

Foraging mode of the chameleon, *Bradypodion pumilum*: a challenge to the sit-and-wait versus active forager paradigm?

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Foraging mode is an important aspect of life history, often associated with traits such as locomotor mode, energy budget, risk of predation and reproductive effort. Because of these life-history associations, classification of foraging mode can be conceptually useful. Lizards figured prominently in the historical development of foraging mode concepts, yet our current understanding is dominated by only two lizard families which are good examples of the two extreme modes, sit-and-wait vs. active foraging. A great deal of lizard phylogenetic diversity remains unrepresented. Chameleons are a highly derived lizard taxon for which we have very little behavioural or ecological data, and no foraging mode data. Because chameleons are so unusual, it is not possible to predict where they will fit within the bimodal paradigm. I studied time budget and foraging mode in the Cape dwarf chameleon, *Bradypodion pumilum*, in Stellenbosch, South Africa. Several approaches were taken to assess foraging behaviour. First, lag-sequential analysis was applied to compare rates behaviours associated with observed eating events, which did not support a sit-and-wait foraging mode. Second, the number of moves per minute (MPM) and per cent time moving (%TM) were compared with those of other lizard taxa from the literature. Foraging in *B. pumilum* was found to be most consistent with an active foraging mode, although the MPM is unusually low. Thus I propose classification of *B. pumilum* as a cruise forager. Sufficient data are available to define a discriminant function for active vs. sit-and-wait modes among lizard species, which classifies *B. pumilum* as active and additionally lends statistical support for good separation between foraging modes. These findings are discussed in relation to the evolution of foraging modes in chameleons and other lizard families. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 84, 797–808.

ADDITIONAL KEYWORDS: adaptation – foraging behaviour – lag-sequential analysis – life history – lizards – movement rates.

INTRODUCTION

Predators have classically been described as utilizing one of two foraging mode strategies: sit-and-wait vs. active. The majority of lizard species can be placed into one of these two categories. Moreover, the paradigm has been useful as an organizing concept for lizard ecologists because the strategies are associated with much ecological variation (Pianka, 1973; Huey & Pianka, 1981; Vitt *et al.*, 2003).

Actively foraging lizards are characterized by their frequent wandering movements. They eat prey as it is

encountered. Sit-and-wait lizards remain still for long periods of time, running out to capture prey as it appears before them. These modes have many important life-history correlates. Active foragers range widely, eat sedentary prey, are themselves eaten by sit-and-wait predators, expend more energy on a daily basis, and have small clutch sizes. By contrast, sit-and-wait predators have small, defined home ranges, eat mobile prey, seem optimized for expending little energy, and have large clutches. Thus, foraging mode is potentially useful for conceptually integrating various aspects of life history, including reproductive effort (Vitt & Congdon, 1978; Vitt & Price, 1982), energy budget and diet (Bennett & Gorman, 1979; Anderson & Karasov, 1981; Huey & Pianka, 1981), habitat preference and locomotor mode (Moermond,

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1979), and food dispersion and costs of acquisition (Schoener, 1969, 1971).

Lizards have figured prominently in the development of foraging mode concepts, yet our current understanding has been dominated by two families – the Iguanidae (sit-and-wait) and Lacertidae (mainly active). Many lizard families remain unsampled. Perhaps partly because of this taxonomic bias, recent studies have challenged the validity of the dichotomous paradigm, resulting in a more complex picture of foraging behaviour (Tollestrup, 1980). Some studies challenge the restriction to two modes, suggesting additional categories (e.g. ‘saltatory foraging’: Eifler & Eifler, 1999; ‘cruise foraging’: Regal, 1978). Others have found that the two modes are adequate, but not fixed, with lizards able to switch modes (Pietruszka, 1986; Greeff & Whiting, 2000). The most damaging critiques of the bimodal paradigm suggest that the two strategies are not well separated and therefore do not represent true modalities (McLaughlin, 1989; Perry, 1999). However, because these studies have tended to rely on simple analyses of moves per minute (MPM) and per cent time moving (%TM) data, we should at least re-examine the utility of the sit-and-wait vs. actively foraging paradigm using modern statistical techniques before discarding a potentially useful model.

Furthermore, this lack of agreement about foraging modes has hampered progress of our understanding of the evolution of foraging strategies. The debate and uncertainty have left workers without a solid framework for evaluating relevant data. One aim of this paper is to provide a rigorous framework for the comparative analysis of foraging behaviour, so that coupled with increased sampling of taxonomic and ecological diversity, future studies may formally address questions such as: (1) how evolutionarily conservative foraging strategy is, and (2) how foraging strategy evolves within the context of physiological constraints and life-history.

The old-world chameleons (family Chamaeleonidae) are a taxon for which there are no foraging data, yet they pose an interesting challenge to classification in terms of the sit-and-wait vs. active foraging paradigm. Chameleons are highly derived in many aspects of locomotion, behaviour and morphology (Peterson, 1984; Abu-Ghanlyun *et al.*, 1988), and it is difficult to predict a priori which foraging mode they should belong to, because their life history has traits of each modality. Chameleons might be expected to be sit-and-wait foragers because they tend to have large clutches, eat flying insect prey, have great visual acuity and can remain still for long periods of time. In addition, their closest relatives (the iguanids and agamids) also practise sit-and-wait. Alternatively, they could be classified as active foragers because their primary mode of

locomotion is walking rather than running, they tend to move slowly, and eat many small prey. Unfortunately, there have been very few studies on their natural behaviour and ecology (for the few studies which exist see Parcher, 1974; Hebrard & Madsen, 1984; Cuadrado, Martin & Lopez, 2001).

In this study I assess the foraging behaviour of the Cape dwarf chameleon, *Bradypodion pumilum*, in the context of the classic sit-and-wait vs. active foraging paradigm. This is the first report of activity and time budgeting for any chameleon species. I also tested for an association between levels of activity and time of day, ambient temperature, sex, or ontogeny. Foraging mode in *B. pumilum* was examined in three ways. First, because the modes were originally described relative to movement rates and their distribution in time, I applied lag-sequential analysis (Bakeman & Gottman, 1986) to the behaviours preceding observed foraging events. This technique is applied to focal observation data to test for non-random association between a target behaviour and the behaviour preceding it – in this case, prey capture and locomotion, respectively. Second, I conducted classical analysis of %TM and MPM data and compared *B. pumilum* to data collected from the literature. As a final objective, I explored the diversity of foraging modes represented by lizard data currently available and assessed the nature of the dichotomy between sit-and-wait and active modes of foraging using modern multivariate statistics.

MATERIAL AND METHODS

Fieldwork was conducted between 20 October and 5 November 1999 in Stellenbosch, South Africa. Field sites included Stellenbosch Hospital, the banks of streams, and various patches of secondary habitat or suburban gardens in and around the town. Focal observations were videotaped from a distance of 3–5 m and typically lasted 20–30 min. As a precautionary measure, the camera operator hid behind cover when available, but at this distance chameleons did not appear disturbed. Several chameleons walked out of view prematurely, but in no case did an observation last less than 10 min. Each individual was captured at the close of the observation period to confirm sex and record mass and snout–vent length (SVL). All individuals were released at original capture sites. Care was taken to avoid sampling the same individual twice by visiting locations only once or by comparing body size measurements. Perch characteristics – height in cm (PHT) and diameter in mm (PD) – were measured for each lizard at the close of the focal observation at the lizard’s location where first sighted.

Individuals were grouped into three age/sex

categories: adult males, adult females, and juveniles. Juveniles were easily distinguished from adults in the field because they possessed a more drab coloration and were often found on smaller bushes closer to the ground. All lizards identified as juveniles were less than the smallest adult size (55 mm SVL; Burrage, 1973). Adult males and females had similar masses for given values of SVL until c. 75 mm, at which point females can greatly outweigh males. The heaviest female was 16 g at 83 mm SVL, whereas the heaviest male was 11 g at 84 mm SVL.

ANALYSIS OF FOCAL OBSERVATIONS

The occurrence and duration of every action that the focal lizard made was scored from the video replays. Continuous bouts of action were counted as one movement or one display; for example, a string of head bobs with no breaks counted as one bob. Actions were classified into one of four categories for the purposes of analysis: movements, displays, stationary position adjustments, and foraging events (i.e. when the lizard actually ate).

Movements were any motion that resulted in physical displacement of the body. The list of movements scored was as follows: *walk*, *walk-rock*, and *lateral move* (i.e. a sideways shift to the right or left, usually around a branch). Walk-rocks occurred when the lizard walked with a jerking (usually fore-aft) motion. Lateral moves were included because in the three-dimensional habitat of chameleons, lateral moves can expose them to different sides of a bush or tree, and hence a new area in which to forage. *Bradypodion pumilum* produced displays vaguely reminiscent of iguanid push-ups, but with many variations of direction (fore and aft or lateral) and speed (fast displays were jerky, slower displays used a rocking motion). The list of display behaviours observed was: *bob* (up-and-down or side-to-side head display), *jerk* (very fast, exaggerated single motions), *lateral rock* (side-to-side rocking of the body), *rock* (forward and reverse rocking of the body), *push-up*. Stationary position adjustments were postural (i.e. involved no displacement of the body). The behaviours observed were: head movement and body adjustment.

INTRASPECIFIC ANALYSIS OF BEHAVIOURAL DATA

Intraspecific analysis of behavioural data was based on previous studies of foraging behaviour using rates and percentages of movement behaviours. I calculated rates per minute for moves and stationary position adjustments, and rates per hour for foraging events. I calculated the percentage of time spent moving, displaying, and in stationary position adjustments. Descriptive statistics (means with standard errors)

are given for per cent time and rates of behaviour data. However, the rates and proportions were often highly skewed and non-normal. Thus, all statistical tests were conducted on transformed variables which removed skew and provided adequate fit to the normal distribution. The square-root transformation was applied to: per cent time in position adjustments (%TPA), stationary position adjustments per minute (PAPM) and displays per minute (DPM). The negative-inverse square root transformation ($= -1/[\text{sqrt}(X) + 1]$) was applied to per cent time displaying (%TD), per cent time moving (%TM), and number of moves per minute (MPM).

I tested for differences among sex/age classes (adult male, adult female, or juvenile) and for association between time of day or ambient temperature. The effect of age/sex class on behaviour was tested with the following dependent variables: (%TM, %TPA, %TD, MPM, PAPM, and DPM) and age/sex class as the independent variable. Separate ANOVAs were used to test each behaviour singly, and MANOVA to test all behaviours simultaneously. I tested for the association between each behaviour listed above and time of day using separate regression analyses, with time of day as the independent variable. Because sex was not significant in individual ANOVAs above, all individuals were pooled in regression analyses. All statistical analyses were conducted using SAS (SAS Institute, 1989).

LAG-SEQUENTIAL ANALYSIS OF *B. PUMILUM* FORAGING EVENTS

The two foraging modes make different predictions regarding the time distribution of behaviours. Therefore, we can apply lag-sequential analysis (Bakeman & Gottman, 1986) to test whether behaviours (particularly locomotion) immediately preceding foraging events differ from random expectation. Active foragers move frequently and eat prey as they are encountered. Alternatively, sit-and-wait foragers move rarely and run out to capture prey. Thus, a finding that locomotion preceding prey capture occurred at higher than baseline frequencies would support a sit-and-wait modality, whereas a finding that locomotion preceding prey capture occurred at baseline levels would support an active foraging modality.

Lag-sequential analysis is basically an assessment of conditional probability. If behaviours preceding prey capture (Beh1) occur at random with respect to prey capture (Eat), then the probability of observing a particular sequence (Beh1, Eat) is simply the product of their individual frequencies:

$$\text{Expected Frequency (Beh1, Eat)} = \text{Prob(Beh1)} \\ * \text{Prob(Eat)} * N$$

where N is the total number of two-sequence behaviours observed, and $\text{Prob}(\text{Beh1})$ is the number of times that Beh1 is observed in the focal sample dataset divided by the total number of behavioural events observed (and similarly for $\text{Prob}(\text{Eat})$). I tested whether a particular behaviour (BehX) tends to precede prey capture by testing the observed frequency of the two-sequence behaviour (BehX, Eat) against the frequency expected at random (i.e. that BehX occurred at the same frequency as observed during the full-length focal observations). I used a Chi-square test with one degree of freedom. Behaviours were scored as events (rather than state behaviours). In this way, adjacent behaviours during a focal observation were allowed to repeat if there was a time break between behaviours. The LAGS.SAS macro written in SAS was used to compute lag frequencies (Friendly, 2001).

INTERSPECIFIC ANALYSIS OF FORAGING MODE

In keeping with previous lizard foraging behaviour studies, I compared the overall mean %TM and MPM obtained in this study for *B. pumilum* with data from the literature. Data were included if at least five individuals per species were observed and total observation time was at least 60 min. These minimal criteria resulted in the exclusion of many datasets.

Several investigators have provided empirically derived boundaries for classifying lizard foraging modes. Cooper & Whiting (1999) found that sit-and-wait foragers exhibited %TM < 15 and McLaughlin (1989) found an MPM cutoff of 1.0. I used these criteria to separate a %TM vs. MPM bivariate plot into four quadrats. While the exact location of these cutoffs is somewhat arbitrary, they are still useful heuristics for gauging variation in foraging behaviour. The four extremes of the MPM vs. %TM plot were characterized as follows:

- (1) Mostly still or 'stationary': movements infrequent rare and brief (low MPM, low %TM).
- (2) Short spurts: frequent but very short moves (high MPM, low %TM).
- (3) Stop-and-go: frequent moves with short rests (high MPM, high %TM);
- (4) Moving constantly or 'cruising': long moves with few stops (low MPM, high %TM).

I plotted the values for each individual examined in this study and each lizard species from the literature.

TESTING THE BIMODALITY OF FORAGING MODES

I tested the bimodality of foraging modes using discriminant function analysis (DFA) on interspecific MPM and %TM data. I then classified *B. pumilum* using the discriminant function. Interspecific means

for MPM and %TM (from the literature) were negative square root transformed to better approximate a normal distribution. Because I was interested in statistically evaluating assignments of foraging modes made by lizard ecologists, the data were assigned to foraging modes based on sit-and-wait vs. actively foraging classifications made in these studies. The analysis was conducted in SAS using proportional prior probabilities (the proportion of observations in each foraging mode class from the input dataset), and using the default options of parametric classification criteria with pooled covariance matrices. The effectiveness of the discriminant function was cross-validated by jackknife. Briefly, this involved sequentially removing one test observation from the dataset, constructing a discriminant function based on the remaining observations, scoring the classification of the test observation, and repeating the procedure for each observation in the dataset.

RESULTS

Chameleons were active between 08:00 and 18:00, with ambient temperatures ranging between 16 and 27.6 °C (mean 22.6 °C). Sampling effort was uniform throughout the activity period. I observed 24 individuals (5 juveniles, 8 females, and 11 males) for a total of 9.5 h. In total, seven lizards performed 15 foraging events: 17 were not observed to eat, four ate once, two ate three times, and one ate five times (Table 1). Chameleons were never observed running, only walking or climbing (i.e. always with at least one foot touching the substrate) and always on a perch (vegetation or fence). For those individuals which ate prey during the focal observation, the most frequent behaviours were head movements, followed by rock-walk and walk (observed frequencies were 0.393, 0.139, and 0.124, respectively; Table 2).

The study was conducted during the breeding season, yet I did not observe any territorial or aggressive behaviour. In general, chameleons tended to display less frequently than move (Tables 2, 3), and no displays were directed at particular individuals. They were typically found singly and tended to avoid rather than engage nearby conspecifics. In every observed encounter, they would begin to move away when another chameleon came into view.

Analysis of time budget data indicated that chameleons spent the greatest proportion of time being still (69%), followed by in motion (21%), adjusting position (7%), and displaying (2%; Table 3). Males, females, and juveniles do not differ in any one measure of activity (Table 3; all univariate tests are not significant). However, differences in activity among sex/age classes were marginally significant when all variables were tested simultaneously using MANOVA (%TM, %TPA,

%TD, MPM, PAMP, and DPM; Roy's Greatest Root = 0.89, $F_{6,17} = 2.55$, $P = 0.060$). The MANOVA indicated that males and juveniles are generally more active than females. The most important combinations

Table 1. The 11 behavioural sequences leading up to the 15 observed foraging events. Each foraging event is listed as 'Eat'. The number of lags indicates the number of behavioural events before eating (i.e. lag1 behaviours immediately precede eating). In four instances, chameleons ate two prey items in sequence, and both events are listed within the same behavioural sequence. For clarity, the secondary eating events are listed as +1 or +2 events. ID = individual chameleon, Sex = J (juvenile), M (male) or F (female). Behavioural codes are as follows. *Displays*: J = jerk, LR = lateral rock, R = rock. *Movements*: LM = lateral move, W = walk, RW = rock walk. *Position adjustments*: LH = lift head, MH = move head, TH = turn head

ID	Sex	Lag3	Lag2	Lag1	Lag0	+1	+2
1	JF	TH	MH	TH	Eat		
6	JM	W	W	LR	Eat		
6	JM	W	W	RW	Eat	Eat	
6	JM	RW	W	RW	Eat	Eat	
12	M	W	TH	TH	Eat		
13	M	RW	TH	LM	Eat		
19	M	R	RW	R	Eat	RW	Eat
19	M	LR	RW	RW	Eat		
21	M	LH	R	R	Eat		
22	F	J	TH	J	Eat		
22	F	TH	MH	LM	Eat	Eat	

of variables which distinguished groups were a contrast between %TM and MPM (largest eigenvector of the matrix [Inverse of Error of Sum of Squares and Cross Products] * [SSCP matrix for SEX-AGE class]), and %TD (second eigenvector). Comparing mean values in Table 2, males score higher than females and juveniles in %TM, while juveniles score higher than adults in MPM. Mean values for %TD are low for all sex/age classes, but are higher for juveniles (2.1%) and males (2.6%) vs. females (0.9%; Table 3).

Most activities were not related to time of day, with the exception of %TPA, which increased with time (time vs. transformed %TPA regression slope \pm SE = 0.00038 ± 0.00013 ; ANOVA $F_{1,22} = 7.54$, $P = 0.01$). With Bonferroni correction for multiple tests, %TPA dependence on time of day becomes marginally non-significant at $P = 0.07$. None of the activity variables were associated with ambient temperature. Foraging events per hour (0.61–1.96) were similar among sex/age classes (Table 3).

Chameleons were very accurate in targeting prey; those who shot their tongues were 100% successful at capturing prey (15 attempts by 7 individuals). If pursuit was abandoned, it was during or after positioning but always before shooting the tongue. All prey items were small (not identifiable from videotape), and were on (or had just landed on) a plant in proximity to the chameleons.

There were no behavioural associations between prey capture and other behaviours. Four prey items were taken while the chameleons were in motion, the remainder (11) taken by individuals who were still or who moved only to position themselves for better tar-

Table 2. Frequencies of behaviours pooled from the seven lizards which ate during the focal observation period. In total, 338 behaviours were observed. Table columns are as follows: Behaviour = behaviours scored. Descriptions are given in the Material and Methods. The miscellaneous category included the following rare behaviours: curl tail, gular extension (movement of the throat), shake, and yawn. Overall = overall frequency of each behaviour observed during the eight focal observations. Lag1(Eat) = the observed frequency for each behaviour immediately preceding eating events ($N = 15$). Lag2(Eat) and Lag3(Eat) are frequencies for behaviours occurring two and three steps prior to eating, respectively. *significantly different than overall frequency at the 5% level

Behaviour	Overall	Lag1(Eat)	Lag2(Eat)	Lag3(Eat)
Bob	0.021	0	0	0
Lateral Rock	0.068	0.067	0	0.067
Rock	0.036	0.133	0.067	0.133
Push Up	0.021	0	0	0
Jerk	0.041	0.067	0	0.067
Head Movements	0.393	0.133	0.333	0.267
Eat	0.044	0.200*	0.067	0
Lateral Move	0.083	0.133	0.067	0
Rock Walk	0.139	0.267	0.267	0.133
Walk	0.124	0	0.200	0.333
Misc	0.030	0	0	0

Table 3. Time budget data for *Bradypodion pumilum* measured in the present study and sample sizes. Abbreviations are as follows: %TM = per cent time moving; %TPA = per cent time position adjusting; %TD = per cent time displaying; %TS = per cent time still, MPM = moves per minute, PAPM = position adjustments per minute, DPM = displays per minute, FEH = foraging events per hour, PHT = perch height in cm, and PD = perch diameter in mm. *F*-ratios and *P*-values are given for one-way ANOVAs testing for difference among sex/age classes

	Juveniles (<i>N</i> = 5)	Females (<i>N</i> = 8)	Males (<i>N</i> = 11)	All (<i>N</i> = 24)	<i>F</i>	<i>P</i>
%TM	16.7 ± 8.0	12.3 ± 4.0	28.8 ± 7.1	20.8 ± 4.1	1.67	0.24
%TPA	6.5 ± 1.5	7.5 ± 2.5	9.0 ± 3.0	6.5 ± 1.5	0.00	1.00
%TD	2.1 ± 0.7	0.9 ± 0.6	2.6 ± 1.5	2.1 ± 0.7	0.89	0.43
%TS	74.7 ± 8.4	79.3 ± 5.1	59.5 ± 8.0	69.3 ± 4.6	1.70	0.21
MPM	0.77 ± 0.2	0.29 ± 0.0	0.39 ± 0.1	0.43 ± 0.1	2.36	0.29
PAPM	0.63 ± 0.2	0.43 ± 0.1	0.44 ± 0.1	0.47 ± 0.1	0.58	0.57
DPM	0.43 ± 0.1	0.16 ± 0.1	0.22 ± 0.1	0.25 ± 0.0	1.21	0.32
FEH	1.96 ± 1.51	0.61 ± 0.41	1.55 ± 0.72	1.32 ± 0.46		
PHT(cm)	47.5 ± 6.5	131.5 ± 29.4	116.6 ± 24.7	105.6 ± 16.1		
PD(mm)	4.9 ± 1.3	7.2 ± 0.9	12.9 ± 3.7	9.0 ± 1.8		

getting of prey (typically turning the body from being parallel to the perch to being perpendicular and extending the torso in the direction of prey). Eleven behaviours were scored during focal observations (Table 2). Three of these (bob, push-up, and misc.) did not occur within three behavioural events prior to foraging events.

Seven different two-sequence behaviours were observed in which the target (second) behaviour was a foraging event ('Eat' in Table 1). Only 'Eat-Eat' occurred at higher than random frequency ($\chi^2_1 = 8.47$, $P < 0.0036$, significant at the 5% level after Bonferroni correction for multiple tests). Results did not differ if the analysis was conducted on behavioural categories (movements, displays, position adjustments, eating events) rather than individual behaviours. Locomotion behaviours preceding foraging events occurred at baseline frequencies, whether the event or individual was used as the unit of analysis (i.e. counting only the first foraging event per individual lizard).

There was a wide range of variation in %TM and MPM among and within sex/age classes (Fig. 1A). Most notable was that females were concentrated in the 'stationary' quadrat, whereas variation among males covered the entire 'stationary' and 'cruise' quadrats. The species mean for *B. pumilum* was 0.43 MPM and 21%TM, which would classify it as an active forager based on simple comparison to rates from the literature. Plotting of the species mean value places *B. pumilum* in the 'cruise' quadrat (Fig. 1B).

MPM and %TM measured in comparable fashion were compiled from the literature for all available lizard taxa (Appendix, Fig. 1B). Most actively foraging species (one teiid, two skinks, and most lacertids) fell

within the 'stop-and-go' quadrat, with only three falling in the 'cruise' quadrat (one skink and two teiids). Most sit-and-wait foragers fell within the 'stationary' quadrat (all iguanids, agamids, and gekkonids), with only four species in the 'short spurts' quadrat (one cordylid, one skink, and two lacertids). An exception was *Platysaurus broadleyi*, a cordylid species which is generally a classic sit-and-wait predator when feeding on insects (%TM = 4.4), but switches to a greater level of activity when foraging on figs, a seasonally ephemeral but high-energy food resource (%TM = 15.5; Greff & Whiting, 2000).

Discriminant function analysis (DFA) classifies *B. pumilum* as an active forager (Fig. 2). It was able to 'correctly' classify 43 out of 44 lizard species (2% error rate). The misclassified data point lies along the border between the two modes: *Platysaurus broadleyi* (MPM 1.9, %TM 15.5; authors classified as active, DFA classified as sit-and-wait). While the DFA was more heavily dependent on %TM values (Figs 1B, 2), both are important in the low %TM region. For example, lizards which initiated few movements but of longer duration (e.g. 10%TM and 0.1 MPM) would be classified as active, whereas lizards with a greater number of movements of shorter duration (e.g. 10%TM and 1.0 MPM) would be classified as sit-and-wait (Fig. 1B). The transition found by the DFA corresponds roughly with previously used empirical cutoffs of 10–15%TM, but makes a more complex discrimination (note curvilinear grey area in Fig. 1B). The distinction between sit-and-wait vs. active was significantly different in MPM and %TM tested by MANOVA (Roy's Greatest Root = 4.57, $F_{2,41} = 93.65$, $P < 0.0001$)

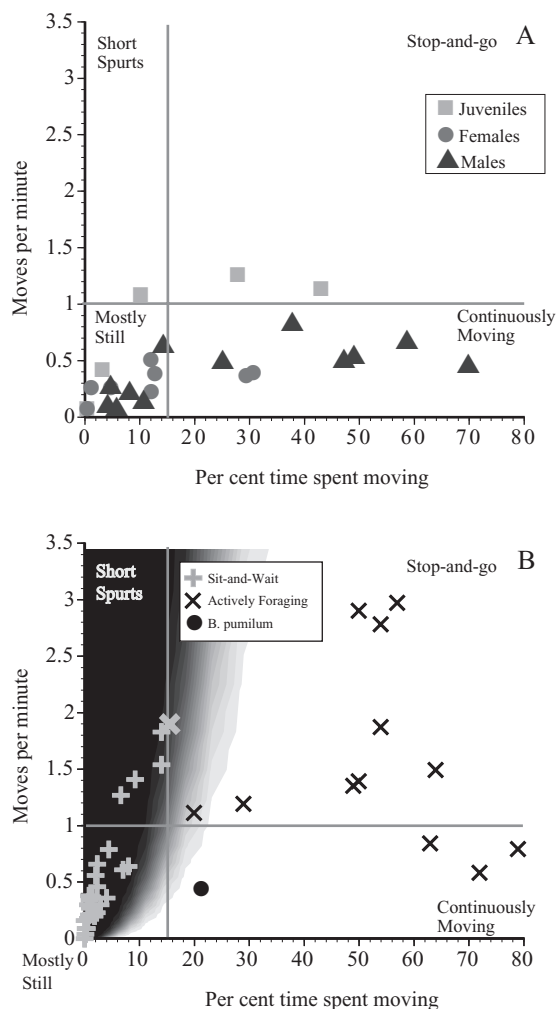


Figure 1. Per cent time moving (%TM) vs. moves per minute (MPM) for all individuals included in the study (A) and for lizard species means obtained from the literature (B). Previously published studies have proposed cut-off values of 15 for %TM and 1.0 for MPM to separate modalities. The modalities are indicated by dashed lines that divide the graph into four quadrats (see text for explanation). The quadrats are labelled with descriptors which characterize the extremes. The posterior probability for classifying species using discriminant function analysis into one of the two foraging modes is indicated in B by shading (black = 100% probability of sit-and-wait; white = 100% probability of actively foraging).

DISCUSSION

INTRASPECIFIC VARIATION IN BEHAVIOUR

I found extensive intraspecific variation in *B. pumilum* foraging behaviour, a finding which is seldom reported in foraging mode studies (although most likely common, as rates of behaviours tend to be

highly variable between and within individuals). Hitherto, most studies have observed very few individuals or observe them for short periods, reducing their utility for commenting on individual variation. Adult observations in this study spanned the range from 'mostly still' (virtually no movement) to extremes of 'cruising'. While examination of Figure 1A indicates that the distribution of %TM is rather platykurtic (spread out), the characterization of chameleons as cruising foragers is appropriate for several reasons. There is no evidence for bimodality (or 'mixed mode') in the movement parameters. Chameleons are clearly different from sit-and-wait foragers which have very little variation about their %TM and MPM statistics (see References in Appendix). Active foragers have similar standard errors to *B. pumilum*, but no further distributional information is available in the literature for comparison.

The finding of intraspecific variation serves as a caution for assessments of foraging mode based on limited data. Some comparative studies report data based on fewer than five individuals or on limited behavioural observations (< 60 min total). While these data may be valuable in the case of rare or inaccessible species, they must be considered tentative in this context.

The sex and age classes of *B. pumilum* differed in activity, with males and juveniles more active than females. This contradicts the finding by Burrage (1973) that females were more active than males during the reproductive season, but confirms findings in another chameleon species (*Chameleo dilepis*) that they are more sedentary (Hebrard & Madsen, 1984). It is not clear whether females have reduced activity, perhaps because of the increased metabolic demands of pregnancy, or whether males have increased activity because they are seeking mates and defending territories. Data from observations made outside the breeding season are needed to resolve this issue.

It is interesting to note, however, that juveniles were also more active than adult females and displayed at levels similar to males, which is more consistent with the hypothesis that females are more sedentary during the breeding season. Also, chameleons seemed to avoid one another. I observed a few chance encounters. When they sighted one another, both quickly changed course and direction, behaviour not consistent with territorial defence.

These findings present several questions for future study, including whether: (1) reproductive females are more 'sedentary'; (2) males range further than females to find mates; (3) dietary intake is related to ranging, and if so, how it impacts daily energy budget; (4) juveniles are active because of dietary needs related to growth or are engaging in active motor learning

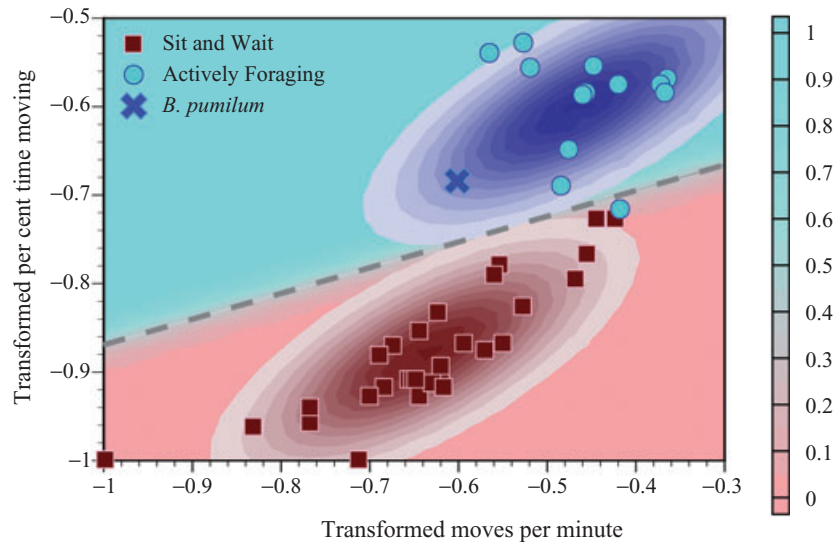


Figure 2. Discriminant function analysis of transformed species-mean data from the literature (negative square root transformation of MPM and %TM). Oval contours indicate density plots for the two foraging mode clusters (lower right [red]: sit-and wait; upper left [purple]: actively foraging). Background shading indicates the posterior probability of species being classified into one of the two foraging mode clusters. The dashed line indicates 50% posterior probability. Symbols indicate foraging modes assigned by previous studies. The labelled gradient bar indicates the probability levels for classification (blue to active foragers, pink to sit-and-wait).

required for their unusual locomotion in a complex 3D habitat.

FORAGING MODE OF *B. PUMILUM*

Lag-sequential analysis revealed that while chameleons were observed to move immediately prior to capturing prey, these movements occurred at similar rates as those observed throughout the focal observation period (Table 2). Movements were not more likely in the three behaviours prior to foraging events relative to the average movement rate computed during the focal observation, as one might expect if *B. pumilum* was a sit-and-wait forager.

Both DFA conducted on %TM and MPM and the empirical %TM cutoff indicate that *B. pumilum* is an active forager. Although %TM = 21 is low for an active foraging species, it is not uniquely so, as two additional species classified as active foragers have values of 20% and 29%. However, *B. pumilum* is unusual in comparison to other active foragers with its low MPM rate of 0.43 (Fig. 1B). An extreme active forager is characteristically walking and searching in a stop-and-go pattern, with frequent stops and starts and changes in direction; it will typically occupy the upper right quadrat of the %TM vs. MPM (Fig. 1A). This is clearly not the case for this chameleon, in which a large percentage of time is spent moving, but few

walks are initiated. Three other species in addition to *B. pumilum* occupy the cruise quadrat – a skink and two teiids (Cooper *et al.*, 2001).

If the 'cruise foraging' behaviour found in *B. pumilum* is characteristic of chameleons, it is likely derived from sit-and wait ancestors, as chameleons are phylogenetically nested within agamids and iguanids (Estes, De Queiroz & Gauthier, 1988). Some key questions that remain to be answered are whether chameleons share the physiological life-history correlates of other active or cruise foragers, or whether they have found some way to evolve high levels of activity at low cost.

Whether very slow locomotion is inexpensive is an open question. I observed low rates of prey capture in *B. pumilum*, indicating low levels of food intake, similar to those of sit-and-wait foragers (appendix Table 1). However, measurements of field metabolic rates, energetic cost of locomotion, and gut content analysis are required to address this issue. If energetic intake is indeed low, then chameleons must have an economical means of maintaining relatively constant activity, potentially providing the exception that proves the foraging paradigm rule, which would truly be adaptation to a novel lizard niche. This seemingly contradictory situation – highly active lizards with low food intake – is a puzzle that awaits further study.

VALIDITY OF SIT-AND-WAIT VS. ACTIVE FORAGING

The boundary between sit-and-wait and active foraging modes established by DFA is a gradient of probability that drops sharply between 10 and 15%TM, which corresponds to values previously cited for empirical cutoffs with the additional qualification that the %TM threshold is correlated with MPM value. A previous study (Perry, 1999) concluded that there was little evidence for bimodality in lizard foraging modes. However, the tests employed (testing against a uniform distribution and visual examination of frequency histograms) were not appropriate. The MPM and %TM data are clearly not uniformly distributed (it is generally extremely difficult to obtain a uniform distribution from frequency data). However, the fact that they are not uniformly distributed does not help to answer the question of whether we can identify the two groups. DFA on suitably transformed data provides an appropriate test of bimodality. While the separation obtained is not absolute, the two modes are sufficiently 'discrete' to separate lizard species by statistical means.

Three data points occur along the border between modes (Fig. 2). The datum which was misclassified is from an unusual situation in which a normally insectivorous species temporarily incorporates fruit into its diet (Greef & Whiting, 2000). When this species is not eating figs, it is well within the sit-and-wait cluster. Two data points may represent species which are truly intermediate. Huey & Pianka (1981) designated these lacertid species as sit-and-wait relative to other lacertids. Thus, the original designation was a relative one applied in relation to more active lacertids, rather than to lizard foraging modes generally. The classification by DFA of these data points may change with the addition of more data.

There was a 'misclassification' of only one datum out of 44, and the general findings are of good separation between lizard foraging modes. Thus investigators should continue to employ the sit-and-wait vs. actively foraging paradigm so long as it remains useful for constructing hypotheses about natural history. The dichotomous classification represents a good major division for the classification of foraging mode, but there is growing support for further refinement. There is good correspondence between the two modes defined by posterior probability of the DFA and the %TM vs. MPM plot with empirical cutoffs (Fig. 1B), such that the 'mostly still' and 'short spurts' regions correspond with sit-and-wait, and 'stop-and-go' and 'continuously moving' regions with active foraging. These subdivisions represent very different movement rates which may be ecologically relevant.

In accord with previous studies, I found that foraging mode is conservative at the family level, suggest-

ing that it represents an important evolutionary constraint. Which general strategy to adopt has apparently been decided early in the evolutionary history of lizard families, as all agamids, cordylids (with the single exception noted previously), iguanids, and gekkonids are sit-and-wait and 'stationary', whereas teiids and lacertids tend more often to be active foragers and 'stop-and-go' (Regal, 1978; Perry, 1999; Vitt *et al.*, 2003).

A novel finding in this study is that, skinks (rather than lacertids) were the most variable taxon, occurring in all four quadrats. Lacertids occurred in three quadrats: 'stop-and-go', 'short spurts', and 'stationary' (Fig. 1B). Why this family retains the flexibility to adapt to a much greater diversity of modes while foraging mode in lizard families is generally conservative should be investigated in future comparative studies.

In addition to the 'cruise', 'stationary' and 'stop-and-go' characterizations discussed above, the fourth variation is 'short spurts' (which corresponds to the saltatory foraging behaviour identified by Eifler & Eifler, 1999). Five species to date fall within this quadrat (two cordylids, two lacertids and one skink). They are similar to sit-and-wait species in terms of %TM, but they have unusually high MPM. The small number of species identified in each of the 'short spurts' and 'cruise' foraging patterns may, however, reflect taxonomic bias in sampling rather than actual diversity of strategies, since early work concentrated on iguanids and lacertids (overwhelmingly 'stationary' and 'stop-and-go' behavioural modes, respectively). Of the eight family/subfamily level taxa represented in the dataset, five were added in the last six years, and all of the 'cruisers' were added in the past two. The species found within the 'short spurts' and 'cruise' quadrats tend to be from recently sampled families. More data from underrepresented families will likely show that these are important variations in lizard foraging behaviour. Clearly, further research into taxonomic and ecological diversity is required.

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APPENDIX

Foraging data for lizard species from the literature. Abbreviations: SS, sample size; TO, total observation time in minutes; FM, foraging mode (SW, sit and wait; AF, active foraging); MPM, moves per minute; %TM, per cent time moving; PCH, prey capture rate per hour. Data were included if both MPM and %TM were given; at least five individuals were observed per species and total observation time was at least 60 min. All prey capture per hour data are listed.

	SS	TO	FM	MPM	%TM	PCH	Reference
CHAMELEONIDAE							
<i>Bradypodion pumilum</i>	24	570	–	0.43	21	1.0	This study
AGAMIDAE							
<i>Acanthocercus a. atricollis</i>	19	>60	SW	0.36	4	10.6	Reaney & Whiting, 2002
<i>Agama atra</i>	24	232	SW	0.27	1	2.3	Cooper <i>et al.</i> , 1999
<i>Agama planiceps</i>	27	240	SW	0.56	2	–	Cooper <i>et al.</i> , 1999
CORDYLIDAE							
<i>Cordylus polysonus</i>	17	157	SW	0.04	0.15	–	Cooper <i>et al.</i> , 1997
<i>Cordylus cataphractus</i>	15	121	SW	0.23	2.2	–	Mouton <i>et al.</i> , 2000
<i>Cordylus cordylus</i>	45	428	SW	0.09	0.27	–	Cooper <i>et al.</i> , 1997
<i>Cordylus niger</i>	36	350	SW	0.09	0.19	–	Cooper <i>et al.</i> , 1997
<i>Platysaurus broadleyi</i> *	78	>60	SW	0.79	4.4	–	Greeff & Whiting, 2000
<i>Platysaurus broadleyi</i> **	78	>60	AF	1.90	15.5	–	Greeff & Whiting, 2000
<i>Platysaurus capensis</i> ***	22	205	SW	1.27	6.6	–	Cooper <i>et al.</i> , 1997
<i>Pseudocordylus microlepidotus</i>	7	70	SW	0.0	0	–	Cooper <i>et al.</i> , 1997
IGUANIDAE							
<i>Anolis polylepis</i>	37	1500	SW	–	–	1.4	Andrews, 1974
<i>Anolis polylepis</i>	138	1182	SW	0.37	1.2	–	Perry, 1996
<i>Cophosaurus texanus</i>	14	129	SW	0.46	2.3	–	Cooper <i>et al.</i> , 2001
<i>Crotaphytus collaris</i>	39	380	SW	0.09	0.4	–	Cooper <i>et al.</i> , 2001
<i>Norops oxylophus</i>	25	244	SW	0.20	1.8	0.8	Vitt <i>et al.</i> , 1995
<i>Oplurus c. cuvieri</i>	26	915	SW	0.30	0.6	–	Mori & Randriamahazo, 2002
<i>Sceloporus clarkii</i>	20	178	SW	0.21	0.8	–	Cooper <i>et al.</i> , 2001
<i>Sceloporus jarrovi</i>	46	455	SW	0.34	0.9	–	Cooper <i>et al.</i> , 2001
<i>Sceloporus virgatus</i>	30	296	SW	0.38	0.8	–	Cooper <i>et al.</i> , 2001
<i>Uma inornata</i>	51	2274	SW	–	2.4	–	Durtsche, 1992
<i>Urosaurus ornatus</i>	30	294	SW	0.66	2.3	–	Cooper <i>et al.</i> , 2001
<i>Uta stansburiana</i>	15	146	SW	0.18	0.6	–	Cooper <i>et al.</i> , 2001
GEKKONIDAE							
<i>Rhotropus barnardi</i>	23	308	SW	0.28	1	1.2	Cooper <i>et al.</i> , 1999
<i>Rhotropus boultoni</i>	24	232	SW	0.29	1	–	Cooper <i>et al.</i> , 1999
<i>Pachydactylus turneri</i>	11	110	SW	0.16	0	–	Cooper <i>et al.</i> , 1999
LACERTIDAE							
<i>Acanthodactylus erythrurus</i>	29	>60	SW	0.64	8	–	Belliure, Carrascal & Diaz, 1996
<i>Eremias lineocellata</i>	15	152	SW	1.54	14	–	Huey & Pianka, 1981
<i>Meroles knoxii</i>	27	235	SW	0.61	7	1.5	Cooper & Whiting, 1999
<i>Meroles suborbitalis</i>	15	123	SW	1.83	14	–	Huey & Pianka, 1981
<i>Ermias lugubris</i>	15	72	AF	2.97	57	–	Huey & Pianka, 1981

APPENDIX *Continued*

	SS	TO	FM	MPM	%TM	PCH	Reference
<i>Eremias namaquensis</i>	25	131	AF	2.78	54	–	Huey & Pianka, 1981
<i>Heliobolus lugubris</i>	14	90	AF	1.49	64	30	Cooper <i>et al.</i> , 1999
<i>Nucras tessellata</i>	11	60	AF	2.90	50	–	Huey & Pianka, 1981
<i>Pedioplanis undata</i>	16	119	AF	1.39	50	2	Cooper & Whiting, 1999
<i>Pedioplanis namaquensis</i>	26	237	AF	1.87	54	16	Cooper & Whiting, 1999
<i>Psammodromus algirus</i>	43	>60	AF	1.11	20	–	Belliure & Carrascal, 1996
TEIIDAE							
<i>Cnemidophorus deppii</i>	39	368	AF	0.84	63	–	Cooper <i>et al.</i> , 2001
<i>Cnemidophorus uniparens</i>	33	272	AF	0.79	79	–	Cooper <i>et al.</i> , 2001
SCINCIDAE							
<i>Eumeces laticeps</i>	25	164	AF	0.58	72	–	Cooper <i>et al.</i> , 2001
<i>Mabuya acutilabris</i>	27	269	SW	0.37	1.4	–	Cooper & Whiting, 2000
<i>Mabuya spilogaster</i>	11	105	SW	0.30	2.9	–	Cooper & Whiting, 2000
<i>Mabuya sulcata</i>	20	118	AF	1.35	49	–	Cooper & Whiting, 2000
<i>Mabuya variegata</i>	16	116	AF	1.19	29	–	Cooper & Whiting, 2000
<i>Oligosoma grande</i>	22	>60	SA	1.41	9.2	1.5	Eifler & Eifler, 1999

*Adult lizards feeding on insects only, sites, insect-rich and insect-poor and sexes pooled.

**Adult lizards feeding on both figs and insects, sexes pooled.

***This population has been renamed *Platysaurus broadleyi*. Lizards were feeding on both figs and insects, W. Cooper, pers. comm.