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A phylogenetic perspective on foraging mode evolution and habitat use in West Indian *Anolis* lizards

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Although many descriptive studies of foraging mode have been performed, the factors that underlie the evolution of foraging mode remain poorly understood. To test the hypothesis that foraging mode evolution is affected by habitat use, we analysed two data sets including 31 species of West Indian *Anolis* lizards. In this genus, the same suite of habitat specialists (or ecomorphs) has evolved on four islands, providing the replication necessary to evaluate the generality of the relationship between foraging mode and habitat use. Using habitat and behavioural data, we conducted phylogenetic comparative analyses to determine whether species of the same ecomorph have evolved similar foraging behaviour and whether differences in foraging mode are associated with differences in habitat use. We found that *Anolis* species show substantial variation in foraging behaviour, including differences in movement and eating rates. Furthermore, variation among ecomorphs indicates that foraging behaviour is related to habitat use, although the specific environmental factors driving foraging divergence are unclear. Our results show that foraging mode is an evolutionarily labile trait that is influenced by evolution of habitat use.

The ecology of feeding has attracted a significant amount of research, including the development of optimal foraging theory (MacArthur & Pianka 1966; Schoener 1971; Stephens & Krebs 1986) and investigation of possible factors shaping the evolution of foraging strategies (Pianka 1966; Curio 1976; Huey & Pianka 1981; O'Brien et al. 1989; Fernández-Juricic et al. 2004). Pianka (1966), in a study of North American desert lizards, identified two strategies for capturing prey: active foraging, in which the foraging animal moves frequently in quest of its prey, attacking the prey as they are encountered, and sit-and-wait foraging, in which the forager motionlessly scans an area for prey and attacks once the prey has been located. In the last four decades, an enormous body of

work has investigated the foraging modes of organisms as disparate as birds, mammals, reptiles, frogs, insects, spiders, ticks and nematodes (reviewed in Cooper 2005a; nematodes: Campbell & Kaya 2002; Lewis et al. 2006). Recurring debates in this field include whether the two aforementioned foraging modes represent discrete alternatives rather than being endpoints on a continuum (Pietruszka 1986; McLaughlin 1989; Perry 1999; Butler 2005; Cooper 2005a, 2007) and whether other distinct alternative foraging modes also exist (e.g. Regal 1983; O'Brien et al. 1989, 1990).

The morphological, ecological and physiological correlates of foraging mode have received considerable attention, as has the possibility that foraging modes are the product of correlated evolution as part of a behavioural syndrome (Sih et al. 2004). Various studies have suggested that sit-and-wait and active foragers differ in a wide variety of organismal traits, including sprint speed,

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endurance, body form, limb length, thermoregulatory and hydric physiology, sensory modalities, and reproductive mode (reviewed in Perry 1999; Miles et al. 2007; Verwaijen & Van Damme 2007). By contrast, why species have evolved to adopt a particular foraging mode has received relatively little attention.

Moermond (1979) suggested that the habitat in which an individual occurs is a critical determinant of foraging mode. In particular, wide-open habitats in which an individual can see great distances would favour a sit-and-wait strategy, whereas more cluttered habitats would require a predator to move more frequently to find its prey (Cooper 2007). Moermond's (1979) study was concerned with lizards, but Robinson & Holmes (1982) subsequently argued that the same considerations applied to the evolution of foraging behaviour in woodland birds. More generally, foraging mode might differ between habitats for a variety of reasons, such as differences in the abundance of a species' predators or prey among habitats (e.g. Lima & Dill 1990; Lima & Bednekoff 1999), but little research has addressed the relationship between structural habitat and foraging mode.

West Indian *Anolis* lizards provide an ideal opportunity to test the hypothesis that foraging mode evolves in response to differences in habitat use. On each island in the Greater Antilles, evolutionary diversification has produced a series of different habitat specialists, termed ecomorphs (Williams 1972; Table 1). Remarkably, more or less the same set of ecomorphs has evolved independently on each island in the Greater Antilles (Williams 1983; Losos et al. 1998). This widespread convergence provides the replication necessary to examine whether foraging mode and habitat evolution are related.

Several authors have noted variation in anole foraging behaviour and suggested that it was related to differences in habitat use. Moermond (1979) and Cooper (2005b), studying Hispaniolan and Puerto Rican species, respectively, found that ecomorph species differed in movement

rate. The lack of evolutionary replication within an island and the small sample sizes (seven species in each study), however, prevented statistical analysis of the relationship between ecomorph class and foraging behaviour.

Using a larger data set comprising 31 species from five islands (see Appendix), and including multiple, independently evolved members of each ecomorph class, we tested the following hypotheses:

(1) Have differences in foraging mode evolved among members of the different ecomorph classes?

(2) If so, do specific features of habitat use that vary among the ecomorphs explain the evolution of different foraging behaviour?

METHODS

We used two data sets collected at different times and on partially overlapping sets of species to examine whether foraging mode evolution corresponded with the evolution of different ecomorph classes. We then used data set 1, for which habitat and behavioural data were more extensive, to further explore the characteristics of behaviour and habitat use that affect foraging mode, including frequency of eating episodes, movement rates during eating episodes, and habitat openness.

Data Collection

Data set 1

For the 14 species in this data set (representing four ecomorph types and species from four islands: Jamaica, Puerto Rico, Dominican Republic and South Bimini, Bahamas), we established an approximately 500 m^2 plot and caught and marked each adult male lizard in the plot. Over a 2–3-week period during summer months in 2004–2006, we performed undisturbed focal observations (7–180 min) of the marked lizards (60–80 h per species), noting all the movement and foraging behaviour. For most species, we located lizards for observation by walking slowly through the habitat until finding an apparently undisturbed subject. However, for some particularly cryptic species (*Anolis angusticeps*, *Anolis bahorucoensis*, *Anolis sheplani* and *Anolis valencienni*), we also located lizards in their sleeping sites before sunrise and observed them upon waking. (There is no evidence that animals observed from daybreak are consistently different in movement rates from those observed at other times of day.) We observed each lizard 1–5 times. We calculated movement rates for each observation and averaged rates for each individual over all observations. Only observations in which the lizard performed more than 0.25 movements per minute (MPM) were included in analyses so as to exclude animals potentially disturbed by our presence. Species' averages were then calculated from an average for each individual.

We measured the following microhabitat characteristics at the time of each observation, at the position of first sighting: perch height, perch diameter and visibility. Perch height and diameter are the classic microhabitat traits with which ecomorphs were defined (Williams

Table 1. Characteristics of ecomorphs*

Ecomorph	Modal perch	Movement type	Morphology
Grass-bush	Grasses or bushes	Jumper	Small; long hindlegs and tail; small toepads
Trunk-ground	Lower tree trunks	Jumper	Very long hindlegs; stocky; small toepads
Trunk	Tree trunks	Runner	Relatively long forelimbs; small, short tail
Trunk-crown	Upper trunks/ branches	Crawler	Short limbs; large toepads
Twig	Canopy twigs/ branches	Crawler	Extremely short limbs and tail
Crown-giant	High in canopy	Walker	Very large body size

*According to Moermond (1981) and Losos (1990).

1972), and visibility is a proxy measure for the structural complexity, or clutteredness, of a habitat. We estimated visibility (i.e. the proportion of the lizard's microhabitat it can see from a given perch) following Johnson et al. (2006). Briefly, to estimate visibility we determined the proportion of two orthogonal planes blocked by each object within a 0.5-m radius around the lizard's head, summed these proportions for all objects within the radius and subtracted this value from 1, providing an estimate of the proportion of space around a lizard in which vision is not obstructed. For each individual observed multiple times, we calculated an average for perch height, diameter and visibility, and from those values we calculated an average for each species. We natural logarithm transformed height and diameter (after adding a value of one to each datum because of the presence of zeros in the data set) and arcsine transformed visibility for use in statistical analyses.

Data set 2

We collected data for males of 27 species (representing all six ecomorph classes and four islands) in this data set in a generally similar way to that just described for data set 1 during summer months in 1987−1989 and in 1997. We found lizards for observation by slowly walking through the habitat until an apparently undisturbed subject was located. We observed lizards for up to 20 min (some lizards disappeared from view before the end of the observation session); we included only individuals watched for at least 5 min and which moved at least five times (five moves in 20 min = 0.25 MPM). Data for Jamaican and Puerto Rican species were previously published in Losos (1990). We observed one species, *Anolis sagrei*, on two islands (Jamaica and Cuba), and we averaged this species' MPM from those two islands for use in analysis.

Ecomorphology and Movement Behaviour

To determine whether the ecomorph categories differ in movement rates (MPM), we first combined the data sets as follows. Using data from the 10 species in both data sets (see Appendix), we determined that MPM values in the two data sets were highly correlated ($r = 0.86$, $P = 0.001$), but values for species' MPM in the first data set were on average 59% of the corresponding values in the second data set. We then divided all MPM data in the first data set by 0.59. For the 10 species common to both data sets, we averaged the first data set (divided by 0.59) and the second data set measures to obtain a single value for each species.

With the combined (31 species) data set, we conducted both a standard (nonphylogenetic) analysis of variance (ANOVA) and a phylogenetic ANOVA, following Garland et al. (1993), with MPM as the dependent variable and ecomorph as the independent variable. In the standard ANOVA, we used Tukey's HSD test to characterize differences between ecomorphs. In the phylogenetic ANOVA, we used the phylogeny from Nicholson et al. (2005), pruned to include only the species in the data set, and with branch lengths made ultrametric using the program r8s (Sanderson 2003).

We conducted a phylogenetic ANOVA because when species are related by a phylogenetic tree, species may not represent statistically independent data points, and consequently the degrees of freedom in a standard ANOVA are inflated (Felsenstein 1985; Harvey & Pagel 1991). Garland et al. (1993) proposed that one solution to this problem is to generate a null distribution for the ANOVA via computer simulation. To accomplish this, we simulated the evolution of MPM by gradual Brownian motion on the empirical phylogeny, assuming that branch lengths in the phylogeny were proportional to time. We estimated the other parameter in the Brownian motion simulation, the rate of evolution of MPM, by calculating the mean square of the independent contrasts from the empirical data and phylogeny; this provides an unbiased estimate of the Brownian motion rate parameter (Garland et al. 1999). Each simulation produced values for each species; using these values, we calculated a value of the F statistic. The P value of the phylogenetic ANOVA was the proportion of the simulations in which the F statistic from the simulated data exceeded the empirical value of F.

A post-hoc means comparison was conducted in a similar way. For each simulated data set, all pairwise t statistics were calculated between all groups. The significance of comparison of the means was evaluated as the fraction of times the absolute value of t from the simulated data sets exceeded its corresponding observed empirical value. With six ecomorph classes, we conducted 15 post hoc pairwise comparisons. At a nominal P value of 0.05, we might expect less than one false significant result to occur by chance; however, when correcting for multiple tests, we found that in many cases, 2−3 comparisons switched from significant to nonsignificant. As others have noted (e.g. Moran 2003), we found this cost in reduced statistical power to exceed the benefit from type I error protection, and hence we do not correct for multiple tests. We provide the results from our pairwise comparisons in Tables 2 and 3, so the data are available for multiple test correction for any who question this approach.

Frequency of Eating Episodes

We determined the frequency of eating episodes (defined as successful prey capture) for each species in data set 1 by determining the proportion of observational periods in which eating was observed. These data were calculated using a total of 594 observed eating episodes for

Table 2. P values from pairwise t tests of movement rates among ecomorphs

	Crown-giant	Grass-bush	Trunk-crown	Trunk-ground	Trunk
Grass-bush	0.757				
Trunk-crown	**0.005**	**0.001**			
Trunk-ground	0.934	0.742	**0.002**		
Trunk	0.075	**0.043**	0.668	**0.033**	
Twig	0.113	0.104	0.172	**0.051**	0.559

Table 3. *P* values from pairwise *t* tests of eating rates among ecomorphs

	Grass-bush	Trunk-crown	Trunk-ground
Trunk-crown	**0.032**		
Trunk-ground	0.713	**0.016**	
Twig	0.063	0.967	**0.015**

the 14 species (average = 42 episodes/species; median = 26.5; range 8–189). To determine whether species in different ecomorphs ate at different overall frequencies, we conducted standard and phylogenetic ANOVAs (as described above) with the proportion of observations in which eating was observed as the dependent variable and ecomorph as the independent variable. To determine whether eating rate is a significant predictor of MPM, we used independent contrasts (Felsenstein 1985) calculated using the IDC program (Revell 2006). MPM contrasts were adequately standardized following Garland et al. (1992), but contrasts for eating rate were correlated with contrast length. Eating rate contrasts were then recalculated after logarithm transforming branch lengths (plus a value of one, as some branch lengths in the phylogeny were zero), a procedure that we found provided adequate standardization. We conducted a linear regression through the origin with eating rate contrasts as the independent variable and MPM contrasts as the dependent variable (Garland et al. 1992). For these analyses, we again used the phylogeny from Nicholson et al. (2005) as described above.

Movement When Eating versus Movement When Not Eating

We divided behavioural observations in data set 1 into two categories: observations in which eating occurred and observations in which eating did not occur. We then calculated the average MPM for each individual for eating and noneating observations, and from these individual averages we determined species averages for both categories. We used repeated measures multivariate analysis of variance (MANOVA), with species' average MPM in eating observations and noneating observations as the dependent variables, and ecomorph as the independent variable, to determine whether species in different ecomorphs move at different rates when they are eating versus when they are not. Within each ecomorph, we determined whether species differed in MPM during eating and noneating observations using paired sample *t* tests.

Microhabitat and Movement Behaviour

To determine the relationship between microhabitat characteristics (height, diameter and visibility) and MPM, we used the habitat and behavioural data in data set 1. Data set 2 contains more species, but does not include visibility data. For this reason, we ran three sets of analyses (data set 1, data set 2, and combined data sets). We

calculated independent contrasts (Felsenstein 1985) as described above for height, diameter, MPM and, in the first data set, visibility. All contrasts in this analysis were adequately standardized following Garland et al. (1992). We performed linear regressions through the origin with MPM contrasts as the dependent variable and contrasts of the transformed microhabitat characteristics as independent variables (Garland et al. 1992).

RESULTS

Ecomorphology and Movement Behaviour

Ecomorphs significantly differed from one another in movement rates (MPM) in both the standard and phylogenetic ANOVAs ($F_{5,25} = 6.19$; standard ANOVA $P = 0.001$; phylogenetic ANOVA $P = 0.002$). The post hoc tests for the two analyses yielded qualitatively similar results, so only results from the phylogenetic post hoc tests are presented here (Fig. 1 and Table 2). Crown-giant, trunk-ground, and grass-bush species had significantly lower movement rates than trunk and trunk-crown species, whereas twig species (which showed highly variable MPMs, see Appendix) did not differ from either group.

Frequency of Eating Episodes

Trunk-crown and some twig species not only moved more frequently than trunk-ground and grass-bush species (see above and Appendix), but they also ate more frequently ($F_{3,10} = 5.49$; standard ANOVA $P = 0.010$; phylogenetic ANOVA $P = 0.021$; Fig. 2 and Table 3). An explicit test of the relationship between movement and eating rates showed that the two were significantly related (regression of contrasts: $F_{1,12} = 3.86$, one-tailed $P = 0.037$; Fig. 3).

Movement When Eating versus Movement When Not Eating

The ecomorphs differed in the extent to which movement rates were increased in observations in which they ate, as indicated by the significant Eat versus Not
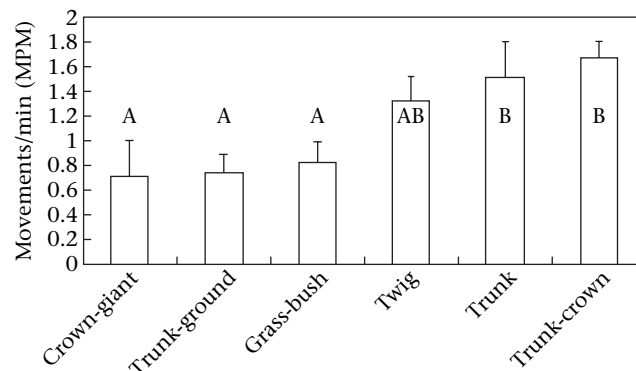

Figure 1. Mean MPM + 1 SE by ecomorph. Ecomorphs with different uppercase letters were significantly different using pairwise *t* tests (the post hoc test for the phylogenetic ANOVA).
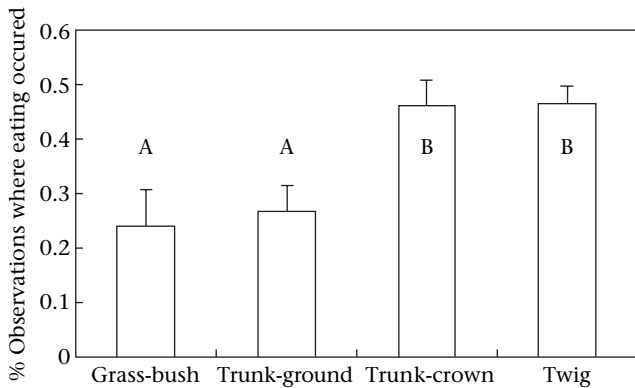
Figure 2. Average percentage + 1 SE of observations in which eating occurred (i.e. frequency of eating episodes) by ecomorph. Ecomorphs with different uppercase letters were significantly different using pairwise *t* tests (the post hoc test for the phylogenetic ANOVA).

Eat*Ecomorph interaction (Table 4). In particular, trunk-crown and twig species moved significantly more often when they were eating than when they were not, whereas the differences in movement rates in trunk-ground and grass-bush were not significant (Fig. 4).

Microhabitat and Movement Behaviour

We found no significant relationship between the three microhabitat variables and MPM in data set 1 (multiple regression of contrasts: $F_{3,10} = 1.85$, $P = 0.20$). In both the larger data set 2 (regression: $F_{1,25} = 1.08$, $P = 0.31$) and the combined data set (regression: $F_{1,29} = 1.02$, $P = 0.32$), height (the only habitat measurement common to both studies) was not a significant predictor of MPM.

DISCUSSION

In the last four decades, researchers have investigated the foraging modes of a wide variety of organisms (see Introduction for references). Furthermore, many studies have revealed a relationship between foraging behaviour and habitat in a range of taxa. For example, in bats, many aspects of foraging are affected by habitat, including echolocation frequency, prey selection and movement route (reviewed in Schnitzler et al. 2003). Adaptations

for prey detection, selection and capture are associated with ecological conditions in insectivores such as moles and shrews (Catania 2005; Catania et al. 2005). Additionally, interspecific differences in foraging behaviour in warblers are correlated with interspecific differences in niche selection and wing morphology; species with short wings mostly forage in dense vegetation, whereas species with relatively long wings usually forage in open areas (Forstmeier & Kessler 2001).

Our results illustrate the strength of using a diverse set of species, occupying a diversity of ecological conditions, to elucidate possible factors shaping the evolution of foraging modes. Anoles are usually considered sit-and-wait predators (Moermond 1979; Perry 1999; Butler 2005; Cooper 2005a, b, 2007). Certainly, in comparison to the other extreme in lizards, such as species that spend more than 60% of their time moving (Butler 2005; Cooper 2005a), anoles would appear more sedentary. Moreover, almost all anole species will at least occasionally adopt the archetypal sit-and-wait position, the 'survey' posture, perched vertically, head down on a tree trunk, in which they scan their surroundings for predators, prey and competitors; some species spend most of their time in this position (Scott et al. 1976; Stamps 1977; Cooper 2005b). None the less, we show, as others have previously (Moermond 1979; Hicks & Trivers 1983; Perry 1999; Irschick 2000; Cooper 2005b), that anoles show substantial variability in their foraging behaviour; the 31 species included in this study span a six-fold range in movement rates. Although we did not measure the percentage of time spent moving, another common metric in foraging studies (Butler 2005; Cooper 2005a), this measure might have yielded even greater interspecific differences, because species that move the most also frequently make movements of a longer duration (Irschick 2000).

Habitat and Foraging Rate

Our findings highlight a relationship between movement rates and the structural habitat commonly used by different species. For example, species that occur on the trunk of the tree and in the branches and canopy (trunk and trunk-crown anoles) move at much higher rates than species that occur on tree trunks near the ground, in the grass and other low-lying vegetation, or on large surfaces
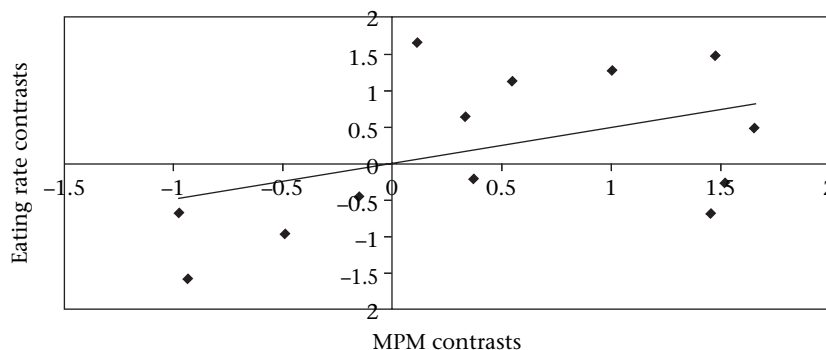

Figure 3. Standardized independent contrasts for average MPM and eating rates. Regression line was forced through the origin.

Table 4. Repeated measures MANOVA comparing movement rates (MPM) in observations where eating occurred versus observations where eating did not occur

	Wilks' λ	df	F	P
Eat versus Not Eat	0.206	1, 10	38.6	<**0.001**
Eat versus Not Eat*Ecomorph	0.337	3, 10	6.6	**0.010**

high in the tree (trunk-ground, grass-bush, and crown-giant ecomorphs). Twig anoles were the only ecomorph that was highly variable: some of the most and least active anoles are members of this class (e.g. Hicks & Trivers 1983; Leal & Losos 2000; Huyghe et al. 2007). These findings parallel the results from studies of other taxa, such as birds, that have shown that the density and structure of the habitat can affect foraging behaviour (e.g. flying patterns and prey selection; e.g. Price 1991; Marchetti et al. 1995; Forstmeier & Kessler 2001).

Anoles are the ultimate multitaskers, and their daily activities are divided between social interactions, which can include displaying to conspecifics and patrolling territory boundaries, and searching for prey and predators. Thus, one might question whether differences in movement rates are actually related to differences in foraging behaviour. Our data show, however, that differences between the ecomorphs in movement rates were associated with differences in foraging and that the differences persisted even when analysis was restricted only to sessions in which feeding was observed. Finally, the observation that the more active species moved more in observations in which they fed compared with observations in which they did not feed, whereas more sedentary species did not differ in activity rates between the two types of observations (Fig. 4), suggests that differences in foraging behaviour may be related to differences in movement rate.

Although movement rate was related to habitat, as indicated by the differences between the ecomorph classes, it is not clear what aspect of the habitat is responsible for these differences. Habitat visibility has been suggested as one factor responsible for differences in foraging rate (Moermond 1979; Cooper 2005b, 2007):
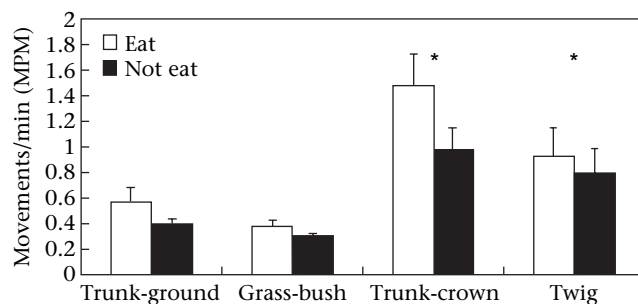
lizards in obstructed habitats should move more often to increase their likelihood of detecting potential prey. Although such differences may explain how individuals change their foraging behaviour depending on the habitat in which they occur (Cooper 2005b), the hypothesis does not generally explain interspecific differences in movement rate: the ecomorphs in the most open habitats, trunk and trunk-ground anoles, vary greatly in movement rates, as do species in some of the most cluttered habitats (grass-bush and trunk-crown anoles; Fig. 5).

Other standard measures of habitat use, height and diameter, are also not generally correlated with movement rate. Although species low to the ground tend to move infrequently, arboreal species span the full range of activity rates. No association with perch diameter is evident, either. Moermond (1979) suggested that the time required to scan the surroundings is the critical determinant of foraging rate. This hypothesis might explain why two ecomorphs in open habitats, trunk and trunk-ground anoles, differ, because trunk-ground anoles survey a vast tract of expanse in the ground below them, whereas trunk anoles scan only the surrounding tree trunk. However, variation in activity rates among species in cluttered habitats would be less explicable in this framework. Our measure of visibility (Johnson et al. 2006) is an important step forward in this sort of mechanistic analysis; further refinement to measure the area surveyed by a lizard is necessary to evaluate Moermond's (1979) hypothesis.

In summary, although evidence strongly suggests that structural habitat use is related to foraging rate in anoles, the mechanistic cause for this relationship is still very much a mystery. Surprisingly, despite decades of work on anoles, many critical aspects of their natural history are still unknown, rendering resolution of these issues difficult.

Comparison to Previous Studies

A number of previous researchers have reported foraging data on anoles (Moermond 1979; Irschick 2000; Cooper 2005b). All these studies included 7–8 species with the exception of Perry (1999), who presented data on 10
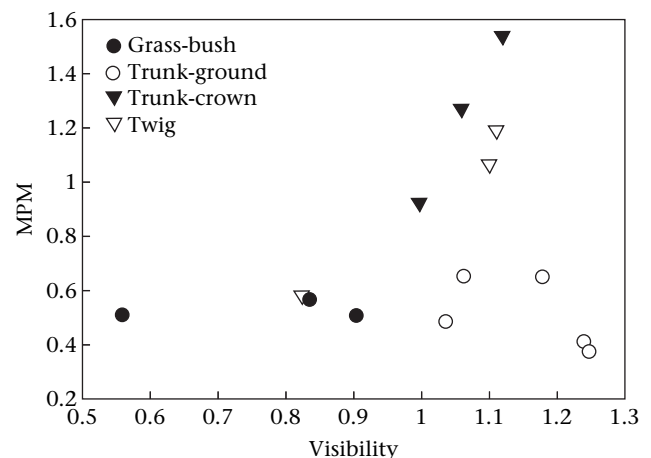
Figure 4. Average MPM for eating versus noneating observations for four ecomorphs. Asterisks indicate ecomorphs for which MPM was significantly greater in eating than in noneating periods.

Figure 5. Transformed average visibility and average MPM for 14 species.

species, however, most of the species in Perry's study were from mainland Central America and thus do not belong to any of the ecomorph classes (Irschick et al. 1997).

For the most part, these studies and ours are consistent in the relative ranking of foraging activity of different species, despite differences in methodologies. The one difference concerns the grass-bush anoles. Perry (1999) and Cooper (2005b) reported grass-bush anoles to be the most active ecomorph class, whereas Moermond (1979) found them to be intermediate to low, and both of our data sets found them to be relatively low. Observational methods are generally the same in these studies, and the differences persist even when comparing data among studies for the same species. Cooper (2005b) showed that grass-bush anole movements differ when they are in different habitats (as also found in Lister & Aguayo 1992 for *Anolis nebulosus* in Mexico), so it is possible that different studies have observed grass-bush anoles in different ways. Resolution of this discrepancy will require further work. We can say with confidence, however, that in our data set, all species were observed in the same way in terms of how lizards were initially detected and watched (except for the particularly cryptic species; see Methods). Moreover, our average observation periods (20−160 min for data set 1; 20 min for data set 2) were generally longer than those of other studies, which may have had some bearing on the results.

Data set 2, from Losos (1990) and unpublished data collected in the same manner, report foraging rates that are consistently higher than in any other study on anole foraging behaviour. In part, this may have resulted because Losos' observation periods were longer than other studies (except our data set 1), and also because Losos excluded individuals that moved fewer than five times for the reason that such individuals may have been inactive because of the presence of the observer. However, we treated data set 1 in the same way and still found a discrepancy. None the less, relative patterns among species were highly consistent between our data sets, and the same qualitative results were obtained when each data set was analysed independently.

Behavioural Syndromes and Foraging Modes in Anoles

Over the last few years, the concept of behavioural syndromes has received considerable attention. A behavioural syndrome is defined as a suite of correlated behaviours exhibited across situations (Sih et al. 2004; Bell 2007). The relationship among morphology, structural niche, locomotion and activity pattern has been previously documented in anoles (Williams 1983; Losos 1994) and has proven to be a major component of *Anolis* evolutionary history. Our results suggest that foraging behaviour can be added to the list of correlated traits associated with each ecomorph category, increasing the possibility of the occurrence of a behavioural syndrome in anoles. However, even after decades of extensive research, the necessary empirical evidence to rigorously test the occurrence of behavioural syndromes in anoles

is currently lacking. Therefore, we encourage further research in this area, particularly in the development of field and experimental studies on multiple aspects of behaviour and their combined effects on individual fitness.

Phylogenetic Perspective on Anole Foraging

Although commonly associated with evolutionary biology, the comparative method was pioneered in ethology (Burghardt & Gittleman 1990; Cuthill 2005 and references therein). Indeed, Tinbergen and his students recognized the value of this approach to elucidate the evolution of behavioural traits and their possible adaptive function (e.g. Cullen 1957). Now, of course, incorporation of phylogenetic information into comparative studies is de rigeur (Felsenstein 1985; Harvey & Pagel 1991).

The diversity of West Indian anoles has proven particularly amenable to the phylogenetic approach; because the same set of habitat specialists has evolved repeatedly across four islands, West Indian anoles provide a powerful system for examining evolutionary questions related to diversification and adaptation in habitat use. Our results clearly indicate that not only is foraging rate an evolutionarily labile trait (as evidenced by the convergence of distantly related members of the same ecomorph class), but also that its evolution is closely linked with adaptation to different habitats.

Anoles provide a more fundamental phylogenetic perspective on foraging mode evolution as well. Most comparative studies of foraging mode have been conducted on a broad taxonomic level and have concluded that most variation in foraging mode in lizards has a deep phylogenetic basis, with some families, such as Iguanidae and Agamidae, being composed entirely of sit-and-wait foragers, whereas other families, such as teiids, being entirely composed of active foragers (e.g. Perry 1999; Butler 2005; Cooper 2005a). By this criterion, all anoles fall squarely within the sit-and-wait camp. However, this perspective overlooks the sometimes-considerable variation that can occur within closely related species. To the extent that differences in foraging mode between families are correlated with differences in morphology, physiology and ecology (reviewed in Miles et al. 2007; Verwaijen & Van Damme 2007), one might expect the same types of differences, perhaps to a less extreme extent, to be evident among anoles. For the most part, relevant data, such as egg mass and energetics, are not available for anoles to test these hypotheses at this time.

More generally, this approach highlights the power of the phylogenetic comparative method: if evolutionary transitions between foraging modes are causally related to adaptive evolutionary change in phenotype, then we might expect to see such associations repeatedly, at multiple levels (between families, within genera) of a phylogeny; adaptive differences that distinguish active-foraging and sit-and-wait families of lizards might also be found among anoles differing in foraging mode. For example, a comparison across lizard families suggests that active foragers have a higher rate of energy input than sit-and-wait foragers (Anderson & Karasov 1981);

correspondingly, our results show that the rate of prey capture is a function of movement rate as well. More detailed investigation of foraging behaviour, energetics and physiology of anoles holds the prospect of further enlightening understanding of foraging mode evolution both among anoles and among lizards in general.

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Appendix

Anolis *species included in the two data sets*

Species	Island	Ecomorph	MPM
Data set 1			
A. bahorucoensis	Hispaniola	Grass–bush	0.51
A. krugi	Puerto Rico	Grass–bush	0.50
A. olssoni	Hispaniola	Grass–bush	0.56
A. cristatellus	Puerto Rico	Trunk-ground	0.41
A. cybotes	Hispaniola	Trunk-ground	0.48
A. gundlachi	Puerto Rico	Trunk-ground	0.37
A. lineatopus	Jamaica	Trunk-ground	0.65
A. sagrei	South Bimini	Trunk-ground	0.65
A. coelestinus	Hispaniola	Trunk-crown	1.27
A. grahami	Jamaica	Trunk-crown	0.92
A. smaragdinus	South Bimini	Trunk-crown	1.53
A. angusticeps	South Bimini	Twig	1.19
A. sheplani	Hispaniola	Twig	0.58
A. valencienni	Jamaica	Twig	1.06
Data set 2			
A. alutaceus	Cuba	Grass–bush	0.64
A. krugi	Puerto Rico	Grass–bush	0.84
A. olssoni	Hispaniola	Grass–bush	1.22
A. poncensis	Puerto Rico	Grass–bush	0.58
A. pulchellus	Puerto Rico	Grass–bush	0.99
A. allogus	Cuba	Trunk-ground	0.51
A. cristatellus	Puerto Rico	Trunk-ground	1.10
A. cybotes	Hispaniola	Trunk-ground	0.89
A. gundlachi	Puerto Rico	Trunk-ground	0.73
A. homolechis	Cuba	Trunk-ground	0.67
A. lineatopus	Jamaica	Trunk-ground	0.82
A. mestrei	Cuba	Trunk-ground	0.59
A. sagrei	Cuba	Trunk-ground	0.57
A. sagrei	Jamaica	Trunk-ground	0.90
A. distichus	Hispaniola	Trunk	1.21
A. loysiana	Cuba	Trunk	1.83
A. aliniger	Hispaniola	Trunk-crown	1.19
A. chlorocyanus	Hispaniola	Trunk-crown	1.17
A. evermanni	Puerto Rico	Trunk-crown	1.27
A. grahami	Jamaica	Trunk-crown	1.74
A. opalinus	Jamaica	Trunk-crown	1.74
A. porcatus	Cuba	Trunk-crown	1.52
A. stratulus	Puerto Rico	Trunk-crown	1.84
A. angusticeps	Cuba	Twig	2.49
A. insolitus	Hispaniola	Twig	0.42
A. valencienni	Jamaica	Twig	1.55
A. garmani	Jamaica	Crown-giant	0.81
A. luteogularis	Cuba	Crown-giant	0.62