by their low MPM and PTM values the three diurnal *Rhotropus* species are all ambush foragers. For *R. barnardi*, the attacks on prey launched by immobile individuals corroborate these findings. This agrees with the qualitative characterization of the genus *Rhotropus* as ambush foragers having sedentary habits by Odendaal (1979), who studied *R. afer*, *R. bradfieldi*, *R. barnardi*, and *R. boultoni*.

Odendaal (1979) believed *R. afer* to be even less active than the other species. Although our statistical tests of this hypothesis did not show significant differences, their power was very low due to small sample sizes. Our limited data agree well with Odendaal's hypothesis. Although differences in frequency of movement might be associated with the terrestrial habits of *R. afer* and the saxicolous habits of the other *Rhotropus* species, all species are ambush foragers with low movement frequencies. The major difference in locomotion that Odendaal noted between *R. afer* and the other species is that the former runs longer distances. Our unrecorded observations confirmed this observation and presumably its cause, which is simply that the terrestrial species is usually farther from refuge from predators. *Rhotropus afer* forages on the ground away from the rock crevices at ground level that it uses as refuges. In contrast, the other species forage on rocks above ground and use nearby crevices as refuges.

The other two gekkonid species, *P. turneri* and *P. porphyreus*, are also ambush foragers having very low MPM and PTM. The results for *P. turneri* are as expected from the qualitative assignment of ambush foraging mode for its congeners, *P. bibroni* and

P. capensis (Vitt and Price, 1982). All five gekkonid species studied here are ambush foragers like the large majority of gekkonid species studied to date (86.67% of 60 species reviewed by Cooper, 1994b; see also Perry, 1995). Based on qualitative accounts, active or mixed foraging is more likely to be found among nocturnal terrestrial gekkonids than in arboreal or saxicolous species such as those studied here (e.g., Arnold, 1984; Henle, 1991), but no quantitative data are available for any terrestrial gekkonid. Such data are needed, especially for those species reported as having mixed or active foraging modes, to attain an understanding of the evolution of foraging in the speciose and ecologically diverse family Gekkonidae.

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