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Ecological Morphology of Locomotor Performance in Squamate Reptiles

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INTRODUCTION

Relationships between morphology, physiology, or biochemistry, on the one hand, and behavior and ecology, on the other, have been widely documented, as this volume attests. Such relationships provide evidence that most, if not all, organisms are to some extent “adapted” to their current environment. Quantifying how well adapted an organism is, or testing the biological and statistical significance of putative adaptations, may, however, be very difficult (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Losos and Miles, chap. 4, this volume). As well, many studies in ecological morphology, and in the conceptually related fields of physiological ecology (Feder et al., 1987) and comparative biochemistry (Hochachka and Somero, 1984), have ignored the crucial intermediate step of organismal performance (Arnold, 1983; Huey and Stevenson, 1979; Losos, 1990b) when trying to correlate morphology with ecology. In this chapter, we review the literature pertaining to the ecological morphology of locomotor performance in reptiles and relate this knowledge to current paradigms and analytical techniques in organismal and evolutionary biology. We will argue that both maximal whole-animal performance abilities (what an animal can do when pushed to its limits; generally measured in the laboratory, and not to be confused with *efficiency*; see Gans, 1991; Lauder, 1991) and behavior (what an animal actually does when faced with behavioral options; best measured in the field) must be considered when attempting to understand the mechanistic bases of relationships between morphology and ecology.

Locomotion is in many ways ideally suited for studies of ecological morphology. Most behavior involves locomotion, and measures of both locomotor performance (e.g., speed, stamina) and its morphological bases (e.g., limb length, heart size) come easily to mind. Some reptiles are good subjects for measurement of locomotor performance in the laboratory (e.g., with race tracks or treadmills), for quantifying its morphological, physiological, and biochemical bases, and for

demographic study and behavioral observation in the field. Measurement of performance is crucial, and reptiles are certainly easier subjects than are some other vertebrate groups, such as birds or bats (Ricklefs and Miles, chap. 2, this volume; Norberg, chap. 9, this volume).

The Morphology → Performance → Fitness Paradigm

“Not infrequently, performance characteristics, measured as maximal speed or endurance, make the difference between eating and being eaten” (Tenney, 1967, p. I–7). The foregoing quotation certainly contains some truth, but actual data indicating the frequency of “close encounters of the worst kind” between predators and prey are few and far between (cf. Castilla and Bauwens, 1991, p. 78; Christian and Tracy, 1981; Hertz et al., 1988; Jayne and Bennett, 1990b).

Studies of ecological morphology implicitly concern fitness and adaptation. Within populations, individual variation in morphology may be related to variation in Darwinian fitness; among populations and higher taxa, morphological variation in Darwinian fitness; among populations and higher taxa, morphological variation may indicate adaptation to different lifestyles. Arnold (1983) proposed a conceptual and statistical—and hence operational—framework for using data on individual variation to study adaptation within populations (fig. 10.1). This paradigm addresses the question of whether natural selection is currently acting on morphology or performance within a single population. Arnold’s (1983) discussion considered multiple morphological characters and multiple measures of performance, as well as correlations within these two levels. He pointed out that multiple regression and path analysis could be used to estimate and test the significance of performance gradients (quantifying the effects of morphology on performance), which can be studied in the laboratory (but see Wainwright, chap. 3, this volume), and fitness gradients (quantifying the effects of performance on fitness), which require field studies (see also Emerson and Arnold, 1989; Wainwright, 1991).

This perspective suggests that intrapopulational variation in morphology may have significant influences on fitness only to the extent that it affects performance. Measures of organismal performance capacities thus become central (cf. Bennett, 1989; Bennett and Huey, 1990; Emerson and Arnold, 1989; Pough,

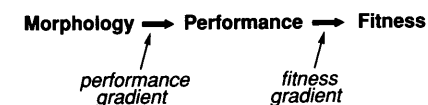


FIGURE 10.1 Simplified version of Arnold’s (1983) original paradigm.

1989), and measures of locomotor performance fall easily into the paradigm. The focus on organismal performance as pivotal is in sharp contrast to many previous studies of locomotor ecology, in which the starting point (and sometimes the ending point) has been measurement of limb proportions (see "Case Studies" below). Moreover, the realization that it is easier to study one or the other rather than both gradients simultaneously, and that both parts of the equation are of interest, has stimulated research.

Physiological and biochemical traits may be included within the category of "morphology," and we will subsequently use morphology as shorthand for all three types of traits. This is not to imply that morphology, physiology, and biochemistry are equivalent, nor are we trying to deny the distinction between "form" and "function." The point is simply that all three types of traits are (generally) at a level of biological organization below the whole-organism, and all may influence organismal performance. Calling all three types of traits "morphology" serves to emphasize that similar tools and approaches are useful for studying their effects on organismal performance (cf. Wainwright, 1991).

Arnold's (1983) paradigm was designed specifically to interface with multivariate quantitative genetics theory (Lande and Arnold, 1983). In the quantitative genetic framework (e.g., Boake, 1994; Brodie and Garland, 1993; Falconer, 1989), adaptive phenotypic evolution consists of two parts: natural selection, which is a purely phenotypic phenomenon, and genetic response, which involves inheritance. Some do not like this separation of selection and inheritance (e.g., Endler, 1986), but we agree with Lande and Arnold (1983) that it has considerable operational advantages in allowing the two elements to be studied independently. It also emphasizes that selection may be futile; if a trait is not heritable, then selection cannot lead to or improve adaptation.

How Does Behavior Fit into the Paradigm?

The place of behavior in the paradigm of figure 10.1 is ambiguous. Arnold (1983) did not mention behavior as a distinct level; subsequently, however, Emerson and Arnold (1989; also Schluter, 1989) have included behavior within the category of morphology. We offer an alternative categorization, as depicted in figure 10.2 (modified from Garland, 1994a).

Many biologists imagine that selection acts most directly on what an animal actually does in nature, that is, its behavior. Performance, on the other hand, as defined operationally by laboratory measurements, generally indexes an animal's ability to do something when pushed to its morphological, physiological, or biochemical limits. (Whether animals routinely behave at or near physiological limits under natural conditions is an important empirical issue for which precious few data exist: Daniels and Heatwole, 1990; Dial, 1987; Garland, 1993;



FIGURE 10.2 Expansion of Arnold's (1983) paradigm to include behavior, as proposed by Garland (1994a).

Garland et al., 1990a; Gatten et al., 1992; Gleason, 1979a; Hertz et al., 1988; MacArthur, 1992; Morgan, 1988; Pough et al., 1992; Seymour, 1982, 1989; van Berkum et al., 1986; Wyneken and Salmon, 1992.) Thus, morphology limits organismal performance, which in turn constrains behavior, and natural and sexual selection act most directly on behavior—what an animal actually does (Garland, 1994a). This modification of Arnold's (1983) original paradigm adds one more level of analysis and places specific emphasis on behavior as the focus of selection. Behavior is seen as a potential "filter" between selection and performance (Garland et al., 1990b).

Further Extensions of the Paradigm

Inserting behavior between performance and fitness seems relatively straightforward (fig. 10.2). But this addition does not necessarily mean the paradigm is complete or general. Many more possible links can be imagined, and a relatively simple chain rapidly becomes a complicated web (e.g., fig. 10.3).

In particular, habitat, broadly defined, is another important factor which may influence behavior, performance capabilities, and even morphology (see also Dunson and Travis, 1991; Huey, 1991). For example, availability of perches or basking sites, their size, and their distribution may affect both what an animal does (e.g., Adolph, 1990b; Grant, 1990; Moermond, 1986; Pounds, 1988; Waldschmidt and Tracy, 1983; see discussion of the "habitat matrix" model below) and what it is capable of doing (e.g., sprint speed in lizards is affected by perch diameter and substrate: Carothers, 1986; Losos and Sinervo, 1989; Losos et al., 1993; Miles and Althoff, 1990; Sinervo and Losos, 1991). Temperature is a habitat characteristic that may affect performance indirectly through its effects on various physiological processes, and by having direct influences on behavior, such as the switches in defensive behavior at low body temperature that occur in some lizards and snakes (Arnold and Bennett, 1984; Crowley and Pietruszka, 1983; Hertz et al., 1982; Mautz et al., 1992; Van Damme, Bauwens et al., 1990; Schiefflen and de Queiroz, 1991). Temperature affects locomotor performance both in absolute terms (Bauwens et al., in press; Bennett, 1990; Garland, 1994b) and, to a lesser extent, relative to other individuals or species. Individual differences in locomotor performance are consistent across temperatures (i.e., fast individuals tend to be fast at all temperatures), but not perfectly so (references in

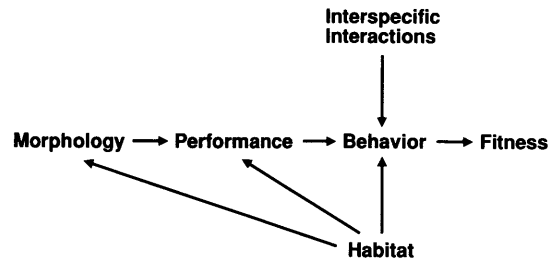


FIGURE 10.3 Inclusion of some other factors that may affect elements of Arnold's (1983) paradigm. Habitat characteristics, such as temperature, may affect basic physiological and biochemical properties as well as behavior (see text). (Of course, behavior and physiology may affect an animal's body temperature; the present diagram is extremely simplified.)

Bennett, 1990; Bennett and Huey, 1990). Thus, the temperature at which an individual happens to be when it encounters a predator may affect its relative fitness (e.g., Christian and Tracy, 1981), and individual differences in thermoregulatory behavior may become crucial (cf. Christian et al., 1985; Waldschmidt and Tracy, 1983).

More subtle habitat effects are also possible. Food in the stomach (Ford and Shuttlesworth, 1986; Garland and Arnold, 1983; Huey et al., 1984), nutritional state (for experiments with mammals, see Brooks and Fahey, 1984, and Astrand and Rodahl, 1986), hydrational state (Moore and Gatten, 1989; Preest and Pough, 1987; Wilson and Havel, 1989, but see Crowley, 1985b; Gatten and Clark, 1989; Stefanski et al., 1989), as well as disease or parasite infection (Schall, 1986, 1990; Schall et al., 1982; but see Daniels, 1985b) all may affect performance ability. Hydrational (Crowley, 1987; Feder and Londos, 1984; Pough et al., 1983; Putnam and Hillman, 1977) or nutritional state may also affect activity levels, that is, behavior. Inter- and intraspecific interactions can also affect behavior in numerous ways (e.g., Fox et al., 1981; Garland et al., 1990a; Henrich and Bartholomew, 1979; Schall and Dearing, 1987; Stamps, 1984). Even hydrational or thermal conditions during incubation or pregnancy can affect locomotor performance of offspring (Miller et al., 1987; Van Damme et al., 1992).

Extending the Paradigm to Population and Species Variation

The paradigm in figure 10.2 can also be applied to understand or predict a relationship between morphology and habitat use among populations or species. The logic of this extension is as follows. First, to the extent that morphological differences among individuals within populations lead to differences in performance abilities that affect fitness, then, assuming the absence of constraints (Maynard Smith et al., 1985), the most "fit" morphology should evolve within

any population (Emerson and Arnold, 1989). Second, to the extent that different morphologies function best in different habitats, then natural selection will tend to favor their evolution in the appropriate habitats. If one has an understanding of which morphologies are best suited in given habitats (based on biomechanical or functional analyses, including optimality models, or on empirical studies of natural selection within populations), then one can test the prediction that taxa have adapted to different environments (Baum and Larson, 1991; Bock and von Wahlert, 1965; Losos and Miles, chap. 4, this volume). Caution must be exercised when taking this view, however, as we have little empirical evidence that any given trait(s) in any given population will have reached its selective optimum by the time we study it (Arnold, 1987; Ware, 1982). Moreover, multiple (sub)optimal solutions, which confer equivalent fitness, may exist (Denny, chap. 8, this volume; Feder et al., 1987; Ware, 1982); depending on the shape of the fitness surface, movement from one peak to another may be difficult.

Although Arnold (1983) suggested path analysis for studying the causes (performance gradients, e.g., fig. 10.5 below) and consequences (fitness gradients) of individual variation in performance (and behavior), path analysis might also be employed to study species-level selection processes (cf. Emerson and Arnold, 1989). For example, rather than values for individuals, data points could be population, species, or clade means for morphological, performance, behavioral, or ecological traits. As components of the "fitness" of a population, species or clade (cf. Futuyma, 1986; Vrba, 1989), one might consider geographic range (cf. Jablonski, 1986), evolutionary longevity, and/or number of descendant populations or species (the latter might require paleontological information; but see Nee et al., 1992). Alternatively, some measure of a population's or of a species' "fitness" or "adaptedness" (Michod, 1986) to its current environment might also be possible, such as physiological tolerances, breadth of the Grinnellian niche (James et al., 1984), or demographic traits (e.g., population density, intrinsic rate of natural increase: cf. Baker, 1978; Birch et al., 1963). To quote Stini (1979, p. 388): "A well-adapted population would be . . . one that enjoys a relatively high probability of survival under conditions highly likely to occur." Of course, a path analysis of comparative data would require proper allowance for phylogenetic non-independence (see below). As noted by Emerson and Arnold (1989, p. 302), "there are no strong theoretical grounds for expecting similar performance topographies at the intra- and interspecific levels and there has been virtually no empirical exploration."

Does Morphology Affect Fitness Directly?

Regardless of how complicated a paradigm one wishes to consider, an outstanding conceptual and empirical issue is whether direct paths exist from morphology to fitness (fig. 10.4). Returning to the original formulation, the most

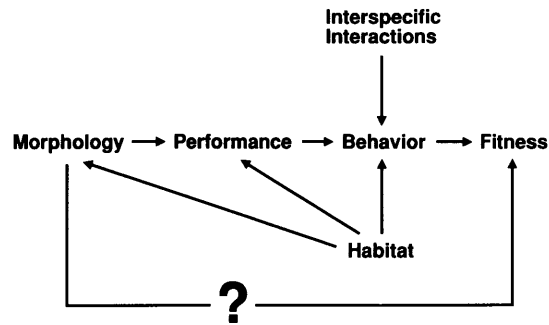


FIGURE 10.4 An outstanding conceptual and empirical issue is whether any direct paths from morphology to fitness are significant (see text).

general path model is one in which all possible effects are depicted, including those directly from morphology to fitness (Arnold [1983, fig. 3] omitted these paths). Consider some hypothetical possibilities. Some individual garter snakes are born with a single or no eyes, an external heart, or a severely kinked tail or spine (Garland, 1988, pers. obs.; Arnold and Bennett, 1988, pers. comm.). These morphological deformities greatly impair locomotor capacities, which in turn limit behavioral options (as compared with “normal” individuals), and would certainly have fitness consequences in nature. In this case, a direct path from morphology to fitness seems unnecessary.

But contemplate two other examples. First, all else being equal (i.e., assuming behavior is unaffected), an albino snake will likely suffer a fitness decrement relative to a normally pigmented individual, because the former will more likely be discovered and eaten by a predator prior to its reproducing. Thus, a direct path appears to exist from morphology (pigmentation) to fitness. Alternatively, if one considers some measure of crypsis as a “performance” variable, then albinism acts through its effects on crypsis (cf. King, 1992), and performance, but not morphology, would seem to have a direct path to fitness, bypassing behavior. But, if an animal could somehow become “aware” that it was differently colored and so alter its behavior to compensate (cf. Morey, 1990), then the effect of albinism might be entirely through the performance → behavior link. Albinism would also affect thermoregulation, making it more difficult for the snake to warm by basking, hence causing it to bask for longer periods of time and increasing its exposure to predators (cf. Andren and Nilson, 1981).

Second, in many species, body size affects the outcome of intraspecific behavioral interactions (Tokarz, 1985; references in Garland et al., 1990a; Faber and Baylis, 1993). This effect may occur simply because size affects strength and stamina, and hence performance at fighting. But in some cases differences in size alone may influence decisions to fight or not, and hence may determine the out-

come of an agonistic interaction before any actual fighting occurs. This example suggests a direct effect of a morphological trait (body size) on behavior, and hence on a component of fitness (dominance rank).

Some might consider it logically impossible that morphology can affect fitness other than through its effects on organismal performance (and hence behavior). The idea is that form only matters if it affects function and hence performance; otherwise, morphological variation is selectively neutral. We would prefer to consider the absence of direct morphology → fitness paths as an hypothesis, subject to empirical test. Such tests might involve measurement of vertebral numbers (in snakes) or limb length (in lizards), as well as locomotor performance and survivorship (cf. Arnold and Bennett, 1988; Jayne and Bennett, 1990b; Tsuji et al., 1989). A significant path from morphology to (a component of) fitness (fig. 10.4) would indicate either a direct effect of morphology on fitness or the presence of some unmeasured (latent) performance variable.

LEVELS AND METHODS OF ANALYSIS

Interpopulation

Although analyses relating morphology, performance, behavior, and fitness (broadly defined) most commonly involve interspecific comparisons (to be discussed below) or, more recently, individual variation, studies of interpopulation differences are essential to evolutionary analyses (Garland and Adolph, 1991; James, 1991). Most previous studies of population (geographic) variation focus on morphometric or allozymic characters (e.g., Zink, 1986), although studies of variation in mitochondrial DNA are now common (e.g., Avise et al., 1987; Lamb et al., 1989). Consequently, phylogenetic analyses of population differentiation cannot be far off (cf. Schluter, 1989; Snell et al., 1984), and we encourage such studies of population differences in locomotor performance and its correlates. If possible, such studies should include a “common garden” approach, in which animals are raised in the laboratory for at least one generation to maximize the probability that observed phenotypic differences are actually genetically based (Garland and Adolph, 1991). Common garden controls are important for studies of different species as well, although most biologists seem less concerned at this level. Population differences in locomotor performance may be consistent across years (Huey and Dunham, 1987), but year-to-year variation in performance exists (Huey et al., 1990) and may confound attempts to correlate morphology with ecology (cf. Wiens and Rotenberry, 1980).

Intrapopulation: Individual, Ontogenetic, and Sexual Variation

Arnold (1983, fig. 10.1) considered studies of individual variation within populations, including effects of morphology on performance (e.g., mechanistic physiology) and the effects of performance on fitness (e.g., direct studies of natu-

ral selection in the wild). Quite a few such studies of reptilian locomotion have been completed since 1983. A major conclusion of these studies is that measures of locomotor performance show substantial and repeatable individual variation within single populations (Bennett, 1987; Bennett and Huey, 1990; Huey et al., 1990; Jayne and Bennett, 1990a; see also Djawdan, 1993; Friedman et al., 1992, on mammals). This variation and repeatability is, of course, a prerequisite for attempts to quantify relationships between morphology and performance (performance gradients) or between performance and behavior, fitness, or ecology (e.g., fitness gradients).

One advantage of studying individual variation is that phylogenetic effects are not a concern. So, for example, the effects of body size can be studied by examining an ontogenetic series (e.g., Garland, 1984, 1985; Jayne and Bennett, 1990a; Pough, 1977, 1978) rather than multiple species. Similarly, the mechanistic correlates of performance variation can be studied (e.g., Garland, 1984, 1985; Garland and Else, 1987; Losos et al., 1989; Tsuji et al., 1989) without concern that phylogenetic effects may confound the results (cf. Losos, 1990a, b, c).

Quantitative Genetic Analysis

Individuals within a population may not provide statistically independent data points, because they are related to varying extents. Quantitative genetics uses this fact to partition observed phenotypic variances and covariances into genetic (due to inheritance, which is analogous to phylogenetic descent; cf. Lynch, 1991) and environmental sources, each of which can be more finely partitioned (Boake, 1994; Brodie and Garland, 1993; Falconer, 1989; Garland, 1994a).

Quantitative genetic analyses are not a traditional part of ecological morphology. They must become an integral part, however, if we are to move towards an understanding of the mechanisms of microevolution. We will not consider quantitative genetic analyses of reptilian locomotor performance in detail. Only a few studies have been completed, all on garter snakes (*Thamnophis*) or lizards (*Sceloporus*, *Lacerta*; reviews in Bennett and Huey, 1990; Brodie and Garland, 1993; Garland, 1994a). All studies to date have relied on analyses of presumed full-sibling families to estimate heritabilities. For many reptiles, gravid females can be captured in relatively large numbers in the field. After offspring are born or hatched in the laboratory, measurements of locomotor performance are made on each. Unfortunately, heritability estimates from sets of full-siblings represent neither a "narrow-sense" nor a "broad-sense" heritability; in addition, multiple paternity will lead to an underestimation of additive genetic effects in full-sibling data sets (Brodie and Garland, 1993; Falconer, 1989; Garland, 1994a; Schwartz et al., 1989). Thus, significant among-family variance in studies of full-siblings suggests heritability, but does not prove it. With one exception (Bauwens et al.,

1987), all studies to date have found significant among-family variance for measures of locomotor performance in reptiles.

Experimental Approaches

Experimental approaches can be used in several ways, for example: (1) to examine the mechanistic bases of performance variation; (2) to mimic the effects of short- or long-term changes that may occur naturally within individuals; (3) to examine the effect of conditions during development on morphology and performance abilities; and (4) to increase the range of variation in organismal performance and so increase statistical power to detect its ecological and selective importance. Experimental approaches have the advantage that they can isolate and study the effects of variation in one variable independent of correlations with other variables (cf. Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Slinker and Glantz, 1985; Wade and Kalisz, 1990). Experimental approaches have been underutilized for analyzing links in the morphology → locomotor performance → behavior → fitness chain (or web) and in ecomorphology in general (but see Benkman and Lindholm, 1991; Carothers, 1986; Hanken and Wake, 1991; Hillman and Withers, 1979; Huey et al., 1991; James, 1991; Jayne and Bennett, 1989; Lauder and Reilly, 1988; Ruben et al., 1987; Webster and Webster, 1988).

Causal mechanistic relationships suggested by correlative studies of individual variation in locomotor abilities (fig. 10.5; e.g., Garland and Else, 1987; Gleeson and Harrison, 1988; John-Alder, 1984a, b, 1990) can be tested with such physiological techniques as blood doping (cf. Withers and Hillman, 1988), but this has scarcely been attempted in reptiles (Gleeson, 1991). Hormonal (John-Alder, 1990; Joos and John-Alder, 1990; Moore and Marler, 1987; Moore and Thompson, 1990) or pharmacological (e.g., John-Alder et al., 1986b) manipulation to change metabolism and performance is also possible. (Levels of some hormones fluctuate rapidly in reptiles, whereas some measures of locomotor performance are quite repeatable, which suggests that the former may have little effect on the latter.) With respect to morphology, the importance of tail length and loss, toe loss, toe fringes, and skin flaps for sprinting and gliding performance in lizards and snakes has also been assessed experimentally (e.g., Arnold, 1984a; Carothers, 1986; Daniels et al., 1986; Formanicwiz et al., 1990; Huey et al., 1990; Jayne and Bennett, 1989; Losos et al., 1989; Marcellini and Keefer, 1976; Pond, 1981).

Within-individual variation in reptilian locomotor performance has been examined as a consequence of several factors, such as physical conditioning (training), feeding, reproductive state, and hormonal state. Physical conditioning studies of the type so common in mammalian exercise physiology (e.g., Brooks

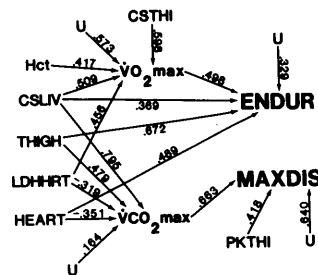


FIGURE 10.5 Path analysis of performance gradients for treadmill endurance at 1.0 km/h (ENDUR) and maximal distance running capacity (MAXDIS) around a circular track in the lizard *Ctenosaura similis* (data from Garland, 1984). For this analysis, only those variables that entered into multiple regression equations as significant predictor (independent) variables and/or that could be explained to a significant extent as dependent variables were considered (see Table 4 of Garland, 1984: SMR was also excluded). Path coefficients were estimated in two ways: first, from standardized partial regression coefficients as described in Nie et al. (1975); second, from the standardized solution output by LISREL Version 4 (Joreskog and Sorbom, 1978), an iterative, maximum likelihood fitting procedure. These two approaches yielded virtually identical results; the figure shows the LISREL results. A variety of path analytic models were fitted with LISREL in order to obtain the model which was judged to best fit the data based on an approximate chi-square-goodness-of-fit statistic and contained no nonsignificant (i.e., $P > .05$) path coefficients (approximate 2-tailed t -tests with 14 degrees of freedom). The path analytic model shown here had a chi-square of 22.4 ($df = 20$, $P = .3199$), indicating an acceptable fit to the data. Individual path coefficients had t -values of between 2.57 and 14.8, which, by comparison with $t_{(14, .05)} = 2.145$, suggests that all paths are significant. CSTHI = thigh citrate synthase activity (per gram of tissue), Hct = hematocrit, CSLIV = liver citrate synthase activity, THIGH = total mass of right thigh muscles, LDH-HRT = lactate dehydrogenase activity in the heart, HEART = heart mass (including atria), PKTHI = thigh pyruvate kinase activity, U = unexplained variation. (See Arnold, 1983; also Sokal and Rohlf, 1981; Bulova, in press; and assumptions in Emerson and Arnold, 1989, p. 299.)

CSLIV is significantly related to ENDUR, $\dot{V}O_2\text{max}$, and $\dot{V}CO_2\text{max}$ (see also multiple regressions in Table 4 of Garland, 1984). Deleting CSLIV from these predictive models resulted in lower coefficients of determination for the multiple regression equations or a higher chi square for the LISREL-fitted path analytic model. Garland (1984) interpreted these results (and data for mammals) as suggesting that liver oxidative capacity plays a significant role in the activity metabolism of ctenosaurs, perhaps via conversion of metabolites during or after activity. Recent studies, however, suggest that the liver is not an important site of lactate metabolism during recovery in amphibians or reptiles (Gleeson and Dalessio, 1989; Gleeson 1991).

and Fahey, 1984; Astrand and Rodahl, 1986) have been attempted only twice with reptiles. These two studies employed very different training regimens and species from different families, yet both failed to improve organismal performance (speed, stamina, maximal oxygen consumption: Garland et al., 1987; Gleeson, 1979b; but see Gleeson, 1991, p. 189). On the other hand, captivity and the accompanying relative inactivity may decrease maximal oxygen consumption ($\dot{V}O_2\text{max}$) (Bennett and John-Alder, 1984; Garland et al., 1987; but see John-Alder, 1984b). Training studies definitely deserve further attention; unfortunately, they can be quite labor-intensive because training regimens cannot be

automated as easily as they can with mammals. An outstanding issue is the extent to which "natural training" occurs in the wild (Burghardt, 1984; Garland et al., 1987). Acclimation and acclimatization of reptilian locomotor performance has been studied only rarely (Gatten et al., 1988; Hailey and Davies, 1986; Kaufmann and Bennett, 1989; Payne and Gatten, 1988), as has seasonal variation, which is in some cases significant (Garland, 1985; Garland and Else, 1987; Gleeson, 1979b; Huey et al., 1990; John-Alder, 1984b). Infection with pathogens or parasites could also be used to lower performance (Schall, 1990; Schall and Dearing, 1987; but see Daniels, 1985b; Schall, 1986).

Body size, which often correlates with locomotor performance (see below), can be manipulated in a variety of ways. For example, variation in diet or in thermal regimen (Sinervo and Adolph, 1989) may affect growth rate and hence age-specific body size; such experimentally induced variation may be useful in studies of static allometry (i.e., within an age class). Sinervo and Huey (1990; Sinervo, 1990; Sinervo et al., 1992; see also Bernardo, 1991; Hahn and Tinkle, 1965; Janzen, 1993; Sinervo and Licht, 1991) have used experimental manipulation of egg size in an attempt to separate the effects of body size per se from other factors that may affect speed or stamina. Embryo manipulation studies are common in mammals (e.g., Atchley et al., 1993; Cowley et al., 1989; Hill and Mackay, 1989; Kirkpatrick and Rutledge, 1988) but apparently have not been attempted in reptiles.

Hydric and thermal conditions during incubation can affect locomotor performance of reptiles (Miller et al., 1987; Van Damme et al., 1992), and such effects may not be uncommon (references in Garland and Adolph, 1991). For example, thermal conditions during pregnancy can affect the number of body and tail vertebrae developed by garter snakes (Fox, 1948; Fox et al., 1961; Osgood, 1978; C. R. Peterson and S. J. Arnold, pers. comm.), which in turn may affect locomotor performance (Arnold and Bennett, 1988; Jayne and Bennett, 1989; M. R. Dohm and T. Garland, in preparation). Many other factors may affect maternal size and/or condition and in turn affect offspring size and/or performance; some of these effects can be controlled for statistically via regression analysis and computation of residuals (Brodie, 1989b; Brodie and Garland, 1993; Garland, 1988; Garland and Bennett, 1990; Tsuji et al., 1989).

Truly evolutionary experiments, involving organismal performance or components thereof, are possible using artificial selection (e.g., Bennett et al., 1990; Garland and Carter, 1994; Hill and Caballero, 1992; Huey et al., 1991; Rose et al., 1987; Schlager and Weibust, 1976), but such experiments have not yet been reported for locomotor performance in any organism. Relatively long generation times may preclude such possibilities for reptiles, although experiments with mice are now being conducted (T. Garland, unpubl.). Direct manipulation of the

germ line (e.g., genetic engineering to produce transgenic mice) is now routine in many animals (see Hill and Mackay, 1989) but has not been attempted with reptiles.

CONFOUNDING ISSUES IN THE STUDY OF PERFORMANCE AND ECOLOGICAL MORPHOLOGY

Measuring "Performance" as Opposed to "Behavior"

Arnold (1983, p. 352) defined performance as "the score in some ecologically relevant activity, such as running speed. . . ." Most estimates of maximal locomotor performance in reptiles are made in the laboratory, although some field estimates are available (e.g., Belkin, 1961; on mammals see Djawdan and Garland, 1988; Garland et al., 1988). In either laboratory or field, however, definition and measurement of "performance" as opposed to "behavior" is not always simple (cf. Friedman et al., 1992; Garland, 1994a, b). For example, if maximal sprint speed is measured by chasing an animal along a race track, how can one be sure that each individual actually runs at its morphological, physiological, or biochemical limits? Animals may vary in their response to stimuli (their "motivation"), such that some run at their physiological limits and others do not. Thus, behavioral variation, just like morphological or physiological variation, can affect laboratory measurements of performance (see also Wainwright, chap. 3, this volume).

In the laboratory, repeated testing of individuals and use of the fastest trial(s) as an index of maximal speed (e.g., Bennett, 1980; Formanowicz et al., 1990; Garland, 1984, 1985, 1988; Gleeson and Harrison, 1988; Huey 1982a; Losos et al., 1989; Marsh, 1988; Marsh and Bennett, 1985, 1986; Sinervo et al., 1991; but see Jayne and Bennett, 1990a, b) may help circumvent motivational problems. (It is well known in human, horse, and dog racing that performances of individuals vary significantly with the competition and setting.) For some performance measures, it may be possible to verify by supplementary tests that physiological limits have been reached. Thus, physiological exhaustion in endurance trials can be supported by testing for loss of righting response (e.g., Huey et al., 1984, 1990), or by measuring whole-body (Arnold and Bennett, 1984) or blood (Djawdan, 1993) lactic acid concentrations. Alternatively, measures of "race quality" can be used in statistical analyses (Tsuji et al., 1989). In any case, what some workers term "performance" others term "behavior" (e.g., Bennett, 1980).

Another possibility is to test for correlations between individual (or interspecific) differences in performance and traits thought to affect performance. If underlying morphological, physiological, or biochemical traits explain (statistically) a large fraction (e.g., 47–89%; Garland, 1984, fig. 10.5; Garland and Else, 1987) of the variance in locomotor performance, then it is unlikely that

variation in performance is due solely to differences in motivation or willingness to run. To date, published studies of individual variation have been somewhat more successful in identifying physiological correlates of endurance than of sprint speed (see "Case Studies" below), which suggests that it may be easier to obtain measures of physiologically limited performance capacities in stamina- than in sprint-type activities.

Some studies of individual variation indicate that measures of "behavior" may show correlations with measures of "performance." For example, antipredator display (Arnold and Bennett, 1984), scored at the end of treadmill endurance trials, showed significantly positive correlations with both treadmill endurance and sprint speed in the garter snake *Thamnophis sirtalis* (Garland, 1988; see also Arnold and Bennett, 1988, on *T. radix* and Brodie, 1992, on *T. ordinoides* concerning the correlation between speed and distance crawled prior to assuming an antipredator display). Arnold and Bennett (1984) previously showed that whole-body lactic acid concentrations of *T. radix* exhibiting antipredator displays (at the end of stamina trials) were similar to those of snakes forced to exercise for thirty minutes. Thus, one might expect the antipredator display to be partly dependent on, and hence limited by, physiological capacities. However, Garland, et al. (1990b) found that, whereas speed and endurance showed significant (although weak) correlations with lower-level morphological, physiological, or biochemical traits, antipredator display did not (see also Arnold and Bennett, 1988). Thus, an alternative interpretation is that underlying variation in some axis of "motivation" (Bolles, 1975) has effects on measures of speed, endurance, and antipredator display (higher scores are more offensive and seem to require more physical exertion), leading to some positive correlation.

The foregoing examples emphasize that caution must be exercised when designing or interpreting measures of locomotor "performance." Our discussions of Arnold's (1983) paradigm and extensions thereof assume that true measures of morphologically or physiologically limited performance can be obtained.

Allometry and its Importance

Body size affects many traits, including locomotor performance (e.g., Dunham et al., 1988; Garland, 1984, 1985; Garland and Huey, 1987; Losos, 1990a, b, c). Variation in body size may therefore obscure or enhance relationships between other traits (Emerson et al., chap. 6, this volume). Unfortunately, much of the older ecomorphological literature has attempted to remove the effect of size by using ratios, which is generally ineffective and potentially misleading (cf. Packard and Boardman, 1988).

The importance of considering allometry can be illustrated with a hypothetical example. Suppose that sprint abilities determine habitat use in lizards. Many

studies of lizards have noted correlations between relative limb length (expressed as a proportion of snout-vent length) and various habitat variables (see "Limb Length and Habitat Use" below), and have implicated differences in locomotor ability as the underlying cause of the relationships. Both within and between species, limb length rarely scales isometrically with snout-vent length (i.e., as individuals or species increase in size, limb length either becomes relatively longer or shorter; see below, figs. 10.7c, 10.8c). Further, within and between species, sprint ability usually increases with body size. Consequently, a relationship may exist between habitat use and body size due to the effect of size on sprint speed. Because relative limb length is partly a function of body size (except when limb length scales isometrically with size), a spurious relationship would exist between relative leg length and habitat use. Our reanalysis of Pianka's (1969, 1986) data illustrates this problem (see discussion below and figs. 10.7, 10.8).

Confounding effects of body size can be controlled in a variety of ways. Perhaps the most common way is to regress each variable of interest (e.g., sprint speed, limb length) on some measure of body size (e.g., body mass, snout-vent length) and then compute residuals. These residuals can then be used in correlation or regression analyses or various multivariate techniques, such as principal components analysis (e.g., Garland, 1984, 1985, 1988; Jayne and Bennett, 1990a, b; Losos, 1990a, b, c). If the effects of additional covariates (e.g., temperature) or categorical variables (e.g., sex, season, population) need to be removed as well, then residuals can be computed from multiple regressions including dummy independent variables (e.g., Garland and Else, 1987; Gatten et al., 1991; Jackson, 1973b; Packard and Boardman, 1988; Sokal and Rohlf, 1981). Regressions to compute residuals need not be restricted to linear models (cf. table 3 of Garland and Else, 1987; Jackson, 1973b; Jayne and Bennett, 1990a; see also Chappell, 1989). With interspecific data, methods that allow for statistical complications due to phylogeny must be used when computing residuals (Garland et al., 1992; Harvey and Pagel, 1991; Losos and Miles, chap. 4, this volume; Martins and Garland, 1991).

The foregoing approach is not without problems, however. We will mention three here (cf. Huey and Bennett, 1987; Tracy and Sugar, 1989). First, least-squares regression analysis assumes that the independent variable contains no measurement error. This assumption is not true of measures of body size, resulting in underestimates of true structural relationships (Harvey and Pagel, 1991; LaBarbera, 1989; Pagel and Harvey, 1988; Riska, 1991; Sokal and Rohlf, 1981). Unfortunately, alternatives to least-squares regression slopes (e.g., reduced major axis, major axis) are not easily employed where multiple independent variables need to be considered. Second, using the same individual measurement of body size (e.g., each animal weighed or measured a single time) as the indepen-

dent variable for a series of dependent variables may result in correlated errors being introduced into all residuals. Such correlated errors can be avoided by taking several measurements of body size (e.g., when speed is measured, when stamina is measured, when limb length is measured; Garland, 1984; Garland and Else, 1987). Third, when correlating the residuals, one degree of freedom should perhaps be lost for each dependent variable for which residuals are computed.

One alternative to the residual approach outlined above is to simply use multiple regression of the dependent variable (e.g., sprint speed) on both a measure of body size and, say, limb length (e.g., Snell et al., 1988). The problem here is that body size and limb length will generally be highly correlated, and the results of multiple regression analyses are unreliable in the face of such multicollinearity (Slinker and Glantz, 1985). We believe that regression of both speed and limb length on body size, then testing for correlation between their residuals, is a more reliable procedure. Alternatively, experimental manipulations that change mass or limb length—but not both—could be helpful in reducing the correlations between independent variables (cf. Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Slinker and Glantz, 1985).

In some cases, the actual value of the allometric exponent is of interest, perhaps in relation to theoretical models of scaling (e.g., Emerson, 1985; Garland, 1985; Harvey and Pagel, 1991; LaBarbera, 1989; Marsh, 1988). Unfortunately, how best to estimate allometric relationships is unclear. As noted above, the independent variable in allometric studies always incorporates some "error variance," which means that slopes will tend to be underestimated. Moreover, for comparisons of population and/or species means, allometric slopes should be estimated phylogenetically, not merely by a regression involving values for tips of a phylogeny (Garland et al., 1992, 1993; Garland and Janis, 1993; Harvey and Pagel, 1991; Losos, 1990c; Lynch, 1991; Martins and Garland, 1991; Purvis and Garland, 1993).

Phylogeny and its Importance

Inheritance of a phenotypic trait cannot be studied without knowledge of the relatedness of individuals. Analogously, the evolution of a phenotypic trait cannot properly be studied without knowledge of phylogenetic relationships. That all organisms are descended in a hierarchical fashion from common ancestors means that no set of taxa can be assumed to be biologically or statistically independent. Phylogenetic non-independence has implications for all aspects of statistical analyses, including hypothesis testing, power to detect significant relationships between traits, and estimation of the magnitude of such relationships (Felsenstein, 1985; Harvey and Pagel, 1991; Losos and Miles, chap. 4, this volume; Lynch, 1991; Martins and Garland, 1991; Pagel, 1993). Several

methods now exist for incorporating phylogenetic information into comparative analyses, and various examples exist in which phylogenetic analyses lead to qualitatively different conclusions (Garland et al., 1991, 1993; Harvey and Pagel, 1991; Nee et al., 1992). It should also be noted that phylogenetic methods for estimating and testing, for example, character correlations, can sometimes *increase*—not just decrease—statistical significance as compared with an inappropriate nonphylogenetic analysis.

As the vast majority of previous comparative studies have been analyzed with inadequate allowance for phylogenetic non-independence, conclusions drawn from them must be viewed with caution. For example, many of the allometric studies we discuss were done nonphylogenetically; practical constraints (e.g., lack of suitable phylogenies: see figs. 10.7, 10.8 below) and time limitations have precluded our trying to redo all of them! Nevertheless, future population- or species-level examination of the morphology → performance → behavior → fitness paradigm should be done with appropriate allowance for phylogenetic non-independence (e.g., Losos, 1990b). An interspecific path analysis, comparable to Arnold's (1983) paradigm for microevolutionary studies (cf. Emerson and Arnold, 1989), would be particularly desirable.

CASE STUDIES

Morphology → Performance

Interspecific differences in locomotor performance are well established in reptiles (e.g., Bennett, 1980; Garland, 1994b; Huey and Bennett, 1987; Losos, 1990b.; van Berkum, 1988; references therein). Population differences have been shown a number of times as well (e.g., Garland and Adolph, 1991; Huey et al., 1990; Sinervo et al., 1991; Snell et al. 1988; but see Bennett and Ruben, 1975). A somewhat surprising finding has been the substantial variation in performance among individuals within single populations (Bennett, 1987; Bennett and Huey, 1990; Huey et al., 1990; Pough, 1989). Sex differences in performance exist and are in some cases due to sex differences in body size; unfortunately, few studies have actually tested for sex differences with adequate sample sizes (e.g., Garland, 1985; Huey et al., 1990; Jayne and Bennett, 1989; Tsuji et al., 1989). Some individual variation in performance ability is due to differences in age and/or size (Garland and Else, 1987; Hailey and Davies, 1986; Marsh, 1988; Pough, 1977, 1978); their effects have been thoroughly separated in only two studies of reptiles (Huey et al., 1990; Sinervo and Adolph, 1989).

Variation in performance calls for both proximate and ultimate explanations. In this section, we consider the former—studies examining the mechanistic bases of performance variation. Note that studies of individual variation in performance and morphology constitute attempts to quantify performance gradients

(Arnold, 1983), although special assumptions are required when individuals of multiple ages are studied (Emerson and Arnold, 1989).

Endurance. Variation in endurance has been less studied than has variation in sprinting ability (see "Sprint Speed" below). Most commonly, endurance is measured as running time to exhaustion on a motorized treadmill. Interspecific comparisons of lizards indicate that treadmill endurance capacity has evolved in concert with both body mass and body temperature (Autumn et al., 1994; Garland, 1994b). Interspecific correlates of endurance have not been studied in detail, but appear to include the energetic cost of locomotion (lower cost leads to higher stamina at a given speed), $\dot{V}O_2$ max, and indices of blood oxygen carrying capacity (Autumn et al., 1994; Bennett et al., 1984; Garland, 1993; Gleeson, 1991; Gleeson and Bennett, 1985; Gleeson and Dalessio, 1989; John-Alder et al., 1983; John-Alder et al., 1986a; Secor et al., 1992). Two populations of *Sceloporus merriami*, which differ in maximal sprint speed, apparently do not differ in treadmill endurance (Huey et al., 1990).

Within populations, treadmill endurance increases ontogenetically in most species of lizards (Garland, 1984, 1994b, unpubl.; Huey et al., 1990; see also Daniels and Heatwole, 1990) and in the two species of snakes that have been studied (Jayne and Bennett, 1990a; Secor et al., 1992), although not necessarily in a linearly allometric fashion (Garland and Else, 1987; Jayne and Bennett, 1990a). Positive static allometry occurs in garter snakes (Garland, 1988; Jayne and Bennett, 1990b).

Morphological, physiological, and biochemical correlates of individual differences in treadmill endurance have been studied in the lizards *Ctenosaura similis* (fig. 10.5) and *Ctenophorus nuchalis* (Garland, 1984; Garland and Else, 1987). Correlations of each variable with body mass were removed by computing residuals from regression equations. After this procedure, several underlying variables were shown to correlate significantly with endurance (e.g., $\dot{V}O_2$ max, thigh muscle mass, enzyme activities). Correlations with $\dot{V}O_2$ max and with thigh muscle mass occur in three of five species studied to date (Garland, 1984; unpublished data on *Callisaurus draconoides* and *Cnemidophorus tigris*; Garland and Else, 1987; John-Alder, 1984b). These studies were the first to document performance gradients for reptilian locomotion.

Treadmill endurance does not correlate with residual hindlimb length in *Sceloporus merriami* (Huey et al., 1990) or in hatchling *S. occidentalis* (Tsuji et al., 1989). However, a small ($r = .218$) but significant correlation exists between treadmill endurance and residual tail length in hatchling *Sceloporus occidentalis* (Tsuji et al., 1989). Treadmill endurance correlates positively with $\dot{V}O_2$ max in *Thamnophis sirtalis* (Garland and Bennett, 1990; Garland et al., 1990b).

Stamina can also be measured by chasing animals around a circular track at top speed until exhaustion and recording total distance and/or time run. Several species of lizards have been so tested, but generalities are not yet apparent (Bennett, 1980, 1989; Garland, 1993; Mautz et al., 1992). Studies of individual variation have also documented morphological and physiological correlates of maximal distance running (or crawling) capacity in both lizards (Garland, 1984, unpub.) and garter snakes (Arnold and Bennett, 1988; Dohm and Garland, unpub.) (see also Gatten et al., 1991, on alligators). Less useful measures of stamina, in terms of comparability and ecological relevance, can be obtained by holding animals in any type of container, prodding them to struggle, and recording the time until cessation of activity, loss of righting response, etc. (Daniels and Heatwole, 1990; Snyder and Weathers, 1977).

Sprint Speed. Sprint speed is the most commonly studied aspect of reptilian locomotor abilities, and a considerable body of research addresses the mechanistic basis of variation in sprinting. At this point, differences in body size and in relative limb length seem to be the most important causal factors.

Within populations of lizards and snakes, sprint speed generally increases with body size (mixed samples: Daniels and Heatwole, 1990; Garland, 1985; Huey, 1982a; Huey and Hertz, 1982; Huey et al., 1990; Losos, 1990c; Losos et al., 1989; Marsh, 1988; Secor et al., 1992; Sinervo, 1990; Snell et al., 1988; static allometry: Arnold and Bennett, 1988; Garland, 1988; Garland and Arnold, 1983; Jayne and Bennett, 1990b; Sinervo, 1990; Sinervo and Adolph, 1989; Sinervo and Huey, 1990; Tsuji et al., 1989). Several exceptions exist (Garland, 1984, unpub.; Brodie, 1989a), however, and the snake *Thamnophis sirtalis* shows a curvilinear allometry (Jayne and Bennett, 1990a).

Evidence for a relationship between speed and size is more equivocal in interspecific comparisons. In a phylogenetic analysis of fifteen Caribbean *Anolis* species, Losos (1990b) has shown that sprint speed and snout-vent length evolved together. By contrast, van Berkum (1986) found no relationship between sprint speed and size among seven species of Costa Rican *Anolis*. At higher taxonomic levels, no simple linear relationship between speed and size appears to exist (Garland, 1982, unpub.; but see Marsh, 1988, p. 131).

Biomechanical models predict a positive relationship between limb length and sprint speed (discussions in Garland, 1985; Losos, 1990b; Marsh, 1988). Indeed, most "cursorial" mammals have elongated legs resulting primarily from increased length of the distal elements (Garland and Janis, 1993; Hildebrand et al., 1985; Janis, in press; references therein). Cursorial lizards also exhibit elongated limbs, but, by contrast, all limb elements seem to increase in length, with no apparent regularity as to which element increases the most (Rieser, 1977).

Many studies have investigated whether the predicted positive relationship between limb length and sprint speed exists in lizards. Given the oft-observed correlation between size and speed, most studies remove the effect of size (see above) on both limb length and speed to examine whether relative limb length correlates with relative sprint speed. Intrapopulation studies have been evenly split: a correlation between relative limb length and sprint speed exists in *Tropidurus albemarlensis* (Snell et al., 1988; but see discussion below), *Sceloporus occidentalis* (Sinervo, 1990; Sinervo and Losos, 1991), *Sceloporus merriami* (Huey et al., 1990), and *Urosaurus ornatus* (D. B. Miles, pers. comm.), but not in *Ctenosaura similis* (Garland, 1984), *Ctenophorus (Amphibolurus) nuchalis* (Garland, 1985), *Leiolepis belliani* (Losos et al., 1989), or hatchling *Sceloporus occidentalis* (Tsuji et al., 1989). Positive interpopulational or interspecific correlations have been reported several times (Bauwens et al., in press; J. Herron and B. S. Wilson, pers. comm.; Losos, 1990c; Miles, 1987, pers. comm.; Sinervo and Losos, 1991; Sinervo et al., 1991; Snell et al., 1988).

Although several theories (e.g., geometric similarity, elastic similarity, dynamic similarity) have been proposed that predict the relationship between size and sprint speed, none adequately explains the available data for mammals or lizards (Chappell, 1989; Garland, 1985). The relationship between limb length, stride length, and sprint speed is perhaps simpler and more intuitive than these theories imply. Snell et al. (1988) argue that the relationship between body size and sprint speed in *Tropidurus albemarlensis* (pooling individuals of both sexes and from two populations) results from the correlation of both variables with hindlimb length, rather than there existing a direct relationship between body size and sprint speed. Stepwise multiple regression analysis indicated that, after allowing for the positive correlation between sprint speed and snout-vent length, individual variation in hindlimb length predicts a significant amount of variation in sprint speed. However, in a second analysis, after hindlimb length is removed, no relationship exists between size and sprint speed. The strong correlation ($r = .93$) between hindlimb length and mass in *Tropidurus* suggests extreme caution in interpreting these results (cf. Slinker and Glantz, 1985). Nonetheless, a reanalysis of data for fourteen species of *Anolis* (from Losos, 1990b, c) reveals a similar pattern: when residuals are taken from regressions on snout-vent length, hindlimb length and sprint speed are still significantly related, but when residuals are taken from regressions on hindlimb length, snout-vent length and speed are not significantly correlated (see also Bauwens et al., in press).

The relationship between other morphological variables and sprint speed has been less studied. Lizards are renowned for their ability to drop their tails to thwart predation; a number of studies have experimentally assessed the effect of tail loss on sprint speed (reviewed in E. N. Arnold, 1988; see also Russell and

Bauer, 1992). Many lizards with experimentally reduced tails run more slowly (Arnold, 1984a; Ballinger et al., 1979; Formanowicz et al., 1990; Pond, 1981; Punzo, 1982), but not *Phyllodactylus marmoratus* (which does not use its tail as a counterbalance: Daniels, 1983), *Sphenomorphus quoyii* (Daniels, 1985a), *Sceloporus merriami* (Huey et al., 1990), or the snake *Thamnophis sirtalis* (Jayne and Bennett, 1989). Although a negative effect on sprint performance may have long-term repercussions, the importance of tail loss in a given predator-prey encounter is probably more a function of predator distraction than of altered lizard escape speed (Dial and Fitzpatrick, 1984; Cooper and Vitt, 1991).

The biomechanics of legless locomotion are poorly understood (Gans, 1975; Jayne and Davis, 1991; Secor et al., 1992). Vertebral numbers may relate to interspecific differences in locomotor performance in snakes (Jayne, 1985, 1986, 1988a, b). Within a population of *Thamnophis radix*, numbers of body and tail vertebrae correlate in an interactive fashion with speed in juveniles (Arnold and Bennett, 1988). Relative tail length also may affect snake sprint speed (Jayne and Bennett, 1989).

The effect of muscle size and composition on sprint performance would seem to be an obvious area for study, but little work has been done to date. Gleeson and Harrison (1988) report significant inverse correlations between sprint speed and muscle fiber areas in desert iguanas (*Dipsosaurus dorsalis*). The low maximal speeds of chameleons appear at least partly related to their having slow-contracting muscles (Abu-Ghalyun et al., 1988; see also Peterson, 1984).

Sprint speed is also affected by temporary changes in body condition. Both gravidity and recent ingestion of food result in increased mass and decreased flexibility and so may have similar effects on sprint performance. Gravidity generally lowers sprint performance in both lizards and snakes (e.g., Brodie, 1989a; Cooper et al., 1990; Garland, 1985; Huey et al., 1990; Van Damme, Bauwens, and Verheyen, 1989). Population differences in the effect of gravidity on maximal sprint speed exist in *Sceloporus occidentalis* (Sinervo et al., 1991). Similarly, a full stomach has, in some cases, been shown to lower speed and/or endurance in lizards and snakes (Ford and Shuttlesworth, 1986; Garland and Arnold, 1983; Huey et al., 1984). Apparently, burst speed may be less sensitive to such effects than is endurance (cf. Cooper et al., 1990; Garland, 1985; Garland and Else, 1987). Further studies of the effects on locomotor capacities of recent feeding, especially in relation to models of optimal foraging, allocation of time and energy to foraging versus reproduction, and associated costs and trade-offs, should prove interesting. Brodie and Brodie (1990) used sprint speed as a bioassay for the effects of tetrodotoxin on garter snakes.

Two caveats must be kept in mind when considering investigations of sprint

speed. First, some animals appear not to sprint at top speed in a race track. For example, maximal reported speeds of desert iguanas (*Dipsosaurus dorsalis*) in race tracks (single fastest individuals) are 10.1 km/h (Bennett, 1980; higher speeds were reported for some other species), 18 km/h (Marsh, 1988; Marsh and Bennett, 1985), and 15.0 km/h (Gleeson and Harrison, 1988), whereas Belkin (1961) reports a maximal field speed of almost 30 km/h and J. A. Peterson (pers. comm.) reports observing similar speeds on a high-speed treadmill (compare also speeds recorded for *Uma notata* in the laboratory [Carothers, 1986] and the field [Norris, 1951]). Why some species do not perform well in a race track is unclear. Alternative techniques for measuring sprint speed, such as high-speed treadmills (J. A. Peterson, pers. comm.; Garland, unpubl.) may circumvent such problems.

Second, measuring acceleration in racetracks is much more difficult than obtaining sprint speed alone, because lizards must sit motionless just in front of the first photocell, then burst along the track when startled. Many species are not so cooperative (but see Carothers, 1986; Huey and Hertz, 1984a), instead struggling and running as soon as being placed in the track. It is unfortunate that measures of acceleration are difficult to obtain, because acceleration, as opposed to just maximal steady-state sprint speed, may be of prime importance in predator-prey interactions (Elliott et al., 1977; Huey and Hertz, 1984a; Webb, 1976).

Jumping. Biomechanical models suggest that body and muscle mass, limb length, location of center of mass, muscle composition, and behavior all can affect jumping performance (Alexander, 1968; Emerson, 1985; Losos, 1990b; Pounds, 1988). The biomechanics of jumping have been investigated only in the legless pygopodid lizard *Delma tinca* (Bauer, 1986) and in *Anolis carolinensis* (Bels and Theys, 1989; Bels et al., 1992).

Considerable variation in jumping ability exists both within and among lizard species (Losos, 1990c; Losos et al., 1989; Losos et al., 1991). Among fifteen species of *Anolis*, body size and jumping ability are positively related (Losos et al., 1991; Losos, unpubl.). Within species, jumping ability increases with size in *Leiolepis belliani* (Losos et al., 1989) and in seven species of *Anolis* (Losos et al., 1991, unpubl.). In addition, positive but nonsignificant relationships also exist in nine of eleven other species of *Anolis* (Losos, unpubl.).

With the effect of size removed, relatively long-legged species of *Anolis* jump relatively farther than do shorter-legged species. Lesser and negative effects of tail and forelimb length on jumping ability also exist in anoles (Losos, 1990c). By contrast, no relationship between relative limb length and jumping ability is evident in *Leiolepis belliani* (Losos et al., 1989). No differences have been de-

tected between males and females in *Leiolepis belliani* (Losos et al., 1989) or in *Anolis frenatus* (Losos et al., 1991), although sample sizes were small in the latter study.

Gliding and Parachuting. Gliding reptiles, including the enchantingly named *Icarosaurus* and *Daedalosaurus*, date to the Permian (Ricqles, 1980). Gliding abilities have been noted in a considerable number of snakes (e.g., *Chrysopelea*: Shelford, 1906; Heyer and Pongsapipatana, 1970) and lizards (*Ptychozoon*: Mertens, 1960; Heyer and Pongsapipatana, 1970; Marcellini and Keefer, 1976; *Holapsis*: Schiotze and Volsoe, 1959). The premier reptilian gliders are the members of the Southeast Asian genus *Draco*, which have evolved flight membranes formed from a patagium stretched over elongated and movable ribs. These lizards can glide for considerable distances; "flights" of over 20 m have been observed in nature, and 60 m in experimental trials (see Colbert, 1967). In other reptiles, gliding ability appears to be enhanced by the presence of flaps of skin along the sides of the body, neck, and tail and between the toes; the ability to increase ventral surface area; and the tendency to adopt an outstretched posture (Mertens, 1960; Oliver, 1951; Russell, 1979). Because the distinction is often not clear, we will use "gliding" throughout the paper to refer to both gliding and parachuting from one arboreal position to another or to the ground (see Rayner, 1981, 1987).

Several studies have experimentally investigated the role of morphology and behavior on gliding ability. Larger individuals of *Leiolepis belliani* have greater wing loading (i.e., mass/surface area) and fall more rapidly (Losos et al., 1989). Wing loading and glide performance were also inversely correlated in *Ptychozoon lionatum* (Marcellini and Keefer, 1976). When surface area is experimentally decreased (by preventing dorsoventral flattening in *Leiolepis belliani* [Losos et al., 1989] and tying lateral cutaneous folds to the body in *Ptychozoon lionatum* [Marcellini and Keefer, 1976]), gliding performance was diminished. The importance of body posture on rate of descent was suggested in *Leiolepis belliani*. Dead lizards, which tumbled rather than falling in a horizontal, outstretched position, fell faster than did live lizards. Further, for a given wing loading, live lizards fell slower, which suggests that behavioral adjustments, such as creating a concave (rather than flat) ventral surface while falling, enhance parachuting abilities (the snake *Chrysopelea ornata* also adopts a similar concave posture when falling [Shelford, 1906]). The importance of gliding as a means of moving through the environment is obvious, particularly in forests in which movement from tree to tree would otherwise require a lizard to climb into the crown or to the ground. Further, Oliver (1951) observed *Anolis carolinensis*

avoiding predators by jumping from trees, gliding to the ground, and running away. Similar behavior is displayed by a number of geckos (Russell, 1979), and perhaps, by spiny-tailed iguanas (*Ctenosaura similis*) over 1 kg in body mass (Garland, pers. obs.).

Conclusions. A variety of ecologically relevant measures of performance have been studied in lizards and snakes. Most attention has been focused on sprint speed, perhaps because it is relatively easy to measure. Although the effects of morphology and physiology on sprinting (and on gliding) capability are theoretically the simplest, we seem to have more empirical information on the mechanistic correlates of variation in endurance. For all measures of performance, the effect of many variables remains to be assessed. Other important aspects of locomotor performance, such as burrowing (Gans et al., 1978), climbing (Losos and Sinervo, 1989; Sinervo and Losos, 1991; see also Thompson, 1990, on rodents), and swimming ability (Bartholomew et al., 1976; Daniels and Heatwole, 1990; Gans, 1977; Gatten et al., 1991; Schoener and Schoener, 1984; Tracy and Christian, 1985; Turner et al., 1985; Vleck et al., 1981) have received little attention.

Performance → Behavior or Fitness/Ecology

Studies using quantitative data to correlate interspecific variation in locomotor abilities with ecology or behavior are relatively rare. In this section, we briefly summarize the data relating endurance and sprint capabilities to behavior, fitness, and ecology, and then address two topics in which the relevance of performance has been more extensively examined: the context-specificity of performance and the relationship of variation in performance capabilities to foraging mode.

Endurance, $\dot{V}O_2$ max, and Anaerobic Metabolism. The relevance of endurance capacity for squamate natural history is just becoming apparent (Garland, 1993, 1994). Treadmill endurance at 1.0 km/h appears to be related to average daily movement distance (cf. Garland, 1983) among nine species of lizards (table 2 of Hertz et al., 1988). Similarly, Loumbourdis and Hailey (1985) suggested a correlation between both active (not verified $\dot{V}O_2$ max) and resting metabolic rates and "lifestyle" of lizards, though further corroboration is necessary (see also Kamel and Gatten, 1983). Various adaptive explanations for the high aerobic capacities ($\dot{V}O_2$ max) of *Cnemidophorus tigris*, *Heloderma suspectum*, and *Varanus* species have been offered (Bennett, 1983; Bickler and Anderson, 1986; Garland, 1993; John-Alder et al., 1983). The uses of anaerobic metabolism in nature, and possible correlations between anaerobic capacities

and lifestyle in reptiles, have been reviewed elsewhere (e.g., Bennett et al., 1985; Gatten, 1985; Pough and Andrews, 1985a, b; Seymour, 1982, 1989; Ultsch et al., 1985).

Sprint Speed. Population differences in wariness have been documented in lizards (Bulova, in press; Shallenberger, 1970), but possible performance correlates have been studied only once. In more open areas on the eastern end of Isla Plaza Sur, Galapagos lava lizards (*Tropidurus albermarlensis*) are warier (i.e., they flee further and earlier when approached by humans) than are lizards from the more vegetated western end of the island (Snell et al., 1988). Lizards living in the more open areas are presumed to be more vulnerable to predation, although data on predation rates are lacking. Males from the eastern population are, indeed, faster than western males, but females do not differ; the morphological basis for the difference in speed among males is unclear.

Four studies have attempted to measure natural selection acting on individual variation in locomotor performance in the field (see Bennett and Huey, 1990). These constitute direct attempts to quantify fitness gradients (fig. 10.1) for reptilian locomotion. Jayne and Bennett (1990b) found that survivorship of garter snakes (*Thamnophis sirtalis*) was positively related to laboratory measures of both speed and distance crawling capacity, although not during the first year of life. R. B. Huey and colleagues (see also Tsuji et al., 1989; van Berkum et al., 1989) conducted a similar study of hatchling fence lizards (*Sceloporus occidentalis*), but the analyses are not yet complete. In both cases, comparisons of families of presumed full-siblings suggest that speed and stamina may be heritable (Garland, 1988; Jayne and Bennett, 1990a; Tsuji et al., 1989; van Berkum and Tsuji, 1987). Miles (1989, pers. comm.) reports significant directional selection on speed in *Urosaurus* lizards. Finally, A. E. Dunham, R. B. Huey, K. L. Overall, and colleagues are continuing a study of selection on locomotor performance in *Sceloporus merriami*, with preliminary results suggesting no significant selection on locomotor performance (pers. comm.). As with almost all studies of selection (Endler, 1986; Wade and Kalisz, 1990), interpretation of these studies is problematical because the causal basis for selection on sprint speed is not understood. In the absence of data on whether lizards and snakes actually use maximum abilities in nature and, if they do, whether variation in maximum abilities is biologically significant, a story can be devised for any result. This is not to suggest that selection studies are unimportant, but, rather, to urge that they be coupled with detailed analyses of natural history and possibly experimental manipulations (Greene, 1986; Hews, 1990; Pough, 1989; Sinervo et al., 1992).

Some information on fitness gradients can be obtained through laboratory studies or controlled trials in seminatural field enclosures (e.g., Schwartzkopf

and Shine, 1992). For example, in laboratory enclosures, Garland et al. (1990a) studied whether social dominance might be related to capacities for speed or stamina in *Sceloporus occidentalis*. In paired encounters between males competing for access to a basking site, winners were significantly faster than were losers, but did not have higher treadmill endurance (see also Hews, 1990; Wilson and Gatten, 1989; Wilson et al., 1989).

Context-Specificity of Performance. Evolutionary specialization to a particular "niche" may come at the expense of lowered fitness (including lower "effectiveness" [Gans, 1991] or energetic efficiency [e.g., Andrews et al., 1987]) in other "niches" ("the jack-of-all trades is master of none" idea [Huey and Hertz, 1984b; Jackson and Hallas, 1986]). If so, then one might predict that performance capability would be context-specific; species, for example, might perform a task best under conditions most similar to those they experience most often in nature (see also Bauwens et al., in press).

To test this idea, Losos and Sinervo (1989) measured sprint speed of four species of *Anolis* on different diameter rods. In nature, the long-legged *A. gundlachi* uses wide structures, whereas the short-legged *A. valencienni* often moves on narrow twigs; the other two species are intermediate in both respects. On wide perches, sprint speed and leg length were directly related among the species; however, on narrow rods, all four species had similar sprint abilities (fig. 10.6). It is understandable why the long-legged species do not use narrow structures in nature: their locomotor capabilities would be impaired. But why should short

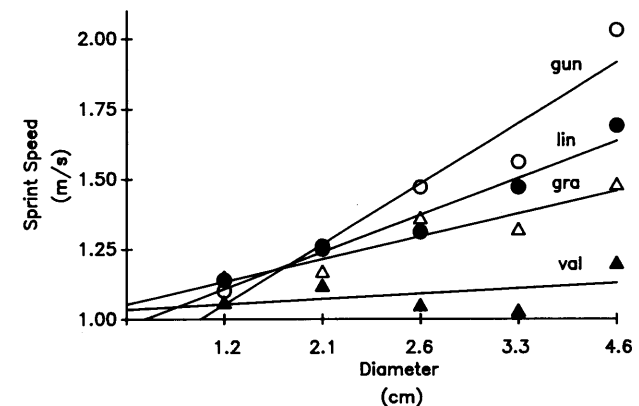


FIGURE 10.6 Interaction between locomotor performance ability and species identity for four species of *Anolis* lizards running on rods of varying diameter (modified from Losos and Sinervo, 1989). Species differences in maximal sprint speed are apparent only on larger rods. gun = *Anolis gundlachi*, lin = *A. lineatopus*, gra = *A. grahami*, val = *A. valencienni*.

legs evolve to utilize narrow structures? *Anolis gundlachi* can run as fast as *A. valencienni* on narrow structures without incurring the latter's 50% sacrifice in speed on broad structures. The answer probably lies in the species' ability to move without difficulty on narrow surfaces ("surefootedness" *sensu* Sinervo and Losos, 1991). In over 75% of the trials on the narrowest rod, *A. gundlachi* stumbled or fell off, whereas *A. valencienni* was much less affected. Consequently, *A. valencienni* seems to have traded the ability to move rapidly on broad surfaces for the ability to move without trouble on narrow ones.

A similar trade-off is apparent among four populations of *Sceloporus occidentalis* (Sinervo and Losos, 1991) and between *S. occidentalis* and *S. graciosus* (Adolph and Sinervo, in preparation). By contrast, relative sprint performance in two chameleon species is consistent across a range of surface dimensions (Losos et al., 1993). In both the *Anolis* and *Sceloporus* cases, field studies are needed to evaluate the relative ecological importance of maximum speed versus sure-footedness. Biomechanical studies should enlighten relationships between limb length, perch diameter, and sprinting (Alexander, 1968; Emerson and Koehl, 1990; Hildebrand et al., 1985; Pounds, 1988).

The foregoing studies underline the importance of measuring performance over a variety of appropriate conditions, of measuring several different aspects of performance, and of considering a variety of behaviors that may relate to performance abilities (cf. Bennett, 1989; Garland, 1993, 1994a, b; Huey and Hertz, 1984a; Sinervo and Losos, 1991).

Foraging Mode and Relative Clutch Mass. Lizards have traditionally been classified either as "sit-and-wait" or as "active" foragers (Pianka, 1966; Regal, 1983; Schoener, 1971), although the distinction represents extremes of a continuum rather than an actual dichotomy (appendix I of Garland, 1993; McLaughlin, 1989; O'Brien et al., 1990; Pietruszka, 1986). A variety of attributes distinguish the two foraging modes among terrestrial lizards. Sit-and-wait (or ambush) foragers tend to be stocky, have short tails, and carry relatively large clutches, whereas active (or "widely foraging" or "cruising") foragers often are slender, with long tails and relatively small clutches (Huey and Pianka, 1981; Vitt and Congdon, 1978; Vitt and Price, 1982; Perry et al., 1990). Relatively little intra-familial variation in foraging mode exists among lizards; hence, interspecific comparisons of foraging types often are confounded by phylogeny (Dunham et al., 1988). However, intrageneric (Huey and Pianka, 1981; Huey et al., 1984) and even intraspecific (Robinson and Cunningham, 1978) variation in foraging mode exists in lacertids (Perry et al., 1990).

The two foraging modes tend to differ in sprint speed and endurance in an expected manner; active foragers have greater endurance, but sit-and-wait for-

agers, which often capture prey by a quick lunge from an ambush site, often show greater sprinting ability (Huey et al., 1984). Further, in interspecific comparisons, foraging mode appears to be associated with differences in resource acquisition and reproductive rates (Anderson and Karasov, 1981, 1988; Karasov and Anderson, 1984; Nagy et al., 1984). Three studies have revealed some morphological and physiological correlates of differences in foraging mode and locomotor performance (Bennett et al., 1984; Garland, 1993, 1994b).

Nonetheless, with the following exceptions, few examples indicate tight relationship between morphology, performance, and foraging mode. Active foraging lizards appear to experience higher predation, and their longer tails may represent an adaptation by increasing the likelihood that a predator will grab the detachable tail, leaving intact the rest of the lizard (Huey and Pianka, 1981; Vitt, 1983). Among snakes, active foragers tend to have longitudinal stripes and flee when approached; longitudinal stripes can give the impression that a moving snake is stationary, making it easy for a predator to lose sight of a fleeing snake. By contrast, more sedentary species often have broken patterns and rely on crypsis or active defense to thwart predators (Jackson et al., 1976; Pough, 1976). Further, antipredator behavior (fleeing versus crypsis) and color pattern (blotched versus striped) are genetically correlated in *Thamnophis ordinoides* (Brodie, 1989b, 1993).

The relationships of clutch size, performance, and foraging mode are better established. Gravidity leads to decreased sprint speed and/or endurance in lizards (e.g., Cooper et al., 1990; Garland, 1985; Garland and Else, 1987; Sinervo et al., 1991; Van Damme, Bauwens, and Verheyen, 1989; but see Huey et al., 1990) and snakes (Brodie, 1989a; Jayne and Bennett, 1990a; Seigel et al., 1987). Thus, active foragers, which rely greatly on sustained locomotion, generally have evolved smaller relative clutch masses (RCM), which minimize these effects (Ananjeva and Shammakov, 1985; Dunham et al., 1988; Huey and Pianka, 1981; Magnusson et al., 1985; Vitt and Congdon, 1978; Vitt and Price, 1982; but see Henle, 1990; again, phylogeny is a confounding factor [Dunham et al., 1988]). Shine (1980), Seigel et al. (1987), and Van Damme, Bauwens, and Verheyen (1989) suggested that locomotor impairment correlated with RCM, but Brodie (1989a) argued that gravidity per se, rather than RCM, is the major cause of decreased locomotor capacities (see also Sinervo et al., 1991). In a similar vein, Shine (1988) argued, based on biomechanical considerations, that a given RCM would hinder snake locomotion more in aquatic than in terrestrial species. He thus interpreted the lesser RCM of aquatic species as adaptive.

A linear relationship between gravidity, decreased sprinting abilities, and increased mortality cannot be assumed. For some species, gravid females may indeed be more vulnerable to predation (Shine, 1980; references in Cooper et al.,

1990), but in other species behavioral shifts may compensate for decreased locomotor performance. For example, the lizards *Lacerta vivipara* (Bauwens and Thoen, 1981) and *Eumeces laticeps* (Cooper et al., 1990), and the snake *Thamnophis ordinoides* (Brodie, 1989a), alter their behavior when gravid, becoming less active and more reliant on crypsis and aggression for defense. Indeed, no increase in mortality was observed for gravid *Lacerta vivipara* (Bauwens and Thoen, 1981; see also Schwartzkopf and Shine, 1992).

Conclusions. Relationships between performance ability and ecology or behavior have been little explored, either intra- or interspecifically. When studies have been conducted, they often are correlational and do not directly examine the causal basis of any correlation. They are thus not able to distinguish selection and sorting (*sensu* Vrba and Gould, 1986). As well, phylogeny confounds most analyses to date. Relationships of foraging behavior, reproductive state, and locomotor performance, however, do seem reasonably well established.

Morphology → Behavior or Fitness/Ecology

Biologists comparing species have long noted correlations between form and lifestyle or habitat (e.g., Bock and von Wahlert, 1965; Gans, 1988; Luke, 1986; Rayner, 1981, 1987; Ricklefs and Miles, chap. 2, this volume; Van Valkenburgh, chap. 7, this volume; references in Wainwright, 1991) and have taken such relationships as evidence that particular morphologies are adaptations (*sensu* Gould and Vrba, 1982) for particular lifestyles or habitats (Harvey and Pagel, 1991). Indeed, such comparisons and interpretations are at the heart of traditional ecological morphology (e.g., Norberg, chap. 9, this volume). Rarely, however, does evidence exist demonstrating that morphological differences actually lead to differences in performance abilities that are appropriate for different habitats. Here, we review studies that have related reptilian locomotor morphology to behavior or ecology, and evaluate the extent to which locomotor performance represents the mechanistic basis of such relationships.

Limb Length and Habitat Use. Several studies have correlated interspecific or interpopulation variation in limb length with differences in microhabitat use or behavior. Usually, however, the effect of variation in limb length on performance and the relevance of differences in performance to variation in habitat or behavior are not investigated. In addition, differences in limb proportions (often expressed as ratios) can be confounded by differences in size (see "Allometry and its importance" above). We first offer a brief discussion of locomotor allometry in lizards.

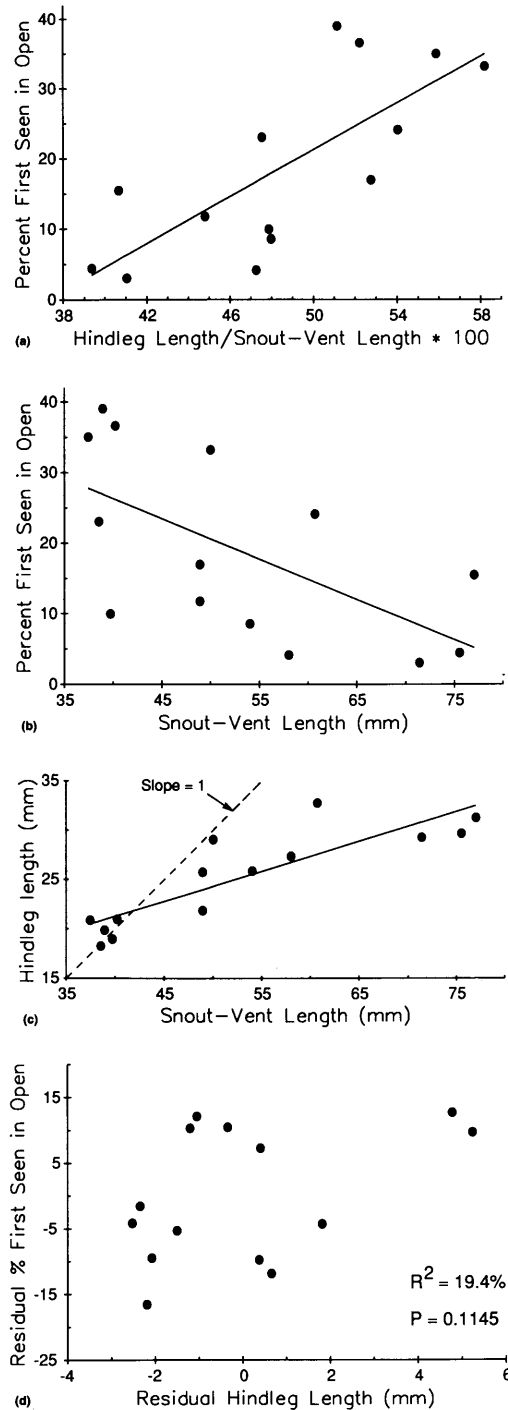
Within most lizard species, hindlimb length shows negative allometry (e.g., Garland, 1985; Kramer, 1951; Marsh, 1988; Pounds et al., 1983), but positive

allometry occurs in a few species (Dodson, 1975; Pounds et al., 1983). Interspecifically, negative allometry of hindlimb length is common among lizards (e.g., figs. 10.7c, 10.8c below; Losos, 1990b). A number of adaptive explanations have been offered to explain these patterns. For example, Dodson (1975) proposed that the positive ontogenetic allometry in two species of *Sceloporus* represented an adaptation for increased home range size and movement in adults, although the underlying mechanism (e.g., increased mobility) for such a relationship was neither specified nor measured. Pounds et al. (1983) hypothesized that positive ontogenetic allometry in *Sceloporus woodi* might relate either to a shift to more arboreal habitats or to reliance on sprinting to avoid predation. Because sprint speed usually increases ontogenetically (see above), Pounds et al. (1983) interpreted the negative allometry observed in four other iguanid species as a means of compensating for the lesser sprinting ability of smaller individuals by increasing the length of their hindlimbs (cf. Grand, 1991, on antelope). Sprint speeds, however, were not measured, and Garland (1985) has argued that data on scaling of limb dimensions alone are inadequate to infer scaling of sprint speed.

The importance of explicitly considering allometry is apparent in a study of fourteen species of diurnal *Ctenotus* skinks in Australia. Pianka (1969) found that relative hindleg length (length of one hindleg/snout-vent length) correlated positively with use of open space (fig. 10.7a). Pianka (1986) inferred that long legs must enhance sprint speed and thus are beneficial in open spaces, whereas, in dense vegetation, long legs actually impede efficient locomotion (see also Jakšić and Nuñez, 1979). (In fact, some *Ctenotus* do fold their legs against the body and use serpentine locomotion to move through clumps of spinifex grass [James, 1989].) Unfortunately, the relationship between relative limb length and habitat is confounded by body size. Larger species use less open habitats (fig. 10.7b) and have relatively shorter legs (fig. 10.7c). When these correlations with body size are removed by regression analysis, a relationship between residual use of open space and residual hindleg length is suggested, but nonsignificant ($P < .12$; fig. 10.7d).

Among species of nocturnal Australian geckos, use of open spaces and relative hindleg length are uncorrelated (data from Pianka, 1986; contrary to analyses of a smaller data set in Pianka and Pianka, 1976; fig. 10.8a). In this case, however, use of open space is not significantly related to svl ($r^2 = .025$, $P = .6652$; fig. 10.8b). Analysis of residuals from regressions on svl (a conservative procedure) also indicates that open-space use is not significantly predicted by relative leg length (figs. 10.8c, d). Both of these examples (*Ctenotus*, nocturnal geckos) deserve phylogenetic reanalyses when suitable phylogenies become available.

A number of other studies have investigated whether a relationship exists between limb proportions and habitat. Longer-legged taxa use more open (includ-

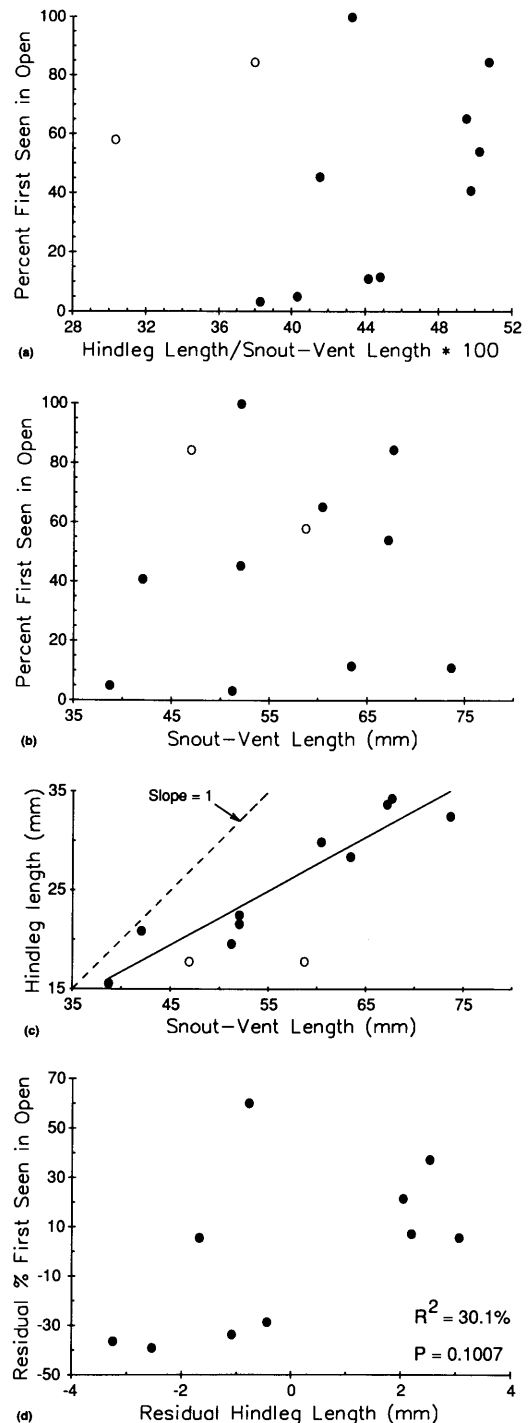


ing large boulders) and/or terrestrial habitats among populations of *Sceloporus woodi* (Jackson, 1973b), among populations in a cline connecting *Liolaemus platei* and *L. lemniscatus* (Fuentes and Jaksic', 1980), and between species of *Sceloporus* (Jackson, 1973a, b) and *Lacerta* (Darevskii, 1967). By contrast, in a study of North American temperate lizard communities, Scheibe (1987) found that large, bulky, and long-legged sit-and-wait foragers occupied extensively vegetated habitats, whereas small, slender, and short-legged active foragers used more open habitats. However, this study is a prime example of the importance of conducting comparative analyses in a phylogenetic context: of the three families represented in the study, only the Iguanidae (twenty-one of twenty-nine species in the study) exhibit substantial variation, most of which is distributed among genera. This phylogenetic non-independence leads, in effect, to a substantial inflation of the inferred degrees of freedom, possibly leading to spurious significant results (cf. Garland et al., 1991). No relationship between limb length and habitat use is evident among *Liolaemus* (Jaksic' et al., 1980) or Brazilian cerrado lizards (Vitt, 1991).

Several other studies have looked for correlates of limb length in lizards. Ananjeva (1977) found that among five species of Russian *Eremias*, limb proportions were related to locomotor behavior (e.g., climbing, burrowing). In addition, insular populations of lacertid lizards in the Adriatic Sea generally have shorter legs than do mainland populations, except on islands with steep cliffs. Kramer (1951) suggested that the lack of predators on islands and the need for clinging and jumping ability on cliffs is responsible for these patterns. Carlquist (1974) discussed other examples of variation in limb proportions.

Interpreting the foregoing results is difficult, because the functional consequences of morphological variation are unknown. Further, the ecological relevance of functional differences (assuming they exist) is usually speculative. Nonetheless, several studies have related limb morphology, functional capabilities, and habitat use. Laerm (1974) compared two species of basilisks which differed in their use of aquatic habitats. The more aquatic *Basiliscus plumifrons*, which has longer legs and wider toe fringes (see below), can run more quickly on water than can *B. vittatus*, which is of similar size.

FIGURE 10.7 (a) Positive relationship between use of open microhabitats and relative hindleg length for 14 species of diurnal *Ctenopus* skinks in Australia (Pianka, 1969; revised data from Pianka, 1986, appendices C.3 and G.3). (b) Negative relationship between percentage first seen in open and snout-vent length, a measure of body size. (c) Deviation from geometric similarity (dashed line) for relationship between hindleg length and snout-vent length. Solid line is least squares linear regression. (d) Nonsignificant relationship between residual percentage first seen in open and residual hindleg length.



Williams (1972) coined the term “ecomorph” to refer to the radiation of *Anolis* lizards in the Greater Antilles. A set of morphologically distinctive species (termed ecomorphs and named for the microhabitat they most commonly use; e.g., “trunk-crown”) occurs on each of the Greater Antilles (i.e., Cuba, Hispaniola, Jamaica, and Puerto Rico [Mayer, 1989; Williams, 1972, 1983]). Comparison of island faunas indicates that not only are the same morphological types present on each island, but that morphologically similar species also are similar in ecology and behavior (Losos, 1990a, b; Moermond, 1979a, b; Rand and Williams, 1969; Williams, 1972, 1983). Although *Anolis* phylogeny is controversial (Burnell and Hedges, 1990; Cannatella and de Queiroz, 1989; Guyer and Savage, 1986, 1992; Williams, 1989), at least three independent radiations have occurred on Jamaica, Puerto Rico, and Cuba-Hispaniola (Williams, 1983).

The ecomorph types differ morphologically in a number of characters, and figure 10.9 confirms that members of each ecomorph type are more similar morphologically to other members of that ecomorph on other islands than they are to more closely related species on the same island (Loso, 1992). Thus, parallel or convergent evolution has occurred. The ecomorphs also differ ecologically (perch height, perch diameter, and distance to the nearest available perch) and behaviorally (frequency of movements, display rate, distance jumped, and relative proportion of runs, jumps, and walks; Losos, 1990a, b; Moermond, 1979a, b; Rand, 1964, 1967; Schoener and Schoener, 1971a, b).

The “habitat matrix” model (Moermond, 1979a, b, 1986; Pounds, 1988) suggests that ecomorphological radiation is driven by adaptation in locomotor morphology and behavior: *Anolis* alter their behavior in different microhabitats; as species evolve habitat specializations they also evolve morphologies appropriate for the behaviors they use. More specifically, the habitat matrix model predicts that as the distance to the nearest perch increases, lizards should jump less frequently but over longer distances; as the surface becomes narrower, lizards should be forced to move more slowly and carefully. Consequently, limb length should correlate with perch diameter and with distance to the nearest perch. Data from twenty-eight species of Costa Rican, Hispaniolan, Jamaican, and Puerto

FIGURE 10.8 (a) Nonsignificant relationship between percentage first seen in open and relative hindleg length for 12 species of nocturnal geckos in Australia (Pianka and Pianka, 1976; revised data from Pianka, 1986, appendices C.3 and G.3). Following Pianka and Pianka (1976, p. 131), two species (open circles) are excluded from subsequent regression analyses. (b) Nonsignificant relationship between percentage first seen in open and snout-vent length. (c) Deviation from geometric similarity (dashed line) for relationship between hindleg length and snout-vent length. Solid line is least squares linear regression. (d) Nonsignificant of relationship between residual percentages first seen in open and residual hindleg length.

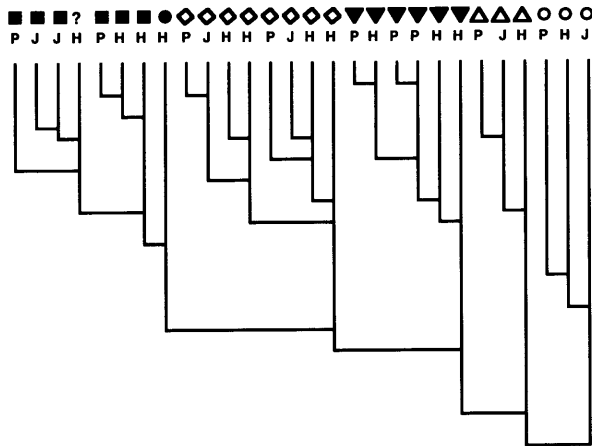


FIGURE 10.9 UPGMA phenogram of the position of *Anolis* lizard species in a multidimensional morphospace (from Losos, 1992). Variables analyzed were forelimb length, hindlimb length, tail length, mass, and lamellae number (all with the effect of snout-vent length removed via computation of residuals from least squares linear regressions), and snout-vent length itself. Members of each ecomorph type (indicated by the different symbols) are more similar morphologically to other members of that ecomorph on other islands than they are to more closely-related species on the same island. Thus, parallel or convergent evolution has occurred.

Rican *Anolis* support these predictions (Losos, 1990b, c, unpubl.; Moermond, 1979a, b; Pounds, 1988).

The predictions of the habitat matrix are predicated on the assumption that variation in morphology affects performance, which is related to differences in ecology and behavior. Studies summarized above (see “Morphology → Performance”) support this assumption. Relative sprinting and jumping abilities (with the effect of size removed) are related to relative limb length. In turn, variation in performance capability correlates with differences in locomotor behavior and microhabitat use (Losos, 1990a, b).

Nonetheless, it is surprising that only a weak relationship was found between absolute performance ability and ecology or behavior. One might expect that an organism’s absolute running and jumping abilities should be important in determining its ecology and behavior, rather than whether it can run or jump well for its size (cf. Huey and Bennett, 1987, p. 1106; “Discussion” in Garland, 1994a, b). Perhaps relative limb length affects ecology and behavior via a relationship with some other aspect of performance, such as endurance or energetic costs of locomotion (Autumn et al., 1994; Full et al., 1990; Full, 1991; Garland and Janis, 1993; John-Alder et al., 1986a; Strang and Stuedel, 1990; references therein). In this scenario, relative jumping and sprinting abilities would also be

correlated with limb length but not necessarily causally involved in the morphology → ecology relationship. A phylogenetically based path analysis (cf. Arnold, 1983) might help to tease apart these relationships.

More generally, the relationships between morphology, performance, and ecology may not be constant across microhabitats (see “Context-Specificity of Performance” above). Rather, species might be adapted to perform best in their own microhabitat, and different microhabitats might select for the optimization of different performance capabilities. Performance tests made under homogeneous conditions might thus obscure why particular morphologies are appropriate for particular “niches.”

A final caveat concerning the functional and adaptive significance of limb length is in order. Muth (1977, p. 718), in a study of *Callisaurus draconoides*, which occupies open areas in often extremely hot North American deserts, concluded that: “Long legs also may function to increase the height of the body in the elevated posture, and to exploit the convective heat loss regime” (see also Arnold, 1984b; Greer, 1989, p. 33). Thus, long limbs may be advantageous both for reducing the threat from predators and for reducing heat load, both of which are likely to be higher in open as compared with closed microhabitats. Given that limb length may affect several abilities (e.g., sprinting, climbing, jumping, moving through grass, thermoregulation, push-up displays), that it varies among individuals and among populations (e.g., Bulova, in press), and that it correlates strongly with both body size and phylogeny, integrated analyses of the evolution of limb length are warranted.

Limbleness. Elongation of the body and loss of the fore- and/or hindlimbs has evolved at least twelve times among squamate reptiles (Edwards, 1985). With the exception of snakes, most legless squamates are either fossorial, use burrows, or shelter under objects on the ground (Gans, 1975); Walls (1942) has argued that snakes evolved from burrowing forms. Several forms of limbless locomotion exist; lateral undulation, however, is common to most limbless vertebrates (Gans, 1975). Undulatory locomotion is also used by some limbed squamates, which fold their legs against the body while moving through fluid (e.g., water, sand) or tangled environments. The evolutionary origin of limblessness appears usually to be associated with the utilization of narrow openings and crevices (Gans, 1975; Gans et al., 1978; Shine, 1986), although in some circumstances nonfossorial locomotor performance may be enhanced by using undulatory locomotion (as in some large Australian skinks; John-Alder et al., 1986a; Garland, pers. obs.). An analysis of the performance capabilities of a series of related species varying in limb dimensions might shed valuable light on the evolution of limblessness.

In snakes, the energetic cost of locomotion during lateral undulation is similar to that predicted for a quadrupedal lizard (or mammal) of similar size (Autumn et al., 1994; John-Alder et al., 1986a), whereas the cost of concertina locomotion is significantly higher (Walton et al., 1990; but see Dial et al., 1987) and the cost of sidewinding significantly lower in at least one species (Secor et al., 1992). As determined on a motorized treadmill, maximal aerobic speeds, and hence endurance capacities at certain speeds, may be rather low in snakes (Garland, 1988; Jayne and Bennett, 1990a, b; Walton et al., 1990; but see Secor et al., 1992) as compared with some lizards of similar size (e.g., Garland, 1984, 1994b; Garland and Else, 1987; John-Alder and Bennett, 1981; John-Alder et al., 1986a). Part of this difference may be related to temperature (cf. Garland, 1994b): existing data for snakes have been taken at temperatures (30°C) somewhat lower than those at which lizards have been measured (35–40°C); however, species from both groups have been measured at or near their mean field-active body temperature.

Toe Fringes. Toe fringes, composed of laterally projecting elongated scales, have evolved at least twenty-six times within seven lizard families (Luke, 1986). The evolution of fringes has been associated primarily with the occupation of windblown sand or water habitats (Luke, 1986). Presumably, fringes work by providing increased surface area and hence less slippage on fluid substrates (Laerm, 1973), and may be more important during acceleration than at maximal speed, when slippage may be minimal (Carothers, 1986, p. 872). Carothers (1986) demonstrated that when the fringes of *Uma scoparia* were removed, the lizards ran more slowly and with lower acceleration on sandy, but not on rubber, surfaces (also see discussion of Laerm's [1974] study of basilisks under "Limb Length and Habitat Use" above).

Conclusions. Although a wealth of data indicate that locomotor morphology and ecology are related among reptiles, we have little hard evidence about the causal basis of this relationship. Information on the ecological consequences of variation in performance abilities and whether the morphology-performance-ecology relationship is constant among habitats is necessary to help elucidate these correlations. Such integrative studies conducted within populations are particularly notable in their absence.

DISCUSSION

Biologists have for many years gathered data documenting relationships between morphology and ecology, as several chapters in this volume attest. Some studies merely describe correlations without considering directly the mechanism by which morphology, physiology, and biochemistry are transduced into be-

havior and ecology. Other studies have argued, sometimes through the use of biomechanical or physiological models (e.g., Emerson et al., chap. 6, this volume; Norberg, chap. 9, this volume; Wainwright, chap. 3, this volume), that morphology must relate to ecology through its effect on organismal performance abilities, but have not actually measured performance. The idea that morphology affects fitness and ecology only through its effects on performance has been formalized in the paradigms discussed above (Arnold, 1983; Emerson and Arnold, 1989; "Introduction" above; fig. 10.1).

The Importance of Behavior

Studies integrating measurements of morphology, performance, behavior, and ecology are rare but increasing in frequency. Those now available indicate that the morphology → performance → fitness paradigm is indeed a useful one for examining natural selection and adaptation in the ecological morphology of reptilian locomotor performance. The simplicity of the paradigm makes it experimentally tractable, but also incomplete. In particular, the role of behavior and habitat must be considered (see "Introduction" above; figs. 10.2, 10.3).

By way of example, consider the role of behavior relative to morphology in gliding reptiles. Numerous arboreal species have evolved structures that increase surface area and hence increase gliding capabilities. However, the most widespread adaptation for increasing gliding ability is a behavioral one: when falling, arboreal species of squamate reptiles, amphibians, and mammals adopt an outstretched posture that maximizes surface area and stability (Oliver, 1951; Russell, 1979). In an early study, Oliver (1951) compared the falling behavior of the arboreal *Anolis carolinensis* to that of the more terrestrial *Sceloporus undulatus*. The anole immediately adopted the outstretched position and landed relatively unharmed; the fence lizard, by contrast, cycled its limbs in an attempt to run and landed forcefully. In a considerably more elegant study, Emerson and Koehl (1990) compared the role of posture and morphological modifications, such as flaps of skin between the legs and toes, in model treefrogs in a wind tunnel. They found that the effect of behavioral and morphological features exhibited by flying frog species, when tested independently, often had quite different effects on the performance of the models. Further, the effect of posture was dependent on morphology.

We have argued that natural selection does not act directly on performance ability, but rather on what an organism does (see "Introduction" above). Selection can act on performance only when individuals are behaving in the same way (e.g., trying to escape from a predator by running away as quickly as possible) and some individuals are better than others, due to their higher performance abilities; otherwise, selection will act on the differences in behavior. Thus, behavior is

a filter through which performance is related to fitness (Garland et al., 1990b), and performance is itself a filter through which morphology is transduced (cf. Ricklefs and Miles, chap. 2, this volume) to determine behavioral options (Garland, 1994a). Behavior can affect the performance → fitness link in two general ways: by negating advantages in performance ability, and by compensating for decrements in ability.

An example of behavior making performance differences irrelevant is presented in a study of crypsis in the Pacific treefrog, *Pseudacris regilla*, which occurs in two color morphs, green and brown. Morey (1990) investigated whether frogs would choose to sit on substrates matching their color, and whether substrate matching affects susceptibility to predation by garter snakes, *Thamnophis elegans*, in laboratory trials. Individual frogs tended to select substrates matching their own color. Laboratory trials were conducted in which one frog matched the substrate and a second did not. Indeed, in the ten trials in which frogs did not move, the snake chose the nonmatching frog nine times. However, in eighteen trials, one of the frogs moved and was immediately attacked regardless of whether its color matched the background. In this example, color gives a performance advantage, crypsis, which leads to increased prey survival only when coupled with the appropriate behavior (nonmovement).

That alterations in behavior can compensate for decreased performance ability has been demonstrated in several contexts. Lizards compensate for diminished locomotor abilities at lower body temperatures either by increasing their approach distance (i.e., the distance at which they will flee from a potential predator) (Rand, 1964; Shallenberger, 1970; but see Bulova, in press) or by switching from flight to aggressive defense (Crowley and Pietruszka, 1983; Hertz et al., 1982; see also Arnold and Bennett, 1984; Schieffelin and de Queiroz, 1991). Lizards and snakes with decreased locomotor abilities due to tail loss (Ballinger, 1973; Dial and Fitzpatrick, 1984; Formanowicz et al., 1990), gravity (Bauwens and Thoen, 1981; Formanowicz et al., 1990), a full stomach (Herzog and Bailey, 1987), or exhaustion (Arnold and Bennett, 1984; Garland, 1988) similarly alter their behavior. In some cases, these behavioral shifts may suffice to eliminate completely the effect of decreased performance on survival (references in Brodie, 1989a; but see references in Cooper et al., 1990; Schwartzkopf and Shine, 1992).

Behavior also acts as an intermediate filter in the performance → fitness link in the context of habitat selection. For example, performance is clearly context-dependent—maximal capabilities are only valuable in habitats in which they can be used. Considering the thermal environment, Waldschmidt and Tracy (1983) demonstrated that *Uta stansburiana* utilize microhabitats that allow them to maintain body temperatures at which they can sprint fastest (cf. Adolph, 1990a;

Christian and Tracy, 1981; Grant, 1990; Grant and Dunham, 1988; Hertz et al., 1988). As the day proceeds, the thermal regimen of microenvironments changes, and the lizards tend to alter their position to maintain their temperature. The role of the structural environment is apparent in *Anolis* communities, where species tend not (but see Huey, 1983) to use habitats in which their locomotor abilities are compromised (see above, "Limb Length and Habitat Use").

Evolutionary adaptation is also mediated via habitat use (Dunson and Travis, 1991; Huey, 1991). In *Anolis* lizards, for example, the optimal temperature for locomotor performance has apparently evolved to match the thermal regimen of their environment (van Berkum, 1986), although some agamid, scincid, and *Sceloporus* lizards are more conservative (Crowley, 1985a; Garland et al., 1991; Hertz et al., 1983; van Berkum, 1988). Similarly, the habitat matrix model (see above) predicts that species utilizing different microhabitats will alter their behavior accordingly and that appropriate morphologies will evolve subsequently. Caribbean anoles exhibit all three components of the model: they shift habitat use in response to a number of factors, including climate and the presence of competitors (e.g., Moermond, 1986; Schoener and Schoener, 1971a, b; and see above); alter their locomotor behavior in different environments (Losos, 1990a; Moermond, 1979a, b; Pounds, 1988); and have evolved appropriate morphologies for their locomotor behavior (see above). Behavioral changes do not always precede changes in morphology and performance abilities, however (cf. Burggren and Bemis, 1990, p. 221). For example, Russell (1979) has shown that the enlarged lateral body folds used by some geckos in parachuting probably originally evolved to enhance crypsis (i.e., they are an exaptation, *sensu* Gould and Vrba, 1982). Similarly, the ability to flatten dorsoventrally in *Leiolepis belliani* may have evolved either as a means of thermoregulation or for social displays; the gliding ability that it entails seems of little significance to this beach-dwelling lizard (Losos et al., 1989). Similarly, the evolution of long legs for thermoregulatory purposes (cf. Muth, 1977; see above, "Limb Length and Habitat Use") might preadapt a lizard for the evolution of high sprint speed (cf. Gans, 1979, on "momentarily excessive construction"). Finally, the agamid *Calotes versicolor* has the ability to swim effectively, but when dropped in water, it swims effectively for a few moments and then becomes disoriented, cycles its limbs ineffectively, attempts to breathe while underwater, and eventually sinks and walks around aimlessly on the bottom (Gans, 1977)! Apparently, this lizard has the functional ability to swim, but not the appropriate behavior to use this ability.

Trade-offs and Correlations of Locomotor Abilities

Potential trade-offs and constraints are of major concern in evolutionary biology, behavioral ecology, and comparative morphology and physiology (e.g., Ar-

nold et al., 1989; Barbault, 1988; Carrier, 1987, 1991; Congdon and Gibbons, 1987; Derrickson and Ricklefs, 1988; Feder and Londos, 1984; Garland and Huey, 1987; Grant and Dunham, 1988; Halliday, 1987; Maynard Smith et al., 1985; Miles and Dunham, 1992; Moermond, 1979b; Rose et al., 1987; Shine, 1988; Sinervo and Licht, 1991; Townsend and Calow, 1981). With respect to locomotion, performance of several functions may be correlated if the functions share a common mechanistic basis (cf. Emerson and Koehl, 1990). Such correlations may limit potential evolutionary pathways and prevent taxa from optimizing several performance abilities simultaneously (cf. Arnold, 1987, 1988; Brodie and Garland, 1993; Emerson and Arnold, 1989). However, predicting the existence of trade-offs based on first principles is not always easy. For example, contrary to simple models suggesting a necessary trade-off based on a dichotomy of fast versus slow muscle fiber types (cf. Gans et al., 1978; Pennycuik, 1991), speed and stamina are not negatively correlated at the level of individual variation (Garland, 1984, 1988; Garland and Else, 1987; Jayne and Bennett, 1990a; Secor et al., 1992), nor are they negatively genetically correlated in either *Thamnophis sirtalis* (Garland, 1988; see also Brodie, 1989b, 1992, on speed and distance crawled in *T. ordinoides*) or *Sceloporus occidentalis* (Tsuji et al., 1989).

Among species of *Anolis*, sprinting, jumping, and clinging ability are positively correlated, in part because all increase with body size (Losos, 1990b, c). With the effect of size removed by computing residuals, however, relative sprinting and jumping ability are still positively correlated, presumably due to the positive relationship of both to relative hindlimb length (Losos, 1990c). These correlations suggest that the evolution of sprinting and jumping ability is likely to be tightly linked. Consequently, the ability of *Anolis* to adapt in some ways to particular microhabitats may be constrained. Similarly, anole species adapt to utilize narrow surfaces such as twigs by evolving short limb length (Losos, 1990a; Williams, 1983), thus trading the ability to move quickly on broad surfaces for enhanced ability to move without difficulty on narrow surfaces (Losos and Sinervo, 1989). As a result, anoles cannot adapt to utilize narrow surfaces and still be able to make long jumps between perches.

Trade-offs may also occur between different types of performance. Chameleons, for example, have specialized for one locomotor task, grasping and moving upon extremely narrow surfaces, at the expense of another, sprint speed. Presumably, changes in the muscle architecture have played an important role in mediating this trade-off (see also Abu-Ghalyun et al., 1988).

Ecological circumstances may also dictate when correlations arise and when they are broken. For example, change in body size may be the path of least resistance when selection is for increased speed, generating among-population correlations of all traits that scale with size. Indeed, body size is often one of the

most heritable traits within populations of many species (Falconer, 1989). In the case of arboreal or cliff-dwelling (cf. Kramer, 1951) species, however, an increase in body size might be selected against, resulting instead in an evolutionary increase in *relative* limb length.

CONCLUSIONS AND SUGGESTIONS FOR THE FUTURE

Our understanding of the ecological morphology of reptilian locomotor performance has increased greatly in the last decade. Many data have been gathered and a unified and general theoretical framework is coming into existence. This framework envisions measures of whole-animal performance as central for attempting to link morphological, physiological, or biochemical variation with behavior, fitness, or ecology. Nevertheless, many relatively simple ideas and hypotheses remain untested or understudied, for example, whether a trade-off between speed and stamina is ineluctable; whether and why limb length correlates with habitat characteristics; the selective importance of ability to recover from exhaustive exercise (cf. Gatten and Clark, 1989; Gatten et al., 1992; Gleeson, 1991; Pough et al., 1992); and possible relationships between locomotor abilities, vagility, and genetic variation (Gorman et al., 1977). Entire groups of reptiles are virtually unstudied (e.g., turtles; but see Dial, 1987; Janzen, 1993; Miller et al., 1987; Wyneken and Salmon, 1992; Zani and Clausen, in press). Studies of performance gradients, relating individual variation in morphology to performance, have been quite successful, but can become much more sophisticated (cf. work in mammalian exercise physiology). Fitness gradients, relating performance to fitness within populations, are starting to be quantified. However, quantitative data on field behavior, as derived from focal animal observations, are uncommon, making it difficult to identify possible selective agents responsible for correlations between laboratory locomotor performance and fitness/behavior/ecology. The lack of quantitative data on field behavior limits both comparisons among species and studies of natural selection (Bennett and Huey, 1990; Garland, 1993; Pough, 1989). For example, it has never even been documented that lizards with greater capabilities for sprinting (as measured in the lab) actually run faster in nature (cf. Garland, 1993; Hertz et al., 1988).

We predict that the next decade will continue to see exciting empirical and conceptual advances, aimed primarily at understanding the evolution of organismal performance (cf. Garland and Carter, 1994). Techniques for sophisticated measurements of locomotor performance and for quantitative genetic (Boake, 1994; Brodie and Garland, 1993) and phylogenetic analyses are now in place and awaiting integrated application. At present, these techniques are still novel enough to merit study in their own right. Soon, however, state-of-the-art studies will involve experimental, quantitative genetic, and phylogenetic analyses of

measurements of morphology, performance, behavior, and fitness (or "adaptedness," when comparing populations or species).

In several cases, certain data sets already exist in partial form; these matrices can be filled in relatively easily. For example, relatively standardized techniques for measuring sprint speed have now been developed, and data on maximal speeds are now available for more than one hundred species of lizards; it is time to relate such data to morphology and to behavior and ecology (cf. Garland et al., 1988; Garland and Janis, 1993; Janis, in press; Losos, 1990b, c). In many cases, the most outstanding need is for quantitative data on field behavior. Comparisons would be greatly facilitated by standardization of methods for taking quantitative measurements of ecology and behavior (e.g., home ranges, movement rates, distances, speeds in nature; cf. Case, 1979; Cooper and Guillette, 1991; Garland, 1993; Huey and Pianka, 1981; Magnusson et al., 1985; Moermond, 1979a, b; Pietruszka, 1986). Another unresolved issue is the extent of behavioral compensation for changes in performance due to a full stomach, gravidity, or lowered body temperature. Behavioral adjustments related to changes in performance due to size and/or age also warrant study (cf. Grand, 1991; Pough and Kamel, 1984; Pounds et al., 1983; Taigen and Pough, 1981). How often does behavior shield performance from the direct effects of selection (fig. 10.2; Garland, 1994a; Garland et al., 1990b)?

Future comparative studies must deal directly with phylogenetic effects (Brooks and McLennan, 1991; Garland et al., 1991, 1992, 1993; Harvey and Pagel, 1991; Lauder, 1991; Losos and Miles, chap. 4, this volume; Lynch, 1991; Miles and Dunham, 1992; Pagel, 1993). As well, many existing studies warrant reanalysis with phylogenetically based methods. Computer programs are now available to do so (e.g., Garland et al., 1993; Lynch, 1991; Martins and Garland, 1991; A. Purvis, pers. comm.), and there is no excuse for not attempting to utilize whatever (even incomplete) phylogenetic information is available (Harvey and Pagel, 1991; Purvis and Garland, 1993). This historical context may be particularly important for investigations concerning the ecomorphology of reptilian locomotion, because many aspects of morphology, performance, and foraging mode seem strongly associated with phylogeny in both lizards and snakes (cf. Miles and Dunham, 1992). As well, many morphological bases—such as limblessness and toe fringes, and behavioral/ecological correlates such as active foraging—of locomotor performance have evolved many times independently in reptiles.

More studies of natural selection acting on individual differences within populations should be done. The available data base for reptilian locomotor performance is exceedingly small (see Bennett and Huey, 1990; Brodie, 1992; Sorci et al., in press). We need to know whether selection on performance is pervasive

or rare, strong or weak, directional or stabilizing. (Unfortunately, quite large samples may be required to detect weak selection, although power can be enhanced by experimental manipulations [Sinervo et al., 1992].) Of particular interest would be studies in which traits at different levels of biological organization are measured simultaneously, such as antipredator display, speed, and scale counts in garter snakes or body mass, relative limb lengths, and endurance in lizards (cf. Lauder, 1990). Only these kinds of studies can tell us whether selection really is stronger for behavior and performance than for lower-level traits (cf. Garland et al., 1990b). Interestingly, Jayne and Bennett (1990b) report selection intensities on locomotor performance in snakes similar to those reported for morphometric traits in birds. Such studies can also tell us whether selection is correlational, favoring, for example, particular combinations of behavior and morphology/physiology (cf. Brodie, 1989b; Garland, 1988, 1994a, b; Huey and Bennett, 1987), and informing us about the form of the fitness function (cf. fig. 3.4 in Feder, 1987; Schluter, 1988). Finally, we might test whether selection ever acts *directly* on morphology (cf. fig. 10.4), although unmeasured characters could confound such analyses (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Wade and Kalisz, 1990).

Although not an easy task, especially with the current difficulties in obtaining long-term funding, some studies of natural selection should be carried out for multiple years (cf. Grant, 1986; Grant and Grant, 1990; Huey et al., 1990). Detection of rare events may be difficult (Buffetaut, 1989; Weatherhead, 1986), but their potential selective and hence evolutionary importance (Grant, 1986; Wiens, 1977; Wiens and Rotenberry, 1980) dictates that substantial effort be expended to study them.

Another important direction for studies of natural selection is toward experimental manipulation to extend the range of natural variation and/or to diminish correlations between independent variables (e.g., performance and body size). Such manipulations can improve statistical power to detect selection acting on individual traits as well as allowing hypotheses suggested by comparative analyses to be experimentally probed (Baum and Larson, 1991; Mitchell-Olds and Shaw, 1987; Sinervo, 1990; Sinervo and Huey, 1990, pers. comm.). Hormonal or pharmacological manipulation, for example, could be used to change performance capacities of individuals, after which one could test for correlations between performance and survivorship in the field (Joos and John-Alder, 1990; John-Alder, 1990, pers. comm.; John-Alder et al., 1986b). Though probably impractical with reptiles, genetic perturbation experiments to detect selection have been successfully performed with invertebrates and with mice (Anderson et al., 1964; Hedrick, 1986).

Studies of natural selection should be integrated with estimates of heritabilities

in nature (cf. Riska et al., 1989), to allow both prediction and reconstruction of microevolutionary phenomena (cf. S. J. Arnold, 1981, 1988). Estimation of field heritabilities (from free-living animals) is difficult but important, as field heritabilities may be considerably lower than those obtained in the laboratory (but see Hedrick, 1986, pp. 552–3).

Correlations between morphology and ecology, and trade-offs and constraints in performance, can be studied at multiple levels, yet integrative studies are uncommon (Emerson and Arnold, 1989; Sinervo, 1990; Sinervo and Licht, 1991). Given the growing information on interspecific variation, quantitative genetics, and physiological bases of locomotor performance, we anticipate studies in which physiological and biomechanical models are used to predict trade-offs in locomotor capacities, which are then tested, at complementary levels, by quantification of (1) genetic correlations within populations (e.g., Garland, 1988) and (2) "evolutionary correlations" through interspecific comparative studies (Garland et al., 1991, 1992; Garland and Janis, 1993; Harvey and Pagel, 1991; Lynch, 1991; Martins and Garland, 1991; Pagel, 1993). Such studies may also allow inferences concerning past patterns of (correlational) selection within populations (S. J. Arnold, 1981, 1988) and the direction of past evolutionary changes (e.g., Larson, 1984; Huey and Bennett, 1987). Of course, macroevolutionary processes, such as mass extinction (Buffetaut, 1989; Jablonski, 1986) and species selection (Arnold et al., 1989; Nee et al., 1992; Vrba, 1989; but see Williams, 1992), may also have influenced the covariation between ecology and morphology that exists for any given set of extant and/or extinct species (cf. Feder, 1987). If so, then patterns of among-population or among-species divergence predicted to have occurred based on known or hypothesized microevolutionary phenomena (e.g., individual selection, genetic correlation) may be obscured (cf. Emerson and Arnold, 1989; Garland and Carter, 1994).

The tools now exist to permit comprehensive studies of the ecological morphology of locomotor performance (cf. Bennett and Huey, 1990). Such studies will be greatly facilitated by interaction of morphologists, physiologists, ecologists, ethologists, geneticists, systematists, and evolutionary biologists. Particularly promising would seem to be collaborations between ecologists doing long-term field studies and morphologists or physiologists with laboratories equipped to measure ecologically relevant aspects of organismal performance (e.g., Huey et al., 1990).

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The Role of Physiological Capacity, Morphology, and Phylogeny in Determining Habitat Use in Mosquitoes

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This volume is intended to deal with ecomorphology, the capacity of morphological features to contribute to and indeed determine the ecological capacities of organisms. Morphological features can influence the ecology of organisms by changing performance, for example, through increased limb length or changes in bill shape (see Garland and Losos, chap. 10, this volume). The majority of morphological changes examined in this light influence behavioral aspects of organismal function such as locomotion, feeding, or sexual attraction.

An equally large number of morphological modifications influence functions which might most commonly be termed physiological or biochemical. The acquisition of novel cell types in the gut capable of the secretion of a strong salt solution certainly qualifies as a morphological change if these cells are morphologically unique. The consequence to the animal of this morphological change would not fall in the realm of what we would typically call a behavioral change, but would instead take the form of an increased capacity to produce concentrated excreta. The ecological consequences of this morphological change might be the capacity to invade highly saline environments previously unavailable to the species.

Before accepting the contention that such physiological changes are adaptive and of ecological significance, we would wish to observe such changes in organisms that had come to occupy a new ecological niche, but not in closely related organisms which retained the ancestral condition and which were excluded from the new niche. We should expect performance testing to demonstrate that the modified organisms possess physiological characteristics necessary for survival in the new niche and that the related forms possessing the ancestral condition could not perform adequately to survive in the niche (see Garland and Losos, chap. 10, this volume). Phylogenetic analysis should indicate that the physiological capability arose simultaneously with the occupation of the new niche (see Wainwright, chap. 3, this volume). Finally, the distribution of the organisms in the field should be in keeping with the contention that the physiological adapta-