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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.

Keywords: *Anolis* lizard; comparative method; ecomorphology; foraging mode; habitat use; movement rate

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?

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).

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