

The evolution of the foraging mode paradigm in lizard ecology

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Always question the paradigm

Carl Gans, 1986

Sometimes a straightforward natural history observation initiates the development of a major area of research in ecology or evolutionary biology. The observation that species numbers increase with island area is one such example. Another is the description by Pianka (1966) and Schoener (1969) of two “distinct” behavioral morphs that differed in their feeding behavior forty years ago. Although other studies described the behavior (see, for example, Kennedy, 1956; Rand, 1967), it was the early publications of Pianka and Schoener that demonstrated the ecological significance of the search strategies. Ostensibly a species’ movement behavior affected its foraging success and consequently was a potential mechanism for resource partitioning. Hence, understanding variation in foraging mode was a foundation for key papers in theoretical and empirical analyses of species interactions (Schoener, 1971). However, ecologists quickly realized the numerous ramifications inherent in the differences between species that ambush prey vs. those that widely search an environment for elusive or concealed prey (see, for example, Eckhardt, 1979).

In a seminal paper, Huey and Pianka (1981) formalized the foraging mode paradigm. Their study elaborated on the potential ecological consequences of variation in search behavior and presented a summary of the traits that were expected to be affected by foraging mode. Using data collected from Kalahari lizards, they corroborated several of the hypothesized differences between ambush and widely foraging lizards. One may ask why their publication was so important. First, many studies on a broad array of vertebrate and invertebrate taxa found that species were readily classified into either ambush foragers or widely foraging species. Second, foraging mode became shorthand

for describing species attributes. Third, as McLaughlin (1989) pointed out, the foraging mode paradigm includes the opportunity to understand how foraging strategies correlate with a suite of behavioral, ecological, physiological, and morphological characters. Thus, their paper provided a framework to explain a myriad of differences between species and hence derive additional hypotheses to explain the diversification of taxa. Consequently, our thinking became focused on examining foraging mode, as a pervasive evolutionary force.

Since the publication of Huey and Pianka (1981), numerous studies related foraging modes to many aspects of lizard ecology, and because so many traits have been correlated with foraging mode, the sit-and-wait vs. active foraging (SW vs. AF) dichotomy emerged as a central paradigm in lizard ecology. Our goal at the onset of this project was to review what has been learned about the foraging biology of lizards in over three decades of research. Specifically, we wanted to know how various aspects of lizard biology covary with foraging mode and how these patterns relate to the initial dichotomous paradigm. Therefore, we asked contributors to address four questions. First, how has a given trait or suite of traits been affected by foraging mode? Second, because differences in foraging mode have been generally related to a deep split in the phylogeny of modern lizards (Perry, 1999), what is the concordance between phylogeny, foraging mode, and a given trait? Third, do traits associated with foraging mode in lizards follow a continuum or is there evidence that foraging mode patterns are clearly dichotomous? And fourth, what are the unresolved questions that need additional study in order to understand the paradigm? By unifying these contributions we believe this volume represents a review of the state of the paradigm at many levels of organismal design, function and ecology. As is evident from the chapters, there is a tremendous amount of information linked with foraging mode. However, at the same time it is also true that each chapter identified major areas of needed research.

This volume has also provided the opportunity to evaluate support for a dichotomous characterization of foraging mode. Clearly, many of the authors supported the existence of a continuum. Although many species do occupy extreme positions on a spectrum describing activity during foraging, a remarkable result emerging from the chapters in this volume is the number of species that are intermediate between ambush and active foragers. Thus, a key question is how to account for the additional variation. Should a third category or continuum be recognized? If so, how would this affect the syndrome of traits that have been intimately tied to the two foraging categories? Certainly, more support exists for the description of *relative* differences in search behavior first

suggested by Pianka (1966) and reiterated by Huey and Pianka (1981). However, categorizing species into one or another mode, albeit convenient, dramatically discounts variation that may relate to other key functional traits and environmental heterogeneity. Consequently, it is prudent to use quantitative traits, moves per minute, percent time moving, or other available variables, to test hypotheses regarding the proximal and ultimate factors that structure variation in search behavior (McLaughlin, 1989).

We have striven to provide future researchers with an integrative description of the behavioral syndrome that is "foraging mode." The volume also serves as a review of the ecological consequences of behavior extended across numerous trait complexes. We know of no other example in vertebrates where an integrative behavioral variable like foraging mode has such an extensive reach into the biology and phylogenetic history of a clade. The central role of foraging mode in lizard biology has spurred investigations in a diversity of fields within ecology, morphology, evolution, and behavior and validated foraging mode as a paradigm in lizard ecology. The paradigm now involves not only the idea of foraging mode variation but the totality of the organismal traits that may or may not covary with foraging strategies.

Evaluating foraging mode variation

A long standing question within the foraging mode paradigm has been whether to treat search behavior as a continuum or a dichotomy. The first classifications of lizards into foraging modes were subjective and as described by Pianka (1973) somewhat arbitrary. The lack of objective criteria for defining the foraging mode was a key weakness early on, yet despite a dichotomous classification most authors concluded that species were arrayed along a continuum, although most taxa investigated tended to occur in the extremes of the continuum. Huey *et al.* (1984) provided some guidelines toward delineating foraging modes by suggesting the use of percent time moving (PTM) as a relative guideline for classifying species. Substantial differences were evident in the treatment of foraging mode. Some authors concluded that two categories were insufficient to capture the observed variation in foraging mode (Regal, 1978). In contrast, Magnusson *et al.* (1985) favored the treatment of foraging mode as a continuum. Most of these suggestions were developed in the absence of quantitative data. As more data were gathered, the categorization ultimately appeared to be arbitrary, with no objective criteria available for distinguishing foraging modes (McLaughlin, 1989). Two early studies (Pietruszka, 1986; McLaughlin, 1989) found partial support for the validity of a dichotomous paradigm; however, more recent studies with increasing

amounts of data (Perry, 1999; this volume, Chapter 1) failed to detect bimodal distribution of search behavior.

One question we pondered was: when did the values for MPM and PTM become formalized to classify species? The use of a value of 1.0 for MPM most likely emerged from the work of McLaughlin (1989), who showed a distinct break between groups of lizard species (see figure 2 in McLaughlin [1989]). There does not appear to be a formal proposal for the use of 10% as a threshold for identifying foraging mode. Huey *et al.* (1984) focused on a range of values to place species into one or another foraging mode. They stressed the relative nature of foraging modes among coexisting taxa. Pietruszka (1986) relied on two measures of foraging behavior: movement rate (meters moved per minute) and foraging movement frequency. The latter variable could be interpreted to be similar to PTM. His study was notable for documenting considerable amounts of seasonal and individual variation in search behavior. Butler (2005) attributed the empirical cut-off of <15% for classifying species to Cooper and Whiting (1999). However, Cooper and Whiting (1999) cite Huey and Pianka (1981) and Perry's unpublished dissertation (Perry, 1995) for a 10%–15% threshold. Reilly and McBrayer (Chapter 10) distinguish a medium or mixed category in familial means between about 10 and 25 PTM, noting, as Schwenk (1994) did, that true active foraging of over *c.* 40 PTM appears independently in the families Teiidae and Varanidae. None of these studies, however, formally tested for the existence of a statistically significant gap separating foraging modes.

We feel that a valuable issue raised in the volume has been to question the biological reality of 'threshold values' to describe foraging modes. Anderson (Chapter 15) provides a thorough description of the full range and complexities of food acquisition modes in lizards. Various authors may use divergent terms to describe the foraging behavior of a species. For example, species in the teiid genus *Aspidoscelis* are often characterized as "extreme wide foragers," active foragers, or intensive foragers. Are these simply different terms for the same behavior or do they represent qualitative differences in behaviors that are not captured by using data on MPM or PTM? Anderson also alludes to similar issues in describing jump–strikes (*e.g.* *Sceloporus*, *Anolis*) and stalk–strikes (*e.g.* *Gambelia*, *Callisaurus*) in species generally thought of as sit-and-wait foragers. He also generates a testable framework of foraging mode states to encourage workers to better describe these complexities. Thus, how one can use objective measures to define a species behavior is another issue raised in the volume. How should the categories of SW or AF be objectively defined or expanded? Additional analyses are necessary to determine the subtleties of variation in feeding behavior. Is it biologically meaningful, in terms of diet

breadth, or feeding success, if a species has a value of 10 for PTM, rather than 14 or 19? The use of broad categories to describe foraging behavior obscures important, yet subtle, differences in the manner in which species locate and acquire prey.

Other efforts have been made to more precisely quantify and thus objectively ascribe foraging mode states, mainly through the inclusion of more traits that characterize feeding behavior. Cooper and Whiting (1999) introduced an additional variable, percentage of attacks while moving (PAM), as a metric to describe and categorize species' foraging modes. They argued that PAM is better able to discriminate between foraging modes because for ambush foragers PAM will equal zero. They also show that PAM is highly correlated with PTM but not with MPM (Cooper and Whiting, 1999; Cooper *et al.*, 2001). Likewise, Cooper *et al.* (2005) and Cooper (2005b) show that average speed, speed while moving, and average duration of movement may be correlated with PAM and PTM.

We suggest another new foraging variable, attacks while stationary (AWS). Attacks while stationary are applicable to both sit-and-wait foragers and active foragers because active foragers often dig up prey while stationary and/or capture prey while engaged in other activities (e.g. basking) although presumably at a much lower rate than while moving. The use of AWS would be complementary to other behavioral metrics. Like PAM, quantification of AWS might be tedious; long hours of observation may be required in order to obtain measurements. However, if investigators were present during the normal activity period of the focal lizards, enough data could be obtained. Although AWS, PAM, PMP, PTM, and other variables may be suitable to quantitatively characterize foraging modes, all of these variables may result in more confusion if analyses are not done to distinguish which variables are most appropriate and where statistically significant gaps exist such that foraging modes may be separated. Interestingly, each of the new variables tends to have a unimodal distribution, which provides further support for the use of a continuum model to describe foraging behavior.

Regardless of whether or not foraging mode is a two-state or multi-state character, major advances were made in lizard biology by authors using a dichotomous classification. This volume is a testament to many of these advances. For example, Vitt (1983) demonstrated significant covariation between tail morphology and autotomy, which was consistent with predictions based on expected differences among species that exploited different foraging modes. The relationship between chemoreception and active or ambush foraging modes was suggested long ago (Evans, 1961), and yet it is only over the past 15 years that Cooper and colleagues have shown this trait to

be a major evolutionary force in the diversification of lizards (see, for example, Cooper, 1994a,b, 2005a). Finally, life history variation has been shown to covary with foraging mode (Dunham *et al.*, 1988; Webb *et al.*, 2003).

However, a key problem in correlative works related to foraging mode in lizards became how to determine the foraging mode of an organism. Although foraging mode was known to influence a myriad of traits, efforts to obtain data that would provide an index into a species feeding behavior have lagged behind other studies. Many questions have become increasingly vexing as we learn more about the intricacies of lizard ecology as it pertains to their foraging. For example, what are the best variables to categorize species? Could we derive thresholds to put species in one foraging group or another? People have discussed thresholds for some time, but what really constitutes a sit-and-wait forager vs. an active forager: is there a real continuum of foraging modes? And finally, does the SW–AF paradigm mirror the r – K selection dichotomy in life history theory? Characterizing species as either “ r –” or “ K –” selected focused much life history theory during the 1970s and 1980s. As additional data were collected, intermediate species were found not to exactly fit the predefined categories, and alternative hypotheses began to come into favor. Ultimately, the r – K continuum was supplanted with other theoretical constructs, yet like SW and AF it was instrumental in guiding our efforts to obtain a handle on the problem.

The foraging mode paradigm: new insights and the need for more data

The chapters included in this book provide the most recent summaries of the consequences and correlates of foraging mode, and meet our goal of reviewing the state of the paradigm at many levels of analysis. Many themes have emerged from these chapters and set the stage for rapid progress across all disciplines. More than anything else, all authors agree that more data are needed on more species. For example, Vitt and Pianka (Chapter 5) point out that it has taken each of them a lifetime to collect all of their dietary data. Yet this Herculean effort still only represents information on *c.* 4.25% of all lizard species. Likewise, Bauer (Chapter 12) calls attention to the fact that our understanding of gecko foraging is rudimentary in that a tiny fraction of gekkonid species have been studied. Gekkotans, which are assumed to be SW, make up 25% of all lizard species. Depending on how they relate phylogenetically to the SW Iguania and the various more widely foraging taxa, they have critical implications on inferences of foraging mode and character evolution. Future work must be focused on this critical polarizing clade. Finally, we hold a feeble understanding of foraging modes in the “other half” of

squamates: snakes. Shine and Wall (Chapter 6) and Beaupre and Montgomery (Chapter 11) not only draw our attention to this, but also make salient points as to *whether* the very idea of foraging mode as we think of it in lizards is applicable to snakes.

The need for more data is also apparent within areas that have made considerable progress and valuable insight. Perry (Chapter 1) highlights several important methodological revisions in how we measure and assign foraging mode states. He also highlights interesting variation in particular groups (*Sceloporus*), as do Miles *et al.* for polychrotines (Chapter 2). Bonine (Chapter 3) and Brown and Nagy (Chapter 4) demonstrate that several physiological parameters (e.g. metabolic rates) generally evolve as predicted, although broad comparative physiological data are scarce. Herrel (Chapter 7) points out that, in the Iguania, much is left to learn about the multiple evolutionary transitions to herbivory and AF from various SW ancestors. In scleroglossans, however, the evolution of omnivory appears to be a first step towards becoming an actively foraging herbivore. Finally, support for the relationship between lingual morphology, chemoreception, and the evolution of foraging mode remains strong (Cooper, Chapter 8). New information on feeding kinematics and behavior (Reilly and McBrayer, Chapter 10) shows that the use of the tongue in prey capture was independently lost in the Anguimorpha and Varanoidea in concert with the appearance of many other convergent traits associated with an increasingly derived chemosensory role of the tongue in the teiids and varanids. Moreover, McBrayer and Corbin (Chapter 9) add the independent evolution of different designs of long, narrow skulls to this pattern. The impacts of new data are important and illustrate the way in which the paradigm continues to foster innovative research with a strong influence in the study of lizard biology.

The second half of the volume addresses plasticity in foraging mode, which remains a severely under-explored topic. Plasticity in foraging mode can arise through ontogenetic, seasonal, annual, or even daily sources of variation, as is the case of nocturnality in geckos (Bauer, Chapter 12). Shine and Wall (Chapter 6) point out that plasticity in foraging mode and diet is the rule in snakes. Their chapter evaluated several mechanistic hypotheses. One major factor dictating dietary shifts is the pronounced change in body size over ontogeny. Small snakes may be constrained to be active foragers, whereas larger snakes may adopt a sedentary, ambush mode of feeding. Seasonal and annual variation in food supplies may also induce shifts in foraging mode. Huey and Pianka (1981) provided one example; Whiting presents another case study in the cordylid species *Platysaurus broadleyi* (Chapter 13). Interestingly Pietruszka (1986) pointed to the fact that a common North American lizard

(*Gambelia wislizenii*) may shift foraging modes seasonally, yet it has not been until just recently that data were brought to bear on this (and it looks as though they do) (Rose, 2004). Habitat structure and heterogeneity have cogent effects on foraging mode plasticity. The lacertids are one of the most variable groups in terms of foraging mode; Vanhooydonck *et al.* (Chapter 14) examine patterns between habitat use, feeding and locomotor behaviour, and the trophic niche of this clade. This chapter identifies functional trade-offs among feeding and climbing performance traits as they relate to the evolution of foraging strategies, diet, and habitat use. Anderson (Chapter 15) provides a detailed essay on foraging plasticity and how we should think about it in terms of levels and patterns of habitat structure. He posits that to understand food acquisition mode we must know the what, when, where, and how of lizard spatiotemporal use patterns within the context basic autecological tasks (feeding, predator evasion, coping with abiotic environment, and reproduction). Finally, Vitousek *et al.* (Chapter 16) examine the most unreptilian strategy of marine herbivory in marine iguanas, where strong sexual selection and cold temperature has led to unique morphological adaptations for their unique herbivorous foraging mode.

The promise of the foraging mode paradigm

We believe that the contributions in this volume will foster and focus a revitalization of work investigating the contribution of foraging mode to understanding the diversification of taxa. We encourage other investigations to avoid diminishing the diversity of feeding behaviors or foraging mode by using dichotomous and broad categories. Such a dichotomous approach constrains the observed variation to fit into the extremes. To be sure, there are examples in the natural world of extreme sit-and-wait or actively foraging species, and these taxa also tend to conform to the predicted ecological and behavioral correlates. However, one wonders whether this too might not be an artifact of history: the teiid (really AF) and iguanid (really SW) lizards of North America have figured strongly in the historical establishment (whether purposefully or by accident) of a dichotomous view in lizards. As additional information on PTM and MPM accumulate from additional, detailed behavioral work, it is likely that more species will fall between strict SW and AF extremes. In short, we might imagine that the categories of SW and AF will ultimately acquire fuzzy boundaries, which will force the revision of the paradigm.

The advantage of the foraging mode paradigm is the clear delimitation of associated predicted ecological and evolutionary consequences. The expanding

database already favors at least a trichotomy of categories, and more data will ultimately lead to a quantitative description of foraging mode. This situation again is analogous to the revision of r - K theory with the introduction of additional factors that can generate more complex variation in life history patterns, e.g. the consideration of how environmental variation would modify survival and reproduction and the explicit inclusion of juvenile and adult vital rates in life history models. Another consideration is how will the paradigm change as additional categories are modified, added or abandoned. Perry *et al.* (1990) demonstrated a significant negative correlation between relative clutch mass (RCM) and moves per minute in lacertid lizards. As more data are collected on the search behavior of lizards in other clades, more exceptions to the rule are discovered. For example, although chamaeleons were long believed to be SW foragers, at least one species (*Bradypodion pumilium*) has now been described as an active forager (Butler, 2005). In addition, Cooper (2005b) portrayed species in a two-dimensional space described by PTM and MPM, yet failed to demonstrate unambiguous clustering of all species into active or sit-and-wait foraging. These conclusions further support the lack of evidence for bimodality in movement data (see, for example, Perry, 1999; this volume, Chapter 1). Indeed, the boundaries separating SW from AF are becoming increasingly blurred. Although it has long been argued that foraging modes diverged early in lizard evolution, the expansion of information on and taxonomic patterns of MPM and PTM in a greater range of species supports the presence of a continuum, alternative interpretations of many organismal trait patterns, and the implications of new contrasting lizard phylogenies clearly show that a dichotomous view of the foraging mode paradigm does not hold all of the answers. The advent of the behavioral variables percentage of attacks while moving (PAM) and attacks while stationary (AWS) may further help quantify the foraging mode continuum. Moreover, it is equally interesting that recent analyses of foraging mode using ancestor reconstruction and independent contrasts suggest multiple transitions in search behavior, with different suites of correlated traits in some lineages and striking patterns of convergence in others.

The future of the foraging mode paradigm lies in the willingness of researchers to depolarize foraging mode. The utility of a polarized, dichotomous view of lizard foraging was evident in generating a research “framework” to attack a problem. That is, by focusing on the extremes of foraging modes, one could test for the existence of differences. However, as more species are studied and better analytical methods are applied to foraging data, we are witnessing a turnover in the strict dichotomous perception of the paradigm. We encourage workers to embrace the variation in foraging modes as exciting, interesting,

and deserving of further investigation. It is the now numerous exceptions to the rule (such as tongue projection in scincomorphans) that must drive the utility of the foraging mode paradigm, if we are to see meaningful advances in the field.

In the future, it will be important to keep in mind how foraging modes are defined and that percent time moving (PTM) and moves per minute (MPM) are relative metrics. Even though species may be categorized as SW, there is still substantial variation in the component variables of foraging mode that can make more detailed analyses interesting. An important methodological advance in this regard may be lag sequential analysis (see Butler, 2005). Lag sequential analysis examines whether a behavior of interest (here locomotion) precedes a particular behavior (foraging) more frequently than would be expected at random. Use of this method will be an important step forward in our ability to separate foraging modes and associated behaviors and further explore the natural variation that is inherent in foraging strategies.

Hence, where should we go from here? What are the burning questions identified by the contributors? Without question, future work must emphasize seasonal variation and within-family variation. Definitive ecological and evolutionary correlates may not emerge when conducting broad interfamilial comparisons. Instead, these correlates may be more enlightening when done on a restricted group of species. Hence, one could focus on North American sceloporines or Kalahari lacertid lizards. Even though the taxonomic representation is not as great, studying a focal clade such as these is likely to be a better control for other factors, e.g., seasonality, habitat, etc. Similarly, work needs to be done addressing possible ontogenetic variation in foraging behavior. Granted, the study of small subadult lizards is difficult, yet on theoretical grounds juveniles face very different energetic, social, and predation-risk challenges compared with adults. It is not only possible that ontogenetic shifts in foraging mode exist, but likely. A starting point might be a study of spiny-tailed iguanas, *Ctenosaura pectinata* or *C. similis*. Juveniles of each species are known to eat insects (*C. pectinata*: Durtsche, 2000; *C. similis*: Van Devender 1982) and later switch to herbivory. Thus, do juveniles start out as sit-and-wait insectivores like many iguanians only to later switch to active foraging herbivory? Another obvious example would be *Pedioplanis* or *Meroles* lizards in the Kalahari. Evolutionary transitions in foraging mode are known in these two genera (AF → SW or mixed foraging) and substantial dietary variation exists within some species from season to season (Pianka, 1986). Thus, seasonal variation in foraging mode is possible but has not been examined in detail (see, for example, Whiting, Chapter 13). Furthermore, closely related species that have more recently diverged in foraging modes may be more likely to

show signs of significant ontogenetic variation. Should the ontogeny of foraging mode be different among species, heterochronic changes in key traits (energy budget, life history, etc.) are likely to be the mechanism of change. These and many other interesting hypotheses have yet to be addressed.

Beyond new avenues of research, several existing lines of investigation warrant deeper consideration. There is a paucity of information on MPM-PTM and related measures of foraging mode across many squamate taxa. To better define broad evolutionary patterns, more data are required for more species. Methodologically these data are simple and inexpensive to collect. Analytically, the use of lag sequential analysis will improve the description of foraging behavior because this approach directly links the locomotor behaviors to foraging behaviors. Using video to collect foraging data may also prove useful. Video is now lightweight and inexpensive; having a permanent record of the movement behaviors and their provenance is certainly valuable. Video data will also allow for analysis of prey capture methods and handling or processing times on a variety of natural prey types. Recent evidence that only the true wide foragers have lost tongue prehension suggests that feeding studies in many more taxa are warranted to tease out the trade-offs between feeding and chemosensory function in lizard tongues.

Along with a general appeal for more data, we specifically need increased sampling of species *within* clades, among *unstudied* clades and in different habitats (e.g. tropics). Several lineages show a wide variation in foraging modes (e.g. lacertids and scincids) and thus our understanding of the factors that effect evolutionary changes in foraging mode may be best examined in such groups. Furthermore, seemingly well understood clades such as polychrotids are now a superb example of how “presumed” foraging modes may not hold up under scrutiny. At the time of writing, no published accounts of foraging behavior are available for varanid, anguid, or xantusid lizards. Granted, many of these lizards are secretive and hard to study; however, given current technologies in telemetry and remote sensing, studies of even these hard-to-observe lizards are possible.

Shifting phylogenies will clearly affect the immediate and long-term future of interpretations of the evolutionary patterns and significance of foraging mode in lizards. Early studies of foraging mode recognized the strong phylogenetic signal associated with the trait (Pianka, 1966, 1973). Indeed, major preliminary analyses of ecological correlates of foraging mode explicitly included a phylogenetic approach (see, for example, Dunham *et al.*, 1988) or acknowledged the tendency for foraging mode to remain conservative within families (Cooper 1994a,b). It is now overwhelmingly apparent that phylogenetic history has played an important role in the evolution of foraging

mode and associated characters. Most contributions in this volume, and for the past 10 or more years, interpreted their data using the phylogeny published by Estes *et al.* (1988). However, new, very different lizard phylogenies (Townsend *et al.*, 2004; Vidal and Hedges, 2005) have appeared recently that may have a dramatic influence on interpretations of foraging evolution described within this volume and elsewhere (both were published late in the preparation of this volume and thus were not seen by many of our authors). At a minimum these new phylogenies change the basal taxa, and thus basal foraging mode states, and lend much stronger support to the independent evolution of many convergent traits in the crown Anguimorpha and Lacertoidea. In addition, if one must consider the Iguania as a crown group rather than the basal and primitive condition (as suggested by new phylogenies), it supports the conclusions of Schwenk and Wagner (2001) and Reilly and McBrayer (Chapter 10) that their radiation demands more respect as a novel, important, and evolutionarily stable strategy among lizards. Like others, we strongly encourage future studies of foraging mode traits to apply all three phylogenies to further explore the utility, and robustness, of phylogenetic hypotheses. Character mapping of foraging mode on the lizard phylogeny also reveals a more complex picture regardless of phylogeny used. There are several transitions in foraging mode from sit-and-wait to active foraging; however, certain families exhibit numerous reversals, e.g. active foraging → sit-and-wait. Future work should be directed toward understanding the factors associated with evolutionary transitions in foraging mode; character mapping is an efficient mechanism to do so.

Finally, future studies should build on the strong database that does exist and add more integrative approaches and thinking. Foraging mode has always represented a composite variable containing several co-adapted traits. The act of searching or watching for prey involves sensory input, integration of that input, and functional and behavioral responses to it. In addition, field conditions, prey biology, community structure, and autecological relevance needs better quantification (Anderson, Chapter 15). As pointed out by Vanhooydonck *et al.* (Chapter 14), quantification of prey availability (field studies) and functionally relevant prey traits (tested in the laboratory, e.g. hardness, escape speed) are necessary to link prey performance to predator performance capacity to patterns of foraging mode. Phenotypes (or species) represent trade-offs among these that have been optimized via natural selection. Thus, studies of foraging mode *require* integrative thinking because the foraging mode concept spans the morphological and physiological parameters of an individual. To use foraging mode as a simple proxy for other ecological traits ignores many of the more interesting trade-offs that are inherent in them.

We encourage future investigators to embrace the integrative nature of foraging mode. Only by doing so can we understand the true pervasiveness and variability that shapes foraging biology in lizards.

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