6 A Comparative Approach to Field and Laboratory Studies in Evolutionary Biology

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1. The Comparative Approach

1.1 Introduction

The comparative method is an important tool for analyzing interspecific patterns at all levels of biological organization. Versatility is one key to the method's success. Consider its diverse applications to issues that emerge from a simple observation that two species of predators differ in movement rate. A comparison of physiological capacities of the two species might pinpoint mechanistic bases underlying differences in movement rate and stamina, a comparison of prey types or of social systems might clarify the significance of movement rate in the ecology and behavior of predators, and a comparison of net energetic gains or of predation risk might hint at the historical pressures that led to the evolutionary divergence in movement rates.

Data in comparative studies are obviously varied and may be gathered from the field, the laboratory, or the literature. Nevertheless, comparative data typically share one characteristic: most are descriptive, not experimental. As a result, conclusions in comparative studies are usually based on static differences or correlations (e.g., stamina is correlated with oxygen transport capacity), not on dynamic responses (e.g., stamina is directly influenced by experimental manipulation of oxygen transport capacity).

In this paper, we evaluate the effectiveness of descriptive comparisons in answering mechanistic, ecological, and evolutionary

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questions. We illustrate our views with field and laboratory data on the evolutionary ecology of foraging mode in lacertid lizards from the Kalahari Desert of Africa.

Four main conclusions emerge from our analysis. First, descriptive comparisons are an efficient and effective way of revealing mechanistic, ecological, and evolutionary patterns in nature. Second, descriptive comparisons nevertheless have limited power in establishing cause and effect. Supplementary manipulative experiments will generally be required to substantiate the ecological processes underlying those patterns. Third, a phylogenetic perspective must accompany comparative studies in evolutionary ecology. A consideration of phylogeny not only guides the selection of species appropriate for comparison, but also suggests the likely direction of past evolutionary change. Fourth, because the analysis of the evolutionary processes that led to current patterns is accessible only by descriptive studies and not by experimental manipulations, definitive answers to evolutionary questions will necessarily be evasive.

1.2 The Problem: Foraging Mode in Kalahari Lacertid Lizards

Many studies of predation are stimulated by natural-history observations on animals in the field (Chapter 7). This one was as well. During a year-long study of the species diversity and ecology of Kalahari lizards, Pianka and Huey noted that different species of lacertid lizards differ conspicuously in foraging mode (Huey and Pianka, 1981; Pianka et al., 1979). Movement patterns of these lizards

TABLE 1: Movement Patterns of Adult Kalahari Lacertid Lizards

Species	Moves/min.	Percent Time Moving	Speed (km/h)
Sit-and-Wait			
EREMIAS LINEOOCELLATA	1.5	14.3	0.07
MEROLES SUBORBITALIS	1.8	13.5	0.06
Widely-Foraging			
E. LUGUBRIS	3.0	57.4	0.31
E. NAMAQUENSIS	2.8	53.5	0.28
NUCRAS TESSELLATA	2.9	50.2	0.37

Modified from Huey and Pianka (1981).

during summer are summarized in Table 1. Some species move more frequently, move a greater proportion of the time, and move farther per hour than did others. Overall movement rates appear dichotomized among these lizards, and interspecific differences are stable even after months in captivity (D. Kairns and P. J. Regal, personal communication). The very active lizards were described as "widely-foraging," whereas the more sedentary lizards were called "sit-and-wait" predators. Dunham (1983) has subsequently developed a more direct method of quantifying foraging mode. Similar differences in foraging mode have been described in many animal taxa (Eckhardt, 1979; Ruben, 1976; Schoener, 1971; Toft, 1981; Webb, 1984), but the differences are not always dichotomous or stable (Huey and Pianka, 1981; Pough, 1983; Taigen and Pough, 1983).

1.3 General Issues in Evolutionary Ecology

This differentiation in foraging mode provokes a series of questions concerning the significance of foraging mode at several levels of biological organization (see Table 2). Some of these questions reflect functional or ecological issues, whereas others reflect evolutionary ones. These questions are general and apply to many biological phenomena,

TABLE 2: Conceptual Issues in Ecological Physiology

Ecological Issues

1) What are the ecological correlates of the phenomenon?

2) What ecological factors maintain contemporary patterns?

Mechanistic Issues

3) What are the physiological, behavioral, and morphological bases of the patterns?

Evolutionary Issues

4) What was the direction of evolutionary change?

5) What selective factors promoted that change?

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not just to predation. We wish to evaluate how well descriptive studies answer these fundamental questions. We will treat these questions in order, except questions 2 and 5, which will be discussed together.

1.4 The Importance of Phylogenetic Control in Comparative Studies

The questions in Table 2 can be addressed with respect to foraging mode by comparing various aspects of the biology of widely-foraging and of sit-and-wait predators. But the validity of answers to those questions depends fundamentally on the criteria used in selecting species for comparison (Clutton-Brock and Harvey, 1984; Harvey and Mace, 1982). All too often, availability or convenience guides the selection of species. Whenever possible, however, closeness of phylogenetic affinity should guide that selection. What attracted us to the Kalahari lacertids was not *just* that they differed in foraging mode, but that close relatives differed in foraging mode -- for such close relationships provided the phylogenetic control necessary for comparative studies.

Why should phylogenetic control be important? Patterns uncovered in comparative studies are the results of unplanned "natural" experiments that have occurred over evolutionary time. Any experiment, whether natural or manipulative, produces unambiguous patterns only when confounding variables such as temperature or size have been controlled. Natural experiments must also attempt to control for coincidental attributes that are a function only of the independent evolutionary histories of the species themselves. In general, the greater the phylogenetic distance between species being compared, the greater the chance that such attributes will confound the comparisons. Thus, the choice of closely related taxa should reduce the risk that coincidental differences will mask significant patterns or perhaps even induce artifactual ones in comparative studies (Jarman, 1982).

An example of how the lack of phylogenetic control can weaken comparative results emerges from an analysis of possible dietary correlates of foraging mode. Invoking some encounter-probability arguments (Gerritsen and Strickler, 1977), Huey and Pianka (1981) predicted that widely-foraging lizards are more likely than sit-and-wait lizards to encounter and eat prey, such as termites, that are patchily and unpredictably distributed (Wilson and Clark, 1977). Comparative dietary data from Africa, North America, and Australia supported their prediction (Huey and Pianka, 1981). However, the North American and Australian data are based on cross-family comparisons. In North

American deserts, for example, the teiid *Cnemidophorus tigris* is a widely-foraging predator, whereas iguanids are generally sit-and-wait predators. Unfortunately, teiids and iguanids differ in several characteristics, not just in movement rate. Specifically, many teiids have relatively well developed olfactory capabilities, whereas most iguanids are more visually oriented (Benes, 1969; Stebbins, 1948). Huey and Pianka (1981) pointed out that these differences should predispose a teiid to uncover more subterranean termites than an iguanid, even if both lizards foraged at the same rate. Although the sensory difference might well have co-evolved with foraging mode (Regal, 1978), it represents an uncontrolled variable that confounds an attempt to use descriptive data as an unambiguous test of a possible causal relationship between movement rate and diet (Huey and Pianka, 1981). Such problems may still occur even when close relatives are being compared (Chapter 2), but they should occur less frequently than when phylogeny is loosely controlled or ignored.

An alternative method that achieves phylogenetic control has been developed by S. J. Arnold (1983; Chapter 10). Individual (rather than interspecific) variation can be compared and correlated: for example, movement rate and incidence of termite eating can be compared among individuals. Arnold's approach is, however, useful only if individual differences are consistent and if the magnitude of the differences is greater than the measurement error.

2. Sequence of Investigation

2.1 Ecological Correlates

The first question we address is: What are the ecological correlates of foraging mode? This question is of interest because of numerous theoretical predictions concerning the relationship between foraging mode and various aspects of an animal's biology, such as diet, survivorship, and social systems. Using standard descriptive data, we can readily determine whether interspecific patterns correspond to predicted patterns.

Table 3 lists a sampling of the traits that we have examined, specific predictions that have been made about differences between widely-foraging and sit-and-wait lizards with respect to those traits, and whether our field data match those predictions. For example, the prediction that widely-foraging lizards should eat relatively more

termites was substantiated by our dietary analyses (above). Where data are available, most theoretical predictions are supported by observed patterns in these Kalahari lizards. Moreover, parallel patterns have been found in other lizard groups (Huey and Pianka, 1981; Magnusson, personal communication), in tropical anurans (Toft, 1981; Taigen and Pough, 1983), and in tropical snakes (Henderson, 1984). Consequently, most patterns appear to be general.

How well do descriptive studies answer questions concerning ecological correlates of foraging mode? They are a very good and efficient way of uncovering patterns in nature, for determining their generality, and for establishing whether theory and observation conform. In general, the types of field data necessary for these evaluations are standard and relatively easy to obtain. Nevertheless, these studies are neither intended nor able to establish cause and effect. Because multiple theories can sometimes generate the same predictions, direct insights into cause and effect will generally require supplementary experimental studies that build on descriptive patterns (Paine, 1977). For example, abundances of termites could be manipulated or monitored, and the potentially differential effects on lizards with different foraging modes could then be observed. The

TABLE 3: Testing Theoretical Predictions Concerning Ecological Correlates of Foraging Mode in Kalahari Lacertid Lizards

Trait	Prediction	Reference for Prediction	Observations Consistent?
Diet	WF[a] eat patchily distributed prey (e.g., termites)	Huey and Pianka, 1981	Yes[1]
	WF encounter more prey per time	Gerritsen and Strickler, 1977	Yes[1,2]
Predation	WF more vulnerable to SW predators	Huey and Pianka, 1981	Yes[1]
Reproduction	WF have smaller relative clutch masses	Vitt and Congdon, 1978	Yes[1]
Home Range	WF have large home ranges	Schoener, 1971	Yes[3]
Social System	WF less territorial	Stamps, 1976	?
"Curiosity"	WF are more curious	Regal, 1978	Yes[4]
Sensory Mode	WF have acute olfactory senses	Regal, 1978	?

[a]WF = Widely-foraging.
[1]Tests from Huey and Pianka (1981)
[2]Tests from Nagy et al., 1984
[3]Huey, Bennett and Nagy (unpubl.)
[4]Kairns and Regal (unpubl.)
? = No relevant data available.

relevant experimental techniques are now well established and have been used and advocated in various contexts by Dunham (1983), Ferguson and Fox (1984), and Helfman (Chapter 9).

2.2 Mechanistic Bases

The second question we wish to address is: What are the mechanistic (physiological, behavioral, or morphological) bases for differences in foraging mode? For example, do widely-foraging and sit-and-wait lizards differ in their capacity for speed and stamina? If so, are these differences reflected in organ systems, organs, or their constituent parts?

Here a problem emerges. Functional issues (see Chapters 2, 3, and 10) can be studied at a variety of levels, as shown in Table 4 -- so which level is most appropriate? The answer depends on the precise

TABLE 4: Establishing Physiological Bases of Foraging Mode

Level	Prediction	Laboratory Observations Consistent?
Whole-Animal Performance	WF[*] have greater stamina	Yes[1]
	S&W[+] have higher burst speeds	Yes[1]
Metabolism	WF have greater aerobic scope	Yes[2]
	S&W have greater anaerobic scope	Yes[2]
Tissue	WF have greater oxygen transport capacity (greater hematocrit and larger hearts)	Yes[2]
	WF muscles are more fatigue resistant	No[2]
	S&W muscles have faster contractile velocities	No[2]
Biochemical	WF muscles have greater activity of aerobic enzymes	No[2]
	S&W muscles have greater myofibrillar ATP-ase activity (index of maximal velocity of shortening)	No[2]

[*]WF = Widely-foraging.
[+]S&W = Sit-and-wait.
[1]Tests from Huey et al. (1984).
[2]Tests from Bennett et al. (1984).

question being asked, for the general question here actually has two subsidiary parts.

(i) Does physiological capacity constrain foraging mode? For example, do sit-and-wait lizards have insufficient stamina to maintain a widely-foraging pace? This question is ecologically motivated.

(ii) Which functional aspects are responsible for an observed difference? This question is mechanistically motivated. This distinction between ecological and mechanistic questions in physiology is sometimes overlooked, but is fundamental (Bartholomew, 1966; Feder, 1984; Huey and Stevenson, 1979). Indeed, this distinction serves as a useful guide in selecting the level appropriate for a given study.

Clearly, ecological questions are best answered by examining whole-animal performance as directly as possible. For example, to establish whether stamina limits foraging mode, one can place lizards on a treadmill moving at normal speeds and then directly compare their capacities for stamina (measured as time until exhaustion, Huey et al., 1984). Similarly, to examine the importance of relative speed in predator-prey encounters, one can measure speed profiles of animals in racetracks and then use these in computer simulations (Huey and Hertz, 1984; Webb, 1976). An even more direct approach would be to stage actual predator-prey encounters.

On the other hand, questions concerning the mechanistic bases of an observed difference in whole-animal performance are necessarily based on other levels. For example, one can examine various components of oxygen transport and of metabolism (Table 4) in an attempt to discover possible bases of observed differences in stamina (Chapter 5; Bennett et al., 1984; Garland, 1984; Ruben, 1983). All too often, however, the performance level is skipped, and lower-level data are used to answer ecological questions. This is inappropriate. The performance of the whole is not always predictable from the performance of an isolated part (Bennett et al., 1984; Feder, 1984; Chapter 2; but see Garland, 1984; Chapter 10). Jimmy the Greek (personal communication) predicts athletic champions based on their past performances, but not on their aerobic scopes or enzyme profiles. Ecologists should do the same.

The risk of using lower-level data to predict whole-animal performance is exemplified in our Kalahari studies, in which differences in whole-animal performance are marked. In general, sit-and-wait lizards had relatively great acceleration and speed but relatively low stamina (Huey et al., 1984). In fact sit-and-wait lizards cannot maintain a widely-foraging pace for even 15 minutes, suggesting that they are physiologically constrained to being sit-and-wait lizards. But our studies

of lower levels of biological organization show differences only at a few levels, not at all (Table 4; Bennett et al., 1984). Clearly, an attempt to infer stamina and speed from contractile properties of muscles or from activities of key enzymes would have led to an incorrect prediction that these species are physiologically similar -- they are not.

Lower-level studies should thus be restricted to answering mechanistic questions (for example, which physiological systems account for observed differences in speed or stamina?). Even in this case the ability of lower-level experiments to answer such questions is sensitive to two problems:

(i) In approaching mechanistic questions, physiologists sometimes focus only on the physiology of the organisms and thus ignore potential interactions with behavior and morphology. This trend is understandable and productive, but it oversimplifies the integral nature of organismal performance (see Chapters 2, 3, and 4). Firing patterns of muscles are controlled by neurons, not by electrodes; and the power output of contracting muscles depends on their insertions on dynamical elements (limbs and jaws), not on force transducers. Physiology and morphology set interactive limits on what is possible, but behavior constrains what actually occurs (Hertz et al., 1982; Chapter 3). More integrative, multi-disciplinary approaches are required in studies of the mechanistic bases of animal performance.

(ii) Despite appearances to the contrary, many comparative "experiments" in physiological ecology (e.g., those listed in Table 3) are descriptive rather than experimental and consequently are subject to our earlier cautions concerning the limits of descriptive analyses in ecology. For example, the cardiovascular system was the only lower-level physiological system in which features were correlated with stamina in the Kalahari lacertids (Table 4). Although this strongly suggests a cause-and-effect relationship (see also Garland, 1984), causality can be established only by supplementary manipulative experiments (e.g., by studying the effect of controlled manipulations of oxygen carrying capacity on stamina). Physiology -- like ecology -- can be a descriptive science.

Finally, whole-animal studies not only provide a framework for mechanistic approaches, but they can also place a new perspective on theoretical issues. Available foraging models assume that stamina is unlimited and that trade-offs do not exist between speed and stamina (e.g., Norberg, 1977); yet neither assumption is generally true (Bennett, 1980; Huey et al., 1984; Webb, 1984; Chapters 3 and 5). An explicit consideration that physiological and morphological capacities are limited should enhance the realism of theoretical models.

2.3 Direction of Evolution

The fourth question (Table 2) concerns the direction of evolutionary change. For example, was widely-foraging or was sitting-and-waiting the evolutionarily derived foraging mode?

This question can be attacked by integrating descriptive field data on foraging mode of several different species with independently established phylogenies (Gittleman, 1981; Lauder, 1981; Ridley, 1983). Figure 1 shows two hypothetical phylogenies, with foraging mode indicated for each of the three species. In the phylogeny on the left, widely-foraging appears (based on parsimony) to be the derived foraging mode; but in the phylogeny on the right, sitting-and-waiting is probably derived (parsimony approaches are not without problems; see Felsenstein [1985]). We have superimposed field observations on foraging mode of several genera of lacertids on a tentative lacertid phylogeny, courtesy of E. N. Arnold (personal communication). Although foraging mode is unknown for many genera, the overall pattern suggests that the sit-and-wait foraging mode is probably derived in African lacertids, with one possible reversal. This pattern may hold for Hispaniolan tree snakes as well (Henderson, 1982).

This type of phylogenetic analysis has been underutilized as an evolutionary tool in most comparative analyses of predation and other problems (but see Feder, 1978; Harvey and Mace, 1982; Ridley, 1983; Arnold, 1984). This may be because most ecologists are not trained to appreciate a phylogenetic perspective or because established phylogenies are rarely available. In any case, phylogenies are an extremely useful tool for comparative studies: phylogenies not only
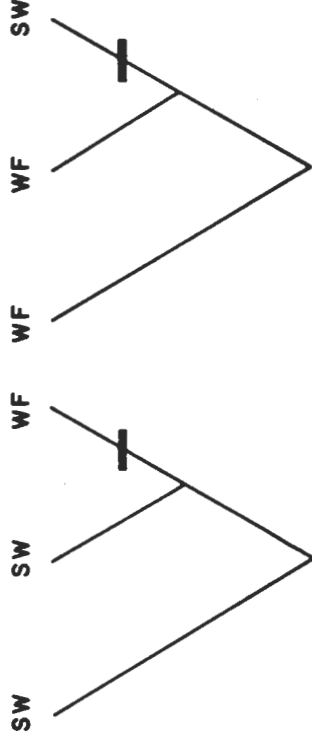

Fig. 1. Hypothetical phylogenies of three species, with foraging mode indicated for each (WF = widely-foraging, SW = sit-and-wait). The horizontal bar indicates an hypothesized evolutionary transition as established by parsimony.

guide the selection of close relatives for comparison (above), but also facilitate the interpretation of evolutionary patterns (Felsenstein, 1985).

2.4 Selective Factors

The final two questions (Table 2) concern selective factors that promote the maintenance and the origin of foraging mode. The question of maintenance is ecological, whereas that of origin is evolutionary.

These are clearly related issues, but a distinction between them is important -- factors that led to the origin of a trait are often different from those that currently maintain the trait. For example, venom of viperid snakes probably evolved initially for enhancing digestion, not for killing prey (Gans, 1978). Similarly, insect "wings" may have evolved initially for temperature regulation, not for flight (Kingsolver and Koehl, 1985).

What factors might be involved in the maintenance of different foraging modes? Theoretical models suggest the following predictions:

(i) If food is abundant, then widely-foraging lizards should have higher net energy gains than do sit-and-wait lizards; but if food is scarce, the reverse is true (Norberg, 1977).

(ii) On the other hand, sit-and-wait lizards, which should be relatively conspicuous to predators, should have lower rates of mortality (Gerritsen and Strickler, 1977).

(iii) If foraging mode influences diet, then differences in foraging mode may reduce interspecific competition (Pianka et al., 1979).

Do widely-foraging lizards have an energetic advantage? Net energy gain (estimated both with doubly labeled water and by short-term growth rates) is higher in widely-foraging lacertids (Nagy et al., 1984). Gross energy gain (size-corrected volumes of food in stomachs) is also higher in widely-foraging lizards (Huey and Pianka, 1981). Net energy gain is higher in widely-foraging teiid lizards than in sit-and-wait iguanids as well (Anderson and Karasov, 1981; Andrews, 1984). Thus, all available data suggest that widely-foraging lizards have higher net energy gains.

Do sit-and-wait lizards have a counteradvantage of reduced predation? Indirect morphological data (relative tail length, which is sometimes used as an index of predation intensity -- see Huey and Pianka [1981]) are supportive: widely-foraging lizards have relatively long tails. Moreover, sit-and-wait lacertids are eaten less frequently than expected (based on apparent densities) by horned adders (*Bitis*

caudalis), a sit-and-wait predator (Huey and Pianka, 1981). Similarly, sit-and-wait lizards in North American deserts (H. W. Greene, personal communication) and in Hispaniola (Henderson, 1984) are eaten relatively infrequently by sit-and-wait snakes. Nevertheless, a direct analysis of the effects of foraging mode on predation rate awaits a capture-recapture study or other approaches.

Do differences in foraging mode reduce interspecific competition in food (Arnold, 1984; Pianka et al., 1979)? Foraging mode seems to influence diet, as discussed above. Nevertheless, experimentally establishing a link between foraging mode and competition may be difficult: the apparent stereotypy of foraging mode in these lizards, as shown in laboratory studies (Kairns and Regal, personal communication), suggests that removal experiments in nature might have little effect on foraging mode (see Schoener, 1974). But, for purposes of argument, assume that sit-and-wait lizards have higher net energy gains, and that differences in foraging mode reduce interspecific competition. Would these patterns -- alone or in combination -- be sufficient to establish an overall selective balance that promotes the coexistence of both foraging modes? Are they the only factors involved?

The question of selective balance is a difficult one in ecology (Paine, 1984). Descriptive studies can at best establish selective advantages and disadvantages associated with each foraging mode but will not establish whether those are of equal and opposite magnitude. Long-term analyses of density, survivorship, and reproductive output as functions of prey availability and of predator abundance may help, but definitive answers to questions concerning the coexistence of foraging modes will be difficult to obtain.

Unfortunately, question 5, which concerns factors that were responsible for the evolution of a trait in the first place, is even more difficult to answer. Recall that sitting-and-waiting is probably the derived foraging mode in lacertids and that sitting-and-waiting might evolve under three scenarios: if food is scarce, if predators are abundant, or if competition is reduced. But without knowing the precise environmental conditions under which evolution took place, and without knowing how abundant is "abundant," we are unable to determine the most reasonable of these scenarios. Moreover, even if those environmental conditions were known from paleontological evidence, we would not be able to use manipulative experiments to test our evaluations, as we can with contemporary issues.

In short, we will often be forestalled from answering questions of the evolutionary origin of complex traits. Much of what we need to know is lost in history, and we are constrained to working with descriptive rather than with manipulative tests. Perhaps the best we will be able to do is to say that the origin of a trait probably isn't related to factor A, but it might be related to factor B or factor C. Our potential to learn about historical phenomena seems inevitably limited. Given that evolutionary questions often provide the ultimate impetus for ecological and physiological research, this is frustrating.

3. Conclusion

We argue that descriptive, comparative studies are very useful in analyses of predation or of other phenomena. For many issues in evolutionary ecology, descriptive approaches are versatile, robust, and efficient: for example, they have uncovered a great deal about foraging mode of Kalahari lacertids. In addition, they set a solid framework for subsequent experimental analyses that more properly address processes involved in cause and effect. But the approach reaches its limits when extrapolating from patterns to processes or when extrapolating from the maintenance of traits to their historical origins.

Acknowledgments

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