

## Foraging modes of some Jamaican, Costa Rican, and Mexican lizards

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**Abstract.** Lizard foraging has played a central role in the evolution of diet, chemosensory sensitivity and morphology, locomotor morphology, and physiological capacities, and has been key character in cladogenesis. Quantitative data needed for comparative studies to establish the phylogeny of foraging modes and identify correlates of foraging mode are available for a tiny fraction of species. We studied foraging in 12 species, including 8 or 9 species for which no quantitative data were available and 12 for which no foraging speed data were available, and noted attacks on prey. Each species had the foraging mode typical for its family, highlighting the stability of foraging mode. A corytophanid, a phrynosomatid, 6 anoles, and 3 gekkonids are ambush foragers, as indicated by low frequency of movement (MPM), low percent time moving (PTM), high average speed (AS), and all but one gecko had the low speed while moving (MS) characteristic of ambushers. The only active forager, the teiid *Ameiva dorsalis*, had higher MPM, PTM, and AS, lower MS, and initiated all attacks on prey discovered while moving. Interspecifically, frequency of movement was positively correlated with percent time moving and average speed. Percent time moving and average speed were highly correlated ( $r = 0.99$ ).

**Keywords:** active foraging, ambush foraging, foraging mode, sit-and-wait foraging, Squamata.

### Introduction

Hunting methods of lizards differ dramatically among species, especially in the importance of movement to search for prey. Pianka (1966) identified two foraging modes over 55 years ago, ambush (= sit-and-wait) foraging (waiting immobile at an ambush post until prey appear), and active foraging (moving through the habitat searching prey). These modes often have been characterized qualitatively, but detailed examination of foraging modes and determination of their correlates requires quantitative measurement of aspects of

foraging. Pianka, his students and others have amassed a large body of data on movements in diverse lizards (e.g. Huey and Pianka, 1981; Vitt et al., 1993; Werner, 1998; Perry, 1999; Cooper, 2005a, 2007a,b; Reilly, McBrayer and Miles, 2007).

Foraging mode has numerous morphological (Cooper, 1996; McBrayer and Corbin, 2007; Miles, Losos and Irschick, 2007), physiological (Anderson and Karasov, 1981; Bonine, 2007), sensory (Cooper, 1995, 1997a,b), ecological (Huey and Pianka, 1981; Anderson, 2007; Vanhooydonck, Herrel and Van Damme, 2007), and behavioral (Huey and Pianka, 1981; Cooper, 1995, 1997a, 2007a) correlates. Foraging modes thus are considered to constitute suites of traits that have undergone correlated evolution to maximize hunting success. Furthermore, the advent of key innovations related to foraging modes appear to have driven major aspects of the evolution of lizard diversity (Vitt et al., 2003). This view, the foraging mode paradigm, has recently been summarized in an edited volume by Reilly, McBrayer and Miles (2007).

Although foraging modes are central to our current views of lizard ecology and evolution, the binary versus continuous nature of foraging mode has remained somewhat controversial. Continuous variation occurs in all movement variables used in foraging studies

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(e.g., Pietruszka, 1986; Perry, 1999; Cooper, 2007a), but cluster analyses have revealed two separate clusters within which the positions of species vary continuously (Cooper, 2005a, 2007a). Recent studies show that two species of chameleons reveal intermediate positions between these clusters (Butler, 2005; Hagey, Losos and Harmon, 2010). As more species, such as chameleons, diverse geckos that have unusual foraging behaviours, and *Chamaeleolis* (Leal and Losos, 2000) are studied, new clusters may appear and gaps between clusters may diminish or disappear. Our current view is that foraging modes exhibit continuous variation with some gaps between groups representing modes. For many purposes, only the degree of activity, which varies continuously, need be considered to establish correlates of foraging mode. On the other hand, it may be useful to categorize groups of species that differ clearly in activity for statistical analyses such as analysis of variance.

Foraging mode has been determined quantitatively using at least two movement variables for about 100 species, approximately 2% of the 5537 species listed in the Reptile Database in August 2011. Limited or no data are available for some major taxa, including Varanidae, Gymnophthalmidae, and Chamaeleonidae (but see Butler, 2005; Hagey, Losos and Harmon, 2011), and others that may have variable or unusual foraging modes (Gekkota, *Chamaeleolis*).

The most widely used foraging variables are number of movement per minute (MPM), percent or proportion of time spent moving (PTM), average speed (AS), and speed while moving (MS). Among these, MPM and PTM have been measured most frequently, but all reveal important aspects of foraging behaviour. Active foragers have higher MPM, PTM, and AS, but lower MS than ambush foragers (e.g., Perry, 1999; Cooper, 2005a, 2007a,b). Far less frequently measured is the proportion of attacks initiated after locating prey while moving (PAM), which is very high in active foragers and very low in ambush foragers, and a related variable, proportion of attacks initiated while immobile (PAS = 1 – PAM) (e.g., Cooper *et al.*, 1999; Williams and McBrayer, 2011). The attack-based variables require more prolonged observations to measure, but do not suffer from the uncertainty about motivation inherent in the movement variables (Anderson, 1993; Perry, 2007).

Our goals in this study were incremental. We sought to increase the number of species and taxa for which quantitative movement variables are available for future comparative studies of foraging mode. Although we planned no broad comparative analyses, another goal

was to characterize the foraging behaviour of each species studied in relations to lizard foraging modes and the foraging behaviour of related species.

## Materials and Methods

We collected data on Jamaica in the Hellshire Hills (*Anolis opalinus*, *Aristelliger praesignus*), on Lime Cay (*Ameiva dorsalis*), on and near the campus of The University of the West Indies, at Mona and Hollywell National Recreation Park (*Anolis grahami* and *Anolis lineatopus*), and Redlight (*Anolis garmani*) in the second half of March and first half of April, 2005. Data for the Costa Rican lizards (*Anolis humilis*, *A. limifrons*, *Basiliscus plumifrons*, *Gonatodes albicularis*, *Hemidactylus frenatus*) were collected during 15–29 May 2006 in lowland tropical forest on the Caribbean slope of Heredia Province. Data for *Uma exsul* were collected by in June 2006 near Villa Bilbao, Viesca in southwestern Coahuila, Mexico (25° 26' 27" N, 102° 55' 15" W). All data were collected during warm sunny intervals when lizards were fully active.

Methods of observing and recording foraging behaviour were those described in Cooper (2005b) and Cooper *et al.* (1999, 2001, 2001, 2005). After locating a lizard by walking slowly through the habitat, the investigator stopped walking while 5–10 m from the lizard and turned to face the lizard directly. After standing still for 2 minutes, the investigator recorded foraging behaviours including all movements other than postural adjustments, the duration of movements, and distance moved (as estimated visually by the researcher). For the ambush foragers infrequent and brief movements allowed us to record data using pen and paper. For the actively foraging *A. dorsalis*, data were recorded on a taped recorder and later transcribed. In addition, WEC recorded the occurrence of feeding attempts by *A. dorsalis*. Sample sizes of the ambush foragers were too small to permit meaningful measurement of attack-based data. A movement (bout of locomotion) terminated when a lizard stopped moving for 2 s. Only adult lizards were observed. Sex was not recorded.

During observations the investigator stood motionless except when movement by a lizard required movement by the investigator to keep the lizard in sight. Our goal was to record behaviour continuously for 10 min. If a lizard moved out of sight or engaged in prolonged social activity, a trial was terminated. Brief times spent in social displaying were excluded from the analyses. The shortest observation interval was 131 s, but only five observations lasted less than 5 minutes. Each lizard

was observed only once, which was ensured by moving to a new location at the end of each focal observation. If the location of the previous focal animal was known, two successive observations of different lizards were sometimes made at or near the same location. Otherwise, the investigator moved beyond the possible location of the previously observed lizard along a transect before making a new observation. For all but one species, a single investigator collected data. For *A. dorsalis*, the data collected by two investigators yielded very similar estimates and were pooled.

From the recorded variables we calculated the number of movements per minute (MPM), the percent time moving (PTM), the average speed in m/min (AS, total distance moved divided by duration of the focal observation), and the speed while moving in m/min (MS, time spent moving divided by distance moved). We also calculated the proportion of all attacks on prey by *A. dorsalis* that were directed at prey detected while the lizard was moving (PAM = proportion of attack while moving). Although broad comparative analysis was not our goal, we computed correlations between pairs of movement variables to ascertain similarities with previously published relationships. Due to the limited range of taxa, the parametric correlations were not corrected for degree of phylogenetic relationship.

## Results and Discussion

*Foraging modes x taxon.*—*Basiliscus plumifrons* is an ambush forager having typically low values of MPM, PTM, and AS, and a high value of MS (table 1). The MPM and PTM values are slightly lower than those recorded for the only other corytophanid studied (Perry, 1999). The AS and MS values, which are the first recorded for a corytophanid species, are indicative of ambush foraging. The AS value is unremarkable, but the MS is higher than previously recorded for any lizard. This presumably reflects greater running speed associated with large body size (Huey and Hertz, 1984) of *B. plumifrons*. When the body size range of lizards is large in comparative studies, estimates of foraging speeds may need to be adjusted for differences in body length. In addition to species listed in table 1, we conducted observations of several *B. vittatus*, but subsequently lost those data. However, our observations are adequate to categorize *Basiliscus vittatus*, like its two congeners, as an ambush forager.

Values of all movement variables for *Uma exsul* (table 1) correspond to ambush foraging. Although *U. exsul* is an omnivore, its ancestral movement pattern has not been

substantially altered from that of related species that are insectivorous. As a member of the phrynosomatid sand lizard clade (*Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma*), it has values of all movement variables that are strikingly similar to those of *Holbrookia propinqua* and *Cophosaurus texanus* (Cooper et al., 2001, 2005). The values were well within the ranges reported for other phrynosomatid lizards, all of which are ambush foragers (Perry, 1999; Cooper et al., 2001, 2005). Ambush foraging is thus highly stable within Phrynosomatidae and is now has been demonstrated quantitatively in six of its genera (Cooper, 2007a).

All of the anoles studied are ambush foragers. Although only 2 observations were made of *A. garmani*, all of its movement variables are indicative of ambush foraging. Values of MPM and PTM (table 1) are close to, but slightly lower than those reported by Irschick (2000) for *A. grahmi* (0.8 and 1.6, respectively) and *A. lineatopus* (0.40 and 0.50, respectively). AS values for these species and *A. opalinus* (table 1) were nearly identical to reported values for other anoles, which ranged from 0.01 to 0.10 for nine species (Cooper, 2005c). Even so, the AS value for *A. grahmi* is the highest yet recorded for an anole. MS values for anoles in this study (table 1) were well within the range typical of ambush foragers, but those for *A. limifrons*, *A. lineatopus* and *A. grahmi* (table 1) were slightly higher than those reported for other anoles (Cooper, 2005c). These findings add substantial data indicating that two additional species of anole are ambush foragers and some data suggesting that a third species may also be an ambusher. All species of *Anolis* studied to date are classic ambushers that move infrequently, spend a very low percentage of time moving, and have both low average speed and high speed while moving.

The three gekkonid species are ambush foragers, as indicated by low MPM, PTM and AS, but MS was variable (table 1). *Aristelliger praesignus* had lower PTM than any previously studied gekkonid and MPM lower than 12 of 13 previously studied species (Werner et al, 1997; Werner, 1998; Perry, 1999, 2007; Cooper et al., 1999; 2001; Vitt et al., 2000; Werner and Chou, 2002). Its AS was also slightly lower and its MS was substantially higher than recorded for any of eight other gekkonids studied previously (Cooper et al., 1999; 2001, 2005; Vitt et al., 2000; Perry, 2007). The MS value (table 1) may be artifactually high because one of the three lizards that moved made a single long, rapid movement that led to an MS of 50.4 for that individual, higher than the reported value for any species. Nevertheless, the available data clearly

**Table 1.** Foraging movement data for several Jamaican, Costa Rican, and Mexican lizard species. MPM – movements per minute, PTM – percent time moving, AS – average speed (m/min), MS – speed while moving (m/min). Data are mean  $\pm$  SE followed by *N* in parentheses. The *N* for each species is identical to that for MPM.

Taxon	MPM	PTM	AS	MS
Corytophanidae				
<i>Basiliscus plumifrons</i>	0.11 $\pm$ 0.04 (15)	0.2 $\pm$ 0.1 (15)	0.1 $\pm$ 0.0 (15)	64.1 $\pm$ 11.1 (7)
Phrynosomatidae				
<i>Uma exsul</i>	0.40 $\pm$ 0.07 (20)	2.1 $\pm$ 0.4 (20)	0.4 $\pm$ 0.1 (20)	24.5 $\pm$ 5.6 (18)
Polychrotidae				
<i>Anolis garmani</i>	0.05 $\pm$ 0.05 (2)	0.1 $\pm$ 0.1 (2)	0.1 $\pm$ 0.1 (2)	15.2 (1)
<i>Anolis grahami</i>	0.31 $\pm$ 0.12 (23)	0.6 $\pm$ 0.2 (23)	0.2 $\pm$ 0.1 (23)	16.3 $\pm$ 3.0 (14)
<i>Anolis humilis</i>	0.14 $\pm$ 0.03 (18)	0.3 $\pm$ 0.1 (18)	0.1 $\pm$ 0.0 (18)	11.9 $\pm$ 4.6 (13)
<i>Anolis limifrons</i>	0.29 $\pm$ 0.11 (8)	0.6 $\pm$ 0.2 (8)	0.1 $\pm$ 0.0 (8)	16.4 $\pm$ 7.5 (7)
<i>Anolis lineatopus</i>	0.26 $\pm$ 0.05 (25)	0.4 $\pm$ 0.1 (25)	0.1 $\pm$ 0.0 (25)	21.9 $\pm$ 2.8 (18)
<i>Anolis opalinus</i>	0.30 $\pm$ 0.06 (19)	0.3 $\pm$ 0.1 (19)	0.1 $\pm$ 0.0 (19)	13.1 $\pm$ 2.4 (16)
Gekkonidae				
<i>Aristelliger praesignus</i>	0.08 $\pm$ 0.02 (4)	0.2 $\pm$ 0.1 (4)	0.0 $\pm$ 0.0 (4)	24.4 $\pm$ 13.0 (4)
<i>Gonatodes albigularis</i>	0.35 $\pm$ 0.05 (14)	0.7 $\pm$ 0.1 (14)	0.0 $\pm$ 0.0 (14)	6.2 $\pm$ 11.3 (13)
<i>Hemidactylus frenatus</i>	0.33 $\pm$ 0.08 (13)	0.8 $\pm$ 0.3 (13)	0.1 $\pm$ 0.0 (13)	7.6 $\pm$ 1.8 (10)
Teiidae				
<i>Ameiva dorsalis</i>	0.76 $\pm$ 0.06 (23)	77.3 $\pm$ 3.5 (23)	2.4 $\pm$ 0.2 (23)	3.4 $\pm$ 0.4 (23)

Ambush foraging by the three gekkonid species that we studied matches the foraging mode of all gekkonids for which data are available with the exception of *Gekko hokuensis*, which has an MPM typical for ambush foragers, but a much higher PTM than other gekkonids (25.5), a value associated with active foraging. Foraging modes have been characterized qualitatively for 54 gekkonid species (Bauer, 2007), of which 9 were considered to be active foragers and one was considered a cruise forager, i.e., to show foraging behaviour intermediate to ambush and active foraging. Quantitative data on foraging movement variables and

PAM are needed to assess the foraging modes of these species and the true extent of variability of foraging mode in Gekkonidae. Although foraging mode is often stable in large taxa, including entire families, ambush foraging occurs frequently in some families that are predominantly active foragers, including Lacertidae and Scincidae (Cooper, 1994a,b). Active foraging is rare or absent in iguanian families. Gekkonidae, which is ecologically diverse, may be an exceptional family because a large majority of species are ambush foragers, but a substantial proportion of species are cruise or active foragers (ca. one fifth).

*Ameiva dorsalis* is an active forager (table 1). Its MPM, PTM and AS values are much higher than those of the remaining species in this study, and its MS is much lower. These findings are typical in indicating that highly active foragers spend more time moving and move greater distances, but move slowly. The slow movements while searching were readily apparent in *A. dorsalis*, which often tongue-flicked and scratched surface litter. MPM is highly variable in teiid lizards (0.14–1.56), including *Ameiva* (0.28–1.56; Anderson, 1993; Vitt et al., 1993, 1995; Vitt, Zani and Barros, 1997; Perry, 1999; Cooper et al., 2001). Thus the value of MPM (table 1) observed for *A. dorsalis* is typical. PTM (table 1) is much higher for *A. dorsalis* than previously recorded for other species of *Ameiva* or *Kentropyx* (Vitt et al., 1993, 1995; Perry, 1999), but appears to be typical for *Aspidoscelis* (Anderson, 1993; Vitt et al., 1993 (and unpublished data); Paulissen, 2001 and personal communication; Cooper et al., 2001, 2005). AS (table 1) is nearly identical to the only other reported value for a congener (*A. festiva*; Perry, 1999) and for the reported range of 0.84–4.15 m/min for all teiids (Cooper, 2007a). MS (table 1) also is similar to the 2.86 m/min reported for *A. exsul* (Perry, 1999), and is slightly below average for all teiids ( $4.53 \pm 0.58$  m/min, 1.92–7.05 m/min,  $n = 11$ ; data from Cooper, 2007a). Eight feeding attempts were observed, all of them initiated while lizards were moving. Thus, PAM = 1.0, the highest possible value predicted for an active forager (Cooper et al., 1999; Williams and McBrayer, 2011). In summary, our data show that *A. dorsalis* is not only an active forager, but among the most active in a family known for active foraging. Why PTM is higher for *A. dorsalis* than for four of its congeners is uncertain, but variation in temperature and insolation are associated with variation in PTM (Verwajen and Van Damme, 2007), and might have varied among the teiid studies.

*Correlations between foraging variables.*—MPM was significantly correlated with PTM ( $r = 0.80$ ,  $df = 10$ ,  $P = 0.002$ ) and AS ( $r = 0.83$ ,  $df = 10$ ,  $P = 0.001$ ), but not MS ( $r = -0.47$ ,  $df = 10$ ,  $P > 0.10$ ). PTM and AS were highly correlated ( $r = 0.99$ ,  $df = 10$ ,  $P < 0.001$ ). PTM was not significantly correlated with MS ( $r = 0.31$ ,  $df = 10$ ,  $P > 0.20$ ). AS and MS were not significantly correlated ( $r = -0.29$ ,  $df = 10$ ,  $P > 0.20$ ). The relationship between MPM and PTM matches findings of previous studies (e.g., Perry et al., 1990; Cooper et al., 2001; Cooper, 2005a,b, 2007a). Because our data were intended to contribute to future large scale phylogenetically informed comparative analyses, we did not conduct

phylogenetic correlations. Nevertheless, the present findings agree with those of a comparative analysis of 57 species in showing that MPM increases as PTM and AS increase, but is unrelated to MS (Cooper, 2007a), which differs between modes and may increase as body length increases. Our findings also agree with the strong positive relationship between PTM and AS (Cooper, 2007a). This relationship is expected if only because AS increases as time spent moving at the same speed increases. The relationship between PTM and MS was not significant in this study, but was significant in the comparative analysis (Cooper, 2007a). In both studies the correlations were negative and almost identical, suggesting that a consistent relationship exists, but was not detected due to small sample size in the present study. The relationship between AS and MS was not significant in either study. This is somewhat surprising because ambush foragers have low AS and high MS. However, AS increases as PTM increases, but the relationship between PTM and MS is weakly negative. These opposing effects of these relationships may preclude a significant relationship between AS and MS.

*Directions for research on foraging mode.*—As more quantitative data on foraging mode become available, foraging data will expand choices of researchers for taxa useful in studies of evolutionary correlates of foraging mode. Statistical power will also be improved. Some likely correlates of foraging mode remain uninvestigated, including escape behaviour, refuge use, and crypsis. Others, such as social structure and utilization of space, have received relatively little attention. Our data make an incremental contribution to this effort. We encourage researchers with access to unstudied taxa, such as Varanidae and Gymnophthalmidae, and other taxa for which minimal data are available to collect data needed to fill major gaps in our knowledge.

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