

Studying the evolution of physiological performance

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1. INTRODUCTION

The study of physiology has largely developed in almost complete independence from the study of evolution. The practitioners, goals and philosophical bases of the fields have been different (Mayr 1982) such that little communication exists between them (see Futuyma 1986; Feder 1987). Nevertheless, the two fields have obvious importance and relevance to each other. The diversity and design of particular functional systems can be properly understood only from the selective, genetic and historical perspectives that evolution provides; and the evolutionary processes of selection and adaptation can be truly understood only when the mechanistic bases underlying functional systems are elucidated (Arnold 1983).

The field of physiological ecology (ecological physiology), a hybrid of comparative physiology and natural history, is a natural place for the interaction of physiology and evolutionary biology to occur. One of its major goals has been to document the role of the environment in shaping the diversity of physiological, morphological and behavioral features of organisms (Feder 1987). Its perspective is therefore fundamentally evolutionary to the extent that it considers how organisms came to be the way they are and how they might change in the future. In practice, however, physiological ecology has been most successful in discovering how various physiological systems work in different animals (e.g. nasal glands in birds and reptiles or the mechanisms of cellulose digestion in ruminants versus non-ruminants: Schmidt-Nielsen 1972) and in analyzing the complex biophysical exchanges of heat and mass between organisms and the environment (Porter 1989). It has been less successful in elucidating why and how particular systems or capacities have evolved. The literature of physiological ecology is, of course, replete with correlations between tolerance capacities of organisms and environmental gradients (e.g. of dehydration resistances of frogs with hydric gradients: Prosser 1986). Nevertheless, adaptation is often simply assumed in such correlative stud-

ies and not tested directly (Gould and Lewontin 1979). Because such evolutionary discussions are typically vague, physiology has – not surprisingly – made little impact on contemporary studies in evolution (Futuyma 1986).

Despite the historical indifference between the fields of evolution and physiology, we believe the potential for productive interchange is now very high. Physiological ecology is branching out into new areas (cf. Feder *et al.* 1987), many of which focus on historical, genetic and evolutionary issues. Several recent papers (e.g. Lauder 1981; Lande and Arnold 1983; Arnold 1983, 1987; Watt 1985; Bennett 1987; Huey 1987; Feder 1987; Koehn 1987; Powers 1987; Huey and Kingsolver 1989; Pough 1989) suggest methods for more rigorous evaluations of evolutionary hypotheses in the hope that evolution and adaptation cease to be bedeviling topics for physiological ecology. We believe that evolutionary biologists and functional biologists will increasingly be able to interact to their mutual profit and understanding, particularly on topics of genetics and natural selection. To this discussion, physiological ecologists can bring a thorough understanding of organismal function, an appreciation for the organism as an integrated unit, and the ability to analyze complex interactive effects of environmental factors on organismal capacities and performance. Most importantly, they can structure and execute experiments to test specific hypotheses about organismal function.

Here we discuss some approaches that we and our colleagues are currently undertaking to investigate aspects of functional capacities of systems and their evolution. To provide a coherent focus, we restrict our examples to studies of maximal locomotor performance (e.g. speed, endurance). Because of its great energetic cost and its intimate dependence on muscle and nervous system physiology, the physiological bases of locomotor capacity have received considerable study from mechanistically oriented physiologists during the past decade. Because of its importance to animal behavior in nature, the ecological and evolutionary consequences of locomotor performance have also been examined by ecologically and evolutionarily oriented physiologists. Indeed, locomotor performance may be the area of physiology in which evolutionarily relevant studies are best developed.

Good reasons exist for expecting that maximal locomotor performance may be of selective and hence evolutionary importance. Maximal athletic performance may well influence an animal's predation success (Elliott *et al.* 1977; Webb 1986), its success in social dominance and reproduction (Garland *et al.* 1990b) and its ability to escape from predators or other noxious factors (Christian and Tracy 1981; Huey and Hertz 1984a). Yet how generally valid are these associations? Is maximal locomotor performance routinely or periodically important to the biology of animals in nature such that the Olympic athlete is a suitable paradigm for animal locomotion

(Hertz *et al.* 1988)? Or, to paraphrase a statement from Ecclesiastes, is the race necessarily to the swift or the battle to the strong? Certainly, the image of a cheetah sprinting after a gazelle is firmly etched in one's mind. Yet, not all animals are cheetahs, and perhaps locomotor capacity is not a significant factor in the lives of most animals. The key issues concern the ecological and evolutionary importance to animals of maximal locomotor capacity. Is, for example, a faster individual more successful in capturing prey? Or is an individual with greater endurance able to spend more time foraging or is it more dominant socially? Is selection on performance constrained by mechanistic and genetic considerations?

To help answer these and related evolutionary questions, we and our colleagues have conducted a series of investigations of locomotion, principally using reptiles as study systems. These studies are designed to test explicit hypotheses involving the evolutionary significance of maximal performance. The general approach that we have used involves the integration of a two-part process. First, using test procedures that are ecologically realistic, we measure maximal performance of individuals in the laboratory. Secondly, relying on detailed information on the background ecology of our study organisms, we then analyze variation in performance (intraspecific, interspecific) from quantitative genetic, ontogenetic, demographic and phylogenetic perspectives. An understanding of the process and pattern of physiological evolution requires such a multi-level approach (Arnold 1983, 1987; Huey and Bennett 1986; Bennett 1987). Studies that focus narrowly on correlative patterns or that test relationships between performance and correlates of fitness only during a short part of an animal's life-cycle are incomplete at best and potentially misleading.

In this chapter, we begin with a short discussion of how we measure and interpret maximal performance. We then address a series of evolutionary issues. First, how variable, repeatable and heritable is maximal performance? In other words, can performance potentially respond to selection? Secondly, what information on the process of natural selection in 'real-time' can we glean from studies of maximal performance in the field? Is selection directional or stabilizing, and what might be the key selective agent(s)? Thirdly, what information on the pattern of selection over evolutionary time emerges from comparative studies? Are historical patterns and real-time processes congruent?

2. MEASURING LOCOMOTOR CAPACITY

In deriving methods to study the evolutionary significance of maximal locomotor performance, we have established and followed two important guidelines:

1. Although locomotion and its components could potentially be studied at a variety of physiological levels (enzyme kinetics to organismal performance *per se*), we concentrate on measures of organismal performance (e.g. speed, endurance) because such measures provide the most direct link between integrated physiological capacities and Darwinian fitness (Bartholomew 1958; Huey and Stevenson 1979; Arnold 1983; Bennett 1989). Lower-level systems, though they sometimes correlate with organismal-level performance (Bennett *et al.* 1984; Garland 1984; Taigen *et al.* 1985; Watt 1985; Koehn 1987; Powers 1987), are generally better suited for analyses of the mechanistic bases of variation in organismal performance, not its ecological consequences.
2. The type of performance being measured as well as the actual test conditions in the laboratory should be ecologically relevant to the natural history of a particular organism (Huey and Stevenson 1979; Bennett 1980; Arnold 1983; Huey *et al.* 1984; Pough 1989). Thus, knowledge of the biology of a given species might dictate the measurement of maximal speed for one species, but of relative agility on a narrow perch for another (Losos and Sinervo 1989). Locomotor tests should be done on an appropriate substrate and slope (Huey and Hertz 1984a; Losos and Sinervo 1989), at ecologically relevant body temperatures (Bennett 1980; Huey and Dunham 1987), during times of normal diel activity (Huey *et al.* 1989), and (when appropriate) in response to multiple environmental or physiological factors (Bennett 1980; Shine 1980; Garland and Arnold 1983; Huey and Hertz 1984a,b; Crowley 1985b; Wilson and Havel 1989; Pough 1989; Huey *et al.* 1990). Moreover, test conditions should allow animals to express normal behavior (e.g. defensive or aggressive responses) during the experiment (Hertz *et al.* 1982; Crowley and Pietruszka 1983; Arnold and Bennett 1984; Garland 1988; Pough 1989). Although it would be naive to think that any laboratory measures of performance will ever perfectly correspond to natural performances (Pough 1989), careful attention to the natural history of an organism should increase the probability that laboratory measurements are meaningful.

For our own studies we measure as many as three aspects of locomotor performance: maximal burst speed in a sprint, maximal capacity for exertion (time or distance to exhaustion while running at high speed) and endurance capacity (time to exhaustion while running at low speed). These variables should depend on relatively independent physiological traits (Table 1), and have generally been found to be independent of each other or have only a very weak positive association (Bennett 1980; Garland 1988; van Berkum *et al.* 1989; Jayne and Bennett 1990a; Huey *et al.* 1990; Shaffer *et al.*, in press). Taken together these variables define a

Table 1

Factors anticipated to limit locomotor performance at different levels of exertion (from Bennett 1989)

<i>Speed</i>	<i>Limiting factor</i>
Slow sustainable speed	Motivation, ultimately fuel
Fast sustainable speed (endurance)	Maximal oxygen consumption
Fast non sustainable speed (maximal exertion)	Anaerobic metabolism
Maximal burst speed	Structure/function of the musculoskeletal complex

'locomotor performance space' that bounds most of the potential capacities for behavior of which an animal is capable (Bennett 1989). [Note, however, that frogs achieve considerably higher rates of oxygen consumption while calling than while engaged in vigorous locomotion (Taigen and Wells 1985; Taigen *et al.* 1985).] As mentioned above, however, the natural history of a particular organism may sometimes dictate that other measures of locomotion (e.g. agility, acceleration) might be relevant as well (Losos, 1990*a,b*).

In interpreting measures of locomotor performance, one must recognize that all behavior (not just locomotor behavior) depends on physical activity and that maximal levels of all behaviors are limited by the same physiology and morphology that limits locomotor activity (Table 1) (Bennett 1989). Therefore, our measurements of locomotor capacity define not only the limits of locomotor capacity *per se*, but also of behavioral 'work' of any type within a given metabolic mode. For example, maximal exertion may provide information on the ability to repel an intruder or perhaps to dig a burrow, not just on the ability to outrun a predator.

To measure maximal speed, we use electronic racetracks that have a series of photocell stations at set intervals along the track (Huey *et al.* 1981; Miles and Smith 1987). When an animal is chased down the track, it breaks the light beams in succession; a computer records the elapsed time until each beam is broken and then calculates the maximal speed over all intervals during a run. Typically, we race each individual several times and analyze the single fastest speed for each individual. Speed is positively correlated with initial acceleration (Huey and Hertz 1984*a*), so the data on individual variation in maximal speed also provide information on individual variation in acceleration.

To measure capacity for maximal exertion, we pursue an animal at high speed around a circular racetrack until it becomes exhausted (judged by

loss of righting response) or assumes a static aggressive or defensive posture (Arnold and Bennett 1984; Garland 1984, 1988). The total distance travelled is a good index of effort, but speed or total time (or distance covered in the first minute or two: Bennett 1980) are also sometimes measured.

To measure endurance capacity, we place an animal on the slowly moving belt of a motor-driven treadmill. The elapsed time until the animal becomes exhausted, as indicated by its falling off the tread and losing its righting response, serves as an index of endurance. Detailed field data on movement rates in nature can suggest an ecologically relevant treadmill speed (Huey and Pianka 1981; Huey *et al.* 1984).

Each of these factors is relatively easy to determine experimentally on large numbers of individuals. Moreover, we can measure performance in each mode on two different days to test for short-term repeatability of the variable. Because performance measurements do not harm the animals, we can conduct release-recapture studies to measure long-term repeatability of individual performance.

A legitimate concern about such measures of locomotor capacity is the extent to which they are influenced by motivational factors. Perhaps speed or endurance measured under laboratory conditions depends more on the willingness of an animal to perform in an artificial situation than on physiological or morphological limits to locomotion, and thus does not represent a true maximal capacity. This possibility is always present when organismal traits are considered, and especially behavioral ones. Accordingly, we and our colleagues have made numerous attempts to determine whether our measurements of locomotor capacity in fact correlate with underlying physiological and morphological systems: if such correlations cannot be found, then performance measurements might reflect motivational differences rather than physiological limitations.

Individual endurance and maximal exertion are in fact generally linked with aerobic metabolic capacity and with anaerobic capacity, respectively (e.g. Garland 1984; Garland and Else 1987). In an important study, Garland (1984) showed that 89 per cent of the size-corrected inter-individual variability in endurance of the lizard *Ctenosaura similis* is explained by only four variables (maximal oxygen consumption, heart- and thigh-muscle mass, and hepatic aerobic enzyme activity) and that 58 per cent of the variability in maximal exertion is correlated with only two variables (maximal carbon dioxide production and anaerobic enzyme activity of skeletal muscle). [Garland's analysis has been criticized (Pough 1989) for analyzing overlapping physiological 'levels', but that criticism does not negate Garland's demonstration of links between physiology/morphology and performance.] Similarly, endurance and maximal exertion of different

species of African lacertid lizards correlate with aerobic and anaerobic capacities, respectively (but not with muscle enzyme activities) (Bennett *et al.* 1984).

For burst speed, studies to date are less comprehensive, but physiological and morphological correlates of variation in speed are now documented for both interspecific (Losos 1990*a,b*; see Section 6) and some intraspecific comparisons (Miles 1987; Snell *et al.* 1988; Tsuji *et al.* 1989; Huey *et al.* 1990; but see Garland 1984, 1985). For example, individual burst speed is strongly correlated with muscle-fiber diameter in desert iguanas (*Dipsosaurus*: Gleeson and Harrison 1988) and with relative limb length in lizards of the genus *Urosaurus* (Miles 1987). However, hindlimb length or thigh-muscle mass has little or no effect on performance of individuals of several taxa (Garland 1984, 1985; Garland and Else 1987; Tsuji *et al.* 1989; Huey *et al.* 1990). Speed in garter snakes (*Thamnophis* spp.) is correlated with the ratio of body to tail vertebrae: animals departing from the mean ratio have lower speeds (Arnold and Bennett 1988; Jayne and Bennett 1989). However, experimental manipulation of tail length over the observed range of variation does not significantly alter speed, and therefore this association is not a simple biomechanical linkage (Jayne and Bennett 1989).

The role of body size on locomotor performance of neonate *Sceloporus occidentalis* has recently been studied using a novel manipulative experiment (Sinervo and Huey 1990). Neonates from a southern population are large at birth and have a high speed and stamina relative to the small neonates from northern populations. To determine whether the differences in performance are merely an allometric consequence of interpopulational differences in body size, Sinervo and Huey (1990) removed some yolk from eggs from the southern population, thereby producing miniaturized neonates equivalent in size to northern hatchlings. Miniaturized southern neonates no longer were relatively fast, but they still maintained high stamina relative to the northern neonates. Thus interpopulational differences in speed are an allometric consequence of differences in egg size, but differences in stamina must also reflect differences in physiology. Size manipulation (Sinervo 1988, 1990) adds an important experimental dimension to studies of the allometry of physiological performance.

Overall, our estimates of locomotor performance appear to have at least a partial mechanistic basis and therefore represent legitimate measures of maximal locomotor capacity. Presumably, measurements of locomotor capacity are also influenced by individual differences in behavior as well (e.g. motivation to sprint). Interestingly, such tendencies may run in families (van Berkum and Tsuiji 1987).

3. STUDY ORGANISMS

Reptiles have numerous attributes that make them suitable and popular systems for physiological and ecological studies (e.g. Milstead 1967; Huey *et al.* 1983; Seigel *et al.* 1987). They may occur in populations of very high density and have relatively low vagility, permitting repeated longitudinal sampling of individuals under field conditions. They are completely independent from parental care at birth, and so ecology and survivorship are uncomplicated by this factor. They can be easily captured and manipulated, and individuals can be marked and returned to field conditions or often kept successfully in captivity for long periods (e.g. Arnold, 1981). Important from the viewpoint of locomotion, they also seem relatively inflexible in adjustment of their locomotor capacities: they neither train physically nor lose capacity under laboratory conditions (Gleeson 1979; Garland *et al.* 1987; but see John-Alder and Joos, in press).

In collaboration with many colleagues, we have concentrated our studies on three taxa: garter snakes (*Thamnophis sirtalis*), fence lizards (*Sceloporus occidentalis*) and canyon lizards (*Sceloporus merriami*). We intentionally selected these species because the availability of background behavioral, ecological and demographic information makes these among the best known of reptiles. This wealth of background information facilitates our ability to pose and to interpret relevant functional hypotheses.

Garter snakes were studied by Jayne and Bennett between 1985 and 1988 in the vicinity of Eagle Lake in northern California. The ecology of this isolated montane population was previously studied extensively by S. J. Arnold and coworkers (e.g. Kephart 1982; Kephart and Arnold 1982). Moreover, the activity physiology of nearby populations and related species is also well known (Arnold and Bennett 1984; 1988; Garland 1988; Garland *et al.* 1990a; Garland and Bennett, in press).

Fence lizards were studied by R. B. Huey, T. Garland Jr, B. Sinervo, J. S. Tsuji and F. H. van Berkum in south-central Washington, near the northern limit of the species' range. Pilot studies were conducted by Tsuji and van Berkum in 1983. A full-scale study was started in 1985 but was terminated after one year when the study area was logged. Fence lizards are well known ecologically, behaviorally and physiologically.

Two populations of canyon lizards in Big Bend National Park, Texas have been studied since 1984 by R. B. Huey, A. E. Dunham, K. L. Overall and R. A. Newman. This study is continuing. These populations have been the focus of long-term ecological and demographic studies (Dunham 1981; Dunham *et al.* 1989). In terms of behavior, ecology and demography, these are the best known populations of lizards.

4. ATTRIBUTES OF LOCOMOTOR CAPACITY

For selection to act on a trait and for evolution to occur, the trait must possess two attributes, namely variability and heritability. Moreover, to facilitate the detection of selection with longitudinal investigations, traits should be repeatable over time, for a single measure of performance will then adequately characterize an individual throughout the interval of the study (Huey and Dunham 1987). Locomotor capacity possesses these attributes.

4.1 Variability

Traditionally, physiological ecologists have shown little interest in documenting inter-individual variability within populations, regarding variability only as an unfortunate feature obscuring central tendency (Bennett 1987). However, high levels of variability are seen in a variety of physiological variables: coefficients of variation are often 10–40 per cent for physiological traits (e.g. Garland 1984; Bennett *et al.* 1989). Locomotor performance capacity is also highly variable among different individuals (e.g. Bennett 1980; Huey and Hertz 1984*b*; Bennett *et al.* 1989; Tsuji *et al.* 1989; Huey *et al.* 1990). For example, size-corrected coefficients of variation for speed, exertion and endurance are, respectively, 27, 28 and 63 per cent for adult lizards (*Ctenosaura similis*: Garland 1984) and 19, 51 and 56 per cent for neonatal snakes (*Thamnophis sirtalis*: Jayne and Bennett 1990*b*). Among neonatal garter snakes, speed, maximal exertion and endurance vary by 10-fold, 20-fold and 100-fold, respectively (Arnold and Bennett 1988; Jayne and Bennett 1990*b*). Similarly, speed and endurance vary 5-fold and 14-fold in neonate fence lizards (*Sceloporus occidentalis*: Tsuji *et al.* 1989) and 3-fold and 14-fold, respectively, in adult canyon lizards (1- to 3-year-old *S. merriami*: Huey *et al.* 1990). Clearly, locomotor capacity shows considerable variability. Interestingly, a few individuals are truly exceptional. For instance, two female canyon lizards had endurance times that were greater than six standard deviations above the population mean (Fig. 1; Huey *et al.* 1990).

4.2 Repeatability

Is the locomotor capacity of an individual animal consistent over time? In other words, is an individual that is relatively fast at one time likely to be relatively fast in the future? Establishing the temporal repeatability of performance through time is a key step in any evolutionary analysis of individual variation, especially in studies that attempt to analyze phenotypic variation among individuals (Arnold 1986; Bennett 1987; Huey and Dunham 1987; Falconer 1989). Significant short-term (day-to-day or week-

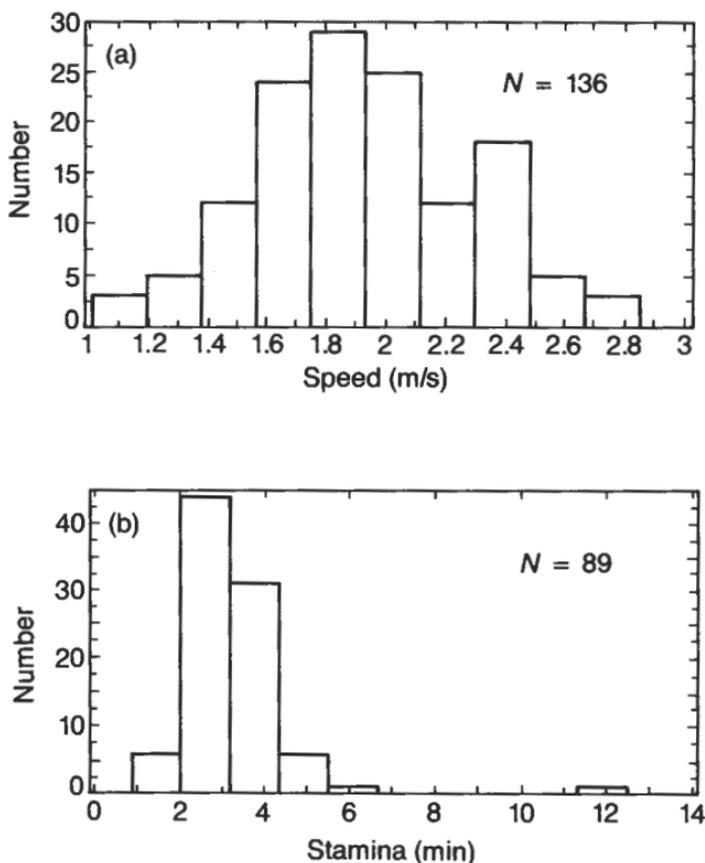


Fig. 1. Histograms of locomotor performance of adult female (aged 1–3 years) canyon lizards (*Sceloporus merriami*) from Boquillas Canyon, Big Bend National Park. (a) Maximal burst speed on a 2-m track, and (b) endurance on a treadmill at 0.5 km/h. Reprinted from Huey *et al.* (1990) with permission.

to-week) repeatability of locomotor performance capacity has been found in nearly every species in which it has been examined (amphibians: Putnam and Bennett 1981; Bennett *et al.* 1989; Shaffer *et al.*, in press; lizards: Bennett 1980; Crowley and Pietruszka 1983; Garland 1984, 1985; Huey and Hertz 1984b; John-Alder 1984; Kaufmann and Bennett 1989; van Berkum *et al.* 1989; Huey *et al.* 1990; mammals: Djawdan and Garland 1988; snakes: Garland and Arnold 1983; Arnold and Bennett 1988; Jayne and Bennett, 1990a). Correlation coefficients of size-corrected locomotor performance between different measurement days are generally 0.5–0.8 in these studies. Repeatability even remains significant among individuals across different physiological states, such as body temperature, again in every species of lizard examined (Bennett 1980; Huey and Hertz 1984b;

Huey and Dunham 1987; Kaufmann and Bennett 1989; van Berkum *et al.* 1989).

The ultimate test of repeatability involves individuals living under field (not laboratory) conditions. This involves measuring the performance of a large sample of individually marked animals, releasing them into the field, and then subsequently recapturing and remeasuring performance of the survivors. Huey and Dunham (1987) found that the speed of an individual *Sceloporus merriami* in two populations was positively correlated with its speed a full year later. Using data from additional years and also controlling for sex, population and age, Huey *et al.* (1990) recently confirmed that speeds of adults (aged 1–3 years) were significantly repeatable for at least one year (Fig. 2), and they demonstrated that endurance was similarly repeatable. One year is a substantial length of time for these small lizards (the cohort-generation time is about 1–1.5 years: A. E. Dunham, personal communication). Moreover, the between-year repeatabilities of speed of lizards are in fact slightly higher than those measured for thoroughbred racehorses and greyhounds, equivalent to those for some morphological traits of birds, and even higher than those for reproductive traits in some birds (see references in Huey and Dunham 1987).

Is locomotor performance stable even during periods of rapid growth? In other words, is a fast neonate likely to be a fast yearling or a fast

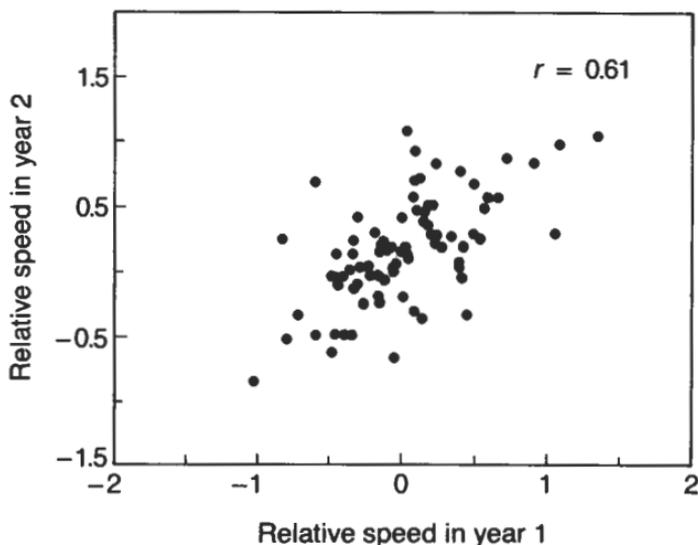


Fig. 2. Relative maximum speed of adult canyon lizards (*Sceloporus merriami*) is repeatable between years ($r = 0.61$, $N = 86$, $P < 0.001$). Relative speeds are actual speeds that have been standardized for population and sex. From data in Huey *et al.* (1990).

adult? van Berkum *et al.* (1989) measured the speed and endurance of almost 300 hatchling fence lizards, *Sceloporus occidentalis* (aged 14 days), released the animals into the field, and then remeasured the speed and endurance of surviving lizards over a year later. Although only a few hatchlings survived, size-corrected endurance (Pearson's $r = 0.77$, $n = 11$, $P < 0.005$) and possibly speed ($r = 0.38$, $n = 12$, $P = 0.06$) were repeatable, even though the lizards had grown by more than 10-fold in mass. Size-corrected speed and endurance were also repeatable over periods of one year (but not 2 years) in a field population of garter snakes, *Thamnophis sirtalis* ($r = 0.25$, $n = 185$, $P = 0.001$ for speed and $r = 0.22$, $n = 166$, $P = 0.005$ for endurance: Jayne and Bennett 1990a).

Recent studies with a salamander (*Ambystoma*: Shaffer *et al.*, in press) provide an interesting counterpoint with studies of reptiles. Although speed and endurance of these salamanders are repeatable within a metamorphic stage, locomotor performances are not repeatable across metamorphic stages. The lack of repeatability presumably reflects the radical shifts in morphology and ecology associated with metamorphosis (Shaffer *et al.*, in press).

In summary, our studies with reptiles demonstrate that individual differences in locomotor performance capacity are repeatable, even over long time intervals in nature, even at different body temperatures, and even in rapidly growing individuals. These demonstrations are important, for high repeatability greatly facilitates attempts to study natural selection on individual performance in nature. These results imply that relative performance capacities of animals do not change radically during the time intervals over which survival is monitored.

4.3 Ontogeny of locomotor performance

Although these former studies examine whether *relative* locomotor performance is stable over 1 or 2 years, they do not describe the stability of *absolute* locomotor performance. Is the average absolute performance of animals of a given age sensitive to between-year changes in the environment? Similarly, does absolute performance change drastically as an animal matures and then ages (Pough 1983, 1989; Taigen and Pough 1985; Huey *et al.* 1990)?

Determining the environmental sensitivity of absolute performance requires comparisons of performance of individuals of equivalent age and sex in different years. In an initial comparison, speeds of canyon lizards in two populations were virtually identical in two years (1984, 1985), suggesting that absolute performance is insensitive to environmental conditions (Huey and Dunham 1987). However, with data from additional

years, significant between-year differences were detected (Huey *et al.* 1990). Interestingly, speed (but not endurance) in a given summer was positively correlated with the cumulative rainfall during the previous winter and spring.

Determining the ontogeny of absolute performance requires comparisons of individuals of different ages. Unfortunately, ontogenetic profiles of physiological performance have received little attention, except during early growth phases (Pough 1989; van Berkum *et al.* 1989; Jayne and Bennett 1990a). The reason is obvious: physiologists rarely know the exact ages of their study animals. This difficulty can be circumvented, however, by conducting physiological studies on populations with individuals marked from near birth because ages are automatically known from mark-recapture data (Huey *et al.* 1990).

The long-term demographic studies of A. E. Dunham and K. Overall made it possible to study the ontogeny of locomotor performance in the lizard *Sceloporus merriami* (Huey *et al.* 1990). In humans and greyhounds (Ryan 1975), maximal speed increases initially with age, reaches a maximum in early adulthood, and then eventually declines during senescence. Do locomotor capacities of *S. merriami* show a similar ontogenetic pattern? Performance might not decline in old adults if mortality rates are so high that few animals actually survive to old age in nature or if only the fastest lizards survive. Speed and endurance are initially low in hatchling *S. merriami* but high in 1-year-olds (young adults). Our sample size of older adults is still limited; however, in regression analyses for lizards 1–3 years old, age actually has a significant positive effect on endurance ($P = 0.003$) but may have a negative effect on speed ($P = 0.053$). In both cases, however, the effects are very weak. Moreover, because the adult age structure of these populations is heavily biased towards 1-year-olds (Dunham 1981), the performance of adult *S. merriami* must be essentially unaffected by age.

We wish to emphasize the importance of considering demography in studies that examine the relationship between performance and fitness. Imagine an investigator who attempts to test the hypothesis that the relative calling (or hopping) ability of male frogs influences their mating ability, but who does not know either the age of individual males or the age structure of the population. If age (independent of size; e.g. see Smith *et al.* 1986) influences performance, then any attempt to analyze a correlation (or the lack thereof) between performance and reproductive success will necessarily be confounded both by age and by the age structure. Knowledge of individual age and of population age structure should be a prerequisite to analyses of performance and fitness (Charlesworth 1980; Huey *et al.* 1990).

4.4 Heritability

Finally, we ask whether locomotor performance capacity has a genetic basis. Or, more properly, is there heritable variation in maximal speed, exertion and endurance, such that these traits have the genetic potential to respond to selection? Knowing the heritability of a trait is required for predictions of the dynamics of evolutionary change (Arnold 1987, 1988; Falconer 1989). However, heritability has been measured for few traits (ecological, physiological or morphological), at least in natural populations. Quantitative geneticists measure heritability in several ways, but the approach used so far for studies of locomotion in natural populations is the most basic. It involves raising full-sib families and then analyzing the patterns of variation within versus among families. Significant heritabilities have been found for speed in horses (Langlois 1980; Gaffney and Cunningham 1988), dogs (Ryan 1975) and humans (Bouchard and Malina 1983*a, b*). Speed, exertion and endurance, as well as defensive behaviors, all have significant heritabilities in garter snakes (genus *Thamnophis*) (Arnold and Bennett 1984; Garland 1988; Jayne and Bennett, 1990*a, b*; Arnold and Bennett, unpublished data). Speed and endurance are heritable in fence lizards (*Sceloporus occidentalis*) (van Berkum and Tsuji 1987; Tsuji *et al.* 1989). Standard and resting, but not maximum, oxygen consumption appear heritable in skinks (*Chalcides ocellatus*) (Pough and Andrews 1984). In all of the listed studies (Table 2), locomotor capacity shows moderate and significant heritability. The estimates based on full-sib breeding designs are, however, only first approximations of heritability; they do not exclude maternal and dominance effects. Experiments using more sophisticated breeding designs are encouraged.

These same full-sib data can address a related genetic issue, specifically the genetic correlation between traits, such as between speed and endurance. Evolutionary ecologists have recently become very interested in genetic correlations, because such correlations can profoundly affect evolutionary responses to selection (Lande and Arnold 1983; Arnold 1987, 1988). If two traits are genetically correlated, then direct selection on only one of the traits will lead to simultaneous evolutionary changes in the correlated trait. Two studies of locomotor performance have thus far addressed this issue. *A priori* might expect a negative genetic correlation between speed and endurance, as they emphasize different types of skeletal muscle fibers and limb proportions. However, Garland (1988) found a positive, rather than a negative, genetic correlation between speed and endurance in neonatal garter snakes. Tsuji *et al.* (1989) found no significant genetic correlation among these variables in hatchling fence lizards. On this very limited basis, the evolution of speed and endurance are predicted to be positively coupled in garter snakes but independent in fence lizards.

Table 2
Broad-sense heritabilities of locomotor performance capacity

Species	Performance	Heritability	Reference
Greyhounds	speed	0.23	Ryan (1975)
Racehorses	speed	0.02–0.65	Langlois (1980)
<i>Thamnophis</i> <i>radix</i>	time-form speed	0.39–0.76 0.59–0.76	Gaffney and Cunningham (1988) Arnold and Bennett (unpublished data)
<i>Thamnophis</i> <i>sirtalis</i>	speed	0.58	Garland (1988)
	speed	0.28	Jayne and Bennett (1990a)
	exertion	0.26	Jayne and Bennett (1990b)
	endurance	0.70	Garland (1988)
<i>Sceloporus</i> <i>occidentalis</i>	endurance	0.68	Jayne and Bennett (1990a)
	speed	0.59	van Berkum and Tsuji (1987)
	speed	0.36	Tsuji <i>et al.</i> (1989)
<i>Drosophila</i> <i>melanogaster</i>	endurance	0.36	Tsuji <i>et al.</i> (1989)
	wing-beat frequency	0.39	Curtsinger and Laurie-Ahlberg (1981)
	power output	0.33	Curtsinger and Laurie-Ahlberg (1981)
<i>Lygaeus</i> <i>kalmii</i>	flight duration	0.20	Caldwell and Hegmann (1969)

5. ANALYZING EVOLUTIONARY PROCESS: NATURAL SELECTION

Several different strategies are used to study the evolutionary adaptation of physiology or other traits (Endler 1986a; Huey and Kingsolver 1989). The one traditionally used by physiological ecologists involves examining comparative data on contemporaneous organisms (e.g. species in different environments) and then deriving *post-hoc* reconstructions of *patterns* that have evolved over historical time (Huey and Bennett 1986, 1987; Bartholomew 1987; Feder 1987); we review examples of this comparative approach later in this chapter. An alternative approach involves studying selection on phenotypic traits in nature (Lande and Arnold 1983; Endler 1986a; Mitchell-Olds and Shaw 1987; Schluter 1989): here one analyzes evolutionary *processes* in real time. This approach has been used very elegantly in several recent studies, especially those by Peter Grant and his colleagues (e.g. Boag and Grant 1981; Grant and Grant 1989) on morphological variation in Darwin's finches. However, the specific protocol we use to study selection on performance was conceived by Arnold and Bennett

(see Arnold 1983). Specifically, we first measure locomotor performance in a cohort of known-age individuals, release them into the field, and then recapture the survivors sometime later. Using a variety of statistical procedures (e.g. multivariate analyses: Lande and Arnold 1983; fitness functions: Schluter 1989; randomization tests: Jayne and Bennett 1990*b*), we test hypotheses concerning whether maximal locomotor capacity of an individual animal is, for example, correlated with growth or survivorship. By monitoring the behavior (e.g. movement rates, social dominance) of these same individuals, one can also test supplementary hypotheses relating maximal locomotor capacities to foraging or social behaviors. In combination, these approaches enable us to determine whether and how maximal performance influences correlates of fitness in real time.

The basic statistical approach can be depicted for the case of direct selection on a single phenotypic trait such as speed. The frequency distribution of speed in an initial cohort of individuals is compared to the distribution of those individuals known to survive the interval of selection (e.g. Fig. 3). The speeds compared are those of the initial cohort before release, on the assumption that speed is repeatable (see above) during the interval of selection. [If the factor, such as speed, is correlated with body size, multivariate techniques are required (Lande and Arnold 1983; Endler 1986*a*; Crespi and Bookstein 1989; Jayne and Bennett 1990*b*.)] These initial distributions may be altered by selection in several ways. If directional selection favored faster individuals between the time of release and recapture, then the survivors should be a relatively fast subset of the original cohort and thus have a significantly greater mean performance. This might be the case if faster individuals were more adept at capturing prey or at avoiding predators. At least theoretically, directional selection could alternatively favor slow individuals, because fast individuals might have a higher risk of injury, as in thoroughbred racehorses, or incur higher energetic costs associated with maintaining 'high-performance' muscles (Goldspink 1981; Taigen 1983). If stabilizing or normalizing selection favored individuals of average speed, then the distribution for the survivors should have the same mean as the initial distribution but a reduced variance. Here we describe results from three such field studies, one with snakes and two with lizards.

5.1 Locomotor capacity of garter snakes

Between 1985 and 1988, Jayne and Bennett (1990*a,b*) followed the effect of locomotor capacity and body size on the survivorship of individual animals in a local population of garter snakes (*Thamnophis sirtalis*) in northern California. In 1985, 40 gravid females were collected, and these later gave birth to 275 offspring in the laboratory. Speed, exertion and endurance were measured within one week of birth, and all of the animals

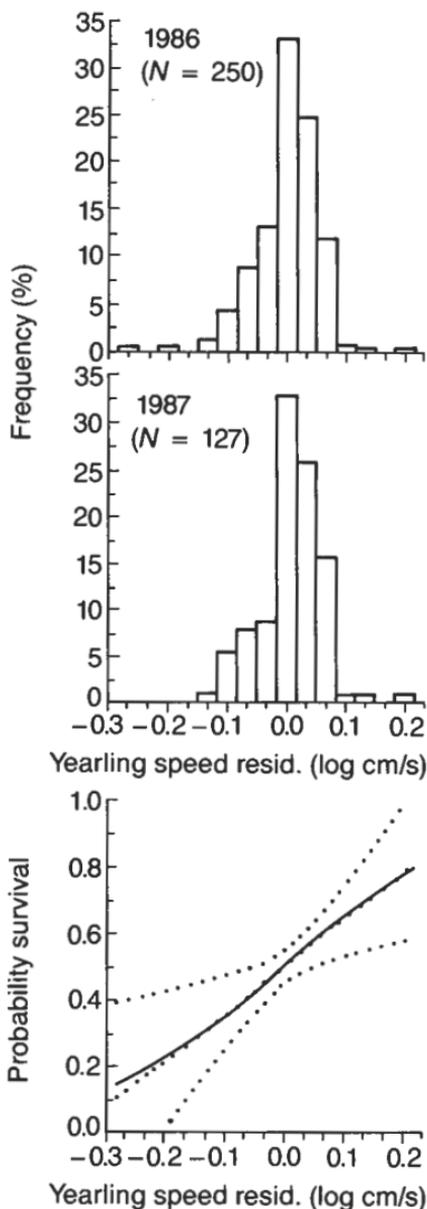


Fig. 3. The effect of speed on survivorship in yearling garter snakes (*Thamnophis sirtalis*). The top panel indicates the distribution of size-corrected residuals of speed of animals released in 1986, and the center panel of the subset of these animals recaptured in 1987. The probability of survival (lower panel) is estimated with both a regression (dotted line with 95 per cent confidence limits) (Lande and Arnold 1983) and a cubic spline function (solid line) (Schluter 1989). Data from Jayne and Bennett (1990b).

were released into their original population within 2 weeks of birth. During the following year, some of these animals were recaptured, remeasured and re-released, along with nearly 400 additional animals resident in the population. Survivorship and locomotor performance were followed for all individuals over a total of 3 years. Because all locomotor parameters were found to be size-dependent and because size positively influenced survivorship of neonates, all of the analyses were carried out on size-corrected residuals.

Locomotor capacity significantly predicted survivorship, but only after the first year of life; all probabilities reported are for one-tailed randomization tests comparing means between years. During the first year, neonate size (length, but not mass) was directly correlated ($P = 0.022$) with survivorship, as has been found in the lizard *Uta stansburiana* (Ferguson and Fox 1984). However, no measure of locomotor performance was directionally associated with survival ($P = 0.19-0.73$). During the second year of life, however, both speed ($P = 0.007$; Fig. 3) and exertion ($P = 0.008$) were positively related to survival, and endurance was nearly so ($P = 0.06$). For snakes older than 2 years, speed continued to be an important correlate of survivorship ($P = 0.001$), and exertion ($P = 0.08$) and endurance ($P = 0.10$) were marginally significant. As snakes in this population do not reach adult size for 3-4 years after birth, this differential mortality associated with size and locomotor capacity occur prior to reproduction. Locomotor capacity is thus under natural selection in this population. In addition, the mass residual on length was found to be under stabilizing selection in yearling snakes ($P = 0.006$): both relatively thin and heavy animals were at a selective disadvantage. Selection intensities (Schluter 1989) on these functions are similar in magnitude to those measured for morphological characters in natural populations of small birds (Bumpus 1899; Boag and Grant 1981; Schluter and Smith 1986).

5.2 Locomotor capacity of fence lizards

To examine selection on speed and endurance, Huey, Garland, Tsuji and van Berkum (unpublished data) captured 49 gravid fence lizards (*Sceloporus occidentalis*) in June 1985. The females were taken to the laboratory, where they laid eggs within 1-2 weeks. When the resulting hatchlings ($N = 296$) were 2 weeks old, we measured their speed, endurance and body size and then released them (age = 3 weeks) on our study area in early August. Six weeks later, shortly before the hatchlings began their first winter dormancy, we recaptured as many of the survivors as possible, remeasured their size and performance, and re-released them. We staged a second recapture the following May, and a third and final

recapture in August, when the subadult lizards were about 13 months of age (these lizards require 2 years to mature). During each recapture we measured the size and performance not only of the lab-raised hatchlings, but also of field-raised hatchlings of the same age (c. 400). Because our recaptures were more frequent than those of the garter snake (above) or canyon lizard (below) studies, we analyze selection over short time intervals (first summer, first winter and first spring through summer), for which performance is highly repeatable (van Berkum *et al.* 1989). For each interval, we can determine whether speed, endurance or body size at the beginning of a time period influenced survivorship as well as growth rate (survivors only).

Based on preliminary analyses, the patterns appear consistent across all three time intervals, for both lab- and field-raised hatchlings. We present here only data on the effect of speed on survivorship for the first interval (from age 3 weeks to 9 weeks, lab-born hatchlings). Comparisons of the distributions of speeds at release for the entire original cohort and for the survivors demonstrate that the survivors were a random subset of the original cohort, at least with respect to speed (randomization test on average performance, $P = 0.35$). Endurance similarly had no effect on survival ($P = 0.17$). Locomotor performance was also uncorrelated with short-term feeding success (indexed by size of fecal pellets from recaptured lizards) or with the growth rates of the survivors. Nevertheless, we did detect two cases of selection. First, survival of the hatchlings during the first winter dormancy was sharply reduced if their tail was broken near the base, suggesting that complete tails may confer survival advantages in dormancy in ways removed from those associated to defense against predators (Bauwens and Thoen 1981). Secondly, the effects of body size on survival were contrary to those observed for garter snakes (above) or for *Uta* (Ferguson and Fox 1984): hatchlings from large eggs had slightly lower survivorship than did hatchlings from small eggs (Sinervo, Huey, Tsuji and van Berkum, unpublished data). In contrast to Lack's (1954) hypothesis of stabilizing selection on egg size, selection in this population is strongly directional and favors small eggs: females that make many small eggs not only produce more hatchlings, but also produce hatchlings with an increased probability of survival.

Because logging of the habitat forced us to terminate this study a year before the lizards reached maturity, we conducted a separate laboratory study to determine whether locomotor performance relates to social dominance in adult males (Garland *et al.* 1990b). Speed, but not endurance, was positively associated with dominance: males that were dominant in paired encounters in the laboratory were typically the faster of the (size-matched) pair.

5.3 Locomotor performance in canyon lizards

Beginning the summer of 1984, Dunham, Huey, Overall and Newman (unpublished data) have been measuring locomotor performance (speed, endurance, or both) of adult individuals (known age) from two marked populations of canyon lizards (*S. merriami*). We can score survivorship for two intervals, 1 month and 10 months after measurement; and we can partition data by age, sex and population. Moreover, because these lizards are also the subject of intensive focal-animal observations, we can search for correlations between locomotor performance and social dominance, territory size, movement rates, etc. This study is still continuing, and preliminary analyses have been conducted only for survivorship for the years 1984–8. So far, neither speed nor endurance correlate with survivorship; and the consistency of this pattern (among years, or between sexes and populations) suggests that the lack of detectable selection is not just an artefact of relatively small sample sizes.

5.4 Summary of selection studies

On the basis of these three studies, particularly with such different results, no general conclusions can be drawn concerning patterns of selection on locomotor performance. On the one hand, selection can occur (e.g. speed of snakes, egg size of lizards) and can be reasonably easy to detect; on the other, selection is not universally strong enough to be detected, and perhaps is not even common. Several different factors may account for these disparate observations.

First, the importance of locomotor performance may be highly population- or other taxon-specific, depending on local conditions of both biotic and abiotic factors. The fence lizard study was carried out near the northern limit of the species, where predators are few and rare. Indirect data (mortality rates, relative clutch mass of females, greater locomotor capacities) suggest that selection may well be stronger in more southern populations (Sinervo 1988). Perhaps a study on southern populations would detect selection on locomotor characteristics. However, we have not been able to detect selection on canyon lizards, in which mortality rates are very high (Dunham 1981). Secondly, perhaps selection on performance characteristics is usually too weak or variable to detect in a short-term study, but will nevertheless produce evolutionary change in performance over time (see Section 6). This is certainly not an unreasonable proposal. Selection on morphological traits is sometimes detectable only intermittently (e.g. Boag and Grant 1981; Grant and Grant 1989), and very weak selection – far too weak to be detectable – can of course lead to evolutionary change (Lewontin 1974). Thirdly, the different results for the snake versus lizard studies probably do not reflect a basic difference between these taxa, for an ongoing study with lizards of the genus *Urosaurus* has

detected significant directional selection on size-corrected speed (D. B. Miles 1989, personal communication). Finally, in some groups, other kinds of behavior may compensate for limited performance capacity, such as increased wariness or aggressiveness (Rand 1964; Bauwens and Thoen 1981; Hertz *et al.* 1982; Crowley and Petruszka 1983). Such behavioral shifts might ameliorate any survival disadvantages of limited performance. These alternatives can only be discriminated by further studies.

5.5 A commentary on our general approach

Maximal locomotor performance is a complex trait that can be interpreted directly (e.g. as probability of escape from predation) or indirectly (e.g. as indices of physical as opposed to Darwinian fitness). Only a broadly based study is likely to derive insights into the evolution of such complex traits. Accordingly, we have developed and advocated a multi-step study that meets rigorous criteria:

1. The temporal and thermal repeatability of performance must be determined.
2. The heritability and genetic correlations involving performance must be known.
3. Correlations between performance and fitness must be measured in demographically established populations and over the life-cycle of the organism.
4. Supplementary manipulative experiments (e.g. Ferguson and Fox 1984; Mitchell-Olds and Shaw 1987; Marden 1989; Garland *et al.* 1990*b*; Sinervo and Huey 1990) should then validate or extend the results of descriptive analyses.

Although our field studies test explicit hypotheses (e.g. speed correlates positively with survivorship, growth rate or feeding success), we fully recognize that such analyses are necessarily descriptive and exploratory. Nevertheless, such exploratory approaches should be a key first step in fitness studies; and only subsequently (or perhaps concurrently) should manipulative experiments (*sensu* Mitchell-Olds and Shaw 1987) be used.

A complementary approach to cohort analysis involves the combination of performance data with focal animal observations (Pough 1989). As mentioned above, we are accumulating such data on *S. merriami* in Big Bend, but several focal animal studies on activity performance have already been completed on anuran amphibians (Wells and Taigen 1984; Sullivan and Walsberg 1985; Walton 1988). None of these studies has demonstrated significant correlations between performance and characters thought to be related to fitness. Whether this reflects biological reality or instead is an artefact of a problem inherent in most focal animal studies – small sample sizes and hence low statistical power – is unknown. In any

case, focal animal studies that demonstrate significant correlations will still require both supplementary demonstrations of the genetic bases of the investigated characters and a search for trade-offs.

6. ANALYZING EVOLUTIONARY PATTERNS: COMPARATIVE STUDIES

Given the diversity of organismal form and function, there is no doubt that organismal features, including locomotor ability, do evolve. Comparisons of functional structures and mechanisms found among organisms living in different environments have been the traditional method of examining patterns of evolutionary diversification in physiology (Prosser 1986; Bartholomew 1987). To be maximally informative, such studies should be undertaken on closely related groups of organisms, so that factors extraneous to the comparison can be minimized (Gould and Lewontin 1979; Huey and Bennett 1986; Huey 1987). One recent extension of traditional comparative approaches involves making comparisons with explicit reference to phylogeny, so, for example, that evolutionary directionality (e.g. primitive vs. derived condition) may be inferred from the pattern (Gittleman 1981; Lauder 1981; Ridley 1983; Felsenstein 1985; Huey and Bennett 1986, 1987; Huey 1987). Here we review several types of comparative studies that evaluate evolutionary patterns of locomotor capacity.

Locomotor capacity is strongly influenced by body temperature in ectotherms (Bennett 1980, 1990), increasing directly with body temperature up to a maximum level (at the optimal body temperature for locomotion, *sensu* Huey and Stevenson 1979), and then declining sharply at still greater temperatures. Lizards unable to achieve their optimal temperatures can be subject to high rates of predation (Christian and Tracy 1981) and have reduced foraging success (Avery *et al.* 1982). Consequently, if maximal locomotor performance is regularly important to fitness, then ectotherms should thermoregulate at temperatures that are near optimal for locomotor performance (van Berkum *et al.* 1986). The thermal dependence of speed has now been studied in more than 50 species of reptiles, mainly lizards (Huey, van Berkum, Bennett and Hertz, unpublished review). With a few interesting exceptions (e.g. van Berkum 1986; Huey and Bennett 1987; Huey *et al.* 1989a), most species thermoregulate at body temperatures that are very close to their optimal body temperatures for sprinting; this pattern suggests that the ability to run quickly is important over evolutionary time.

The above comparative pattern suggests that thermal preferences of reptiles are 'co-adapted' evolutionarily with optimal temperatures. Huey and Bennett (1987) tested this hypothesis by conducting a phylogenetic

analysis of interspecific data on the thermal dependence of speed in Australian lygosomine skinks. These skinks show remarkable variation in laboratory thermal preferences and in the upper temperatures at which their righting response is lost (critical thermal maxima: Greer 1980; Bennett and John-Alder 1986). Using an independently derived phylogeny, Huey and Bennett (1987) found that evolutionary shifts in thermal preferences were positively correlated with shifts in optimal temperatures for sprinting, consistent with the hypothesis that the ability to run quickly is important, at least on an evolutionary time-scale. In one genus (*Eremiascincus*), however, shifts in thermal preference and in optimal temperature appear to have been in opposite directions. Obviously, evolution does not always favor high sprint performance.

An interspecific study on the thermal sensitivity of maximal jump distance in tree frogs (John-Alder *et al.* 1988) found a correspondence between biogeographic distribution and ability to jump at low body temperatures. Northern temperate species that breed early in the season can hop at body temperatures that incapacitate later breeding (sympatric) species; both are less affected by low temperatures than are southern temperate or tropical species.

Another type of interspecific comparison involves searching for correlations between activity levels in nature and maximal performance capacities in the laboratory. For example, the foraging mode of species of frogs correlates with their aerobic capacity for exercise (Taigen *et al.* 1982; Pough 1983; Taigen and Pough 1985). For example, lacertid lizards in the Kalahari Desert of Africa differ strikingly in foraging mode (Huey and Pianka 1981): some ('widely foraging species') move about 50–60 per cent of the time they are out of their burrows, whereas others ('sit-and-wait species') move only about 15 per cent of the time. Locomotor capacity reflects these differences in foraging mode: widely foraging species have relatively high endurance, but relatively low acceleration and speed (Huey *et al.* 1984). These capacity differences are also reflected in organismal metabolic potentials (Bennett *et al.* 1984) and field metabolic rates (Nagy *et al.* 1984). The sit-and-wait mode appears evolutionarily derived in these lacertids (Huey and Bennett 1986).

In an important set of recent studies, Losos (1990*a,b*) has examined the relations between morphology (e.g. relative hindlimb length), locomotor capacity (e.g. speed, jumping ability) and field behavior (movement patterns) in Caribbean lizards of the genus *Anolis*. Because phylogenies are available for these lizards, Losos was able to conduct phylogenetic as well as multivariate comparisons. He found that evolutionary changes in morphology, performance and field behavior were correlated. For example, the evolution of short legs in a lineage is associated in the laboratory with decreased abilities to sprint quickly (Fig. 4) and to jump far. In

nature, such lineages crawl relatively frequently, but jump rarely and for short distances.

Finally, several studies have compared locomotor capacities of populations believed subject to different rates of predation. Selection may have favored faster lizards when exposed to a higher risk of predation (Bakker 1983; Snell *et al.* 1988), although alternative ways of reducing risk (Endler 1986b) could of course be favored. Several studies are consistent with this expectation (Crowley 1985a; Snell *et al.* 1988; Sinervo 1988), but others are not (Huey and Dunham 1987; J. Herron and B. Wilson, personal communication).

Intersexual differences in locomotor capacities may reflect different selection pressures on the sexes. Male lava lizards (*Tropidurus albemarlensis*) in the Galapagos run faster than do the females. Snell *et al.* (1988) suggest that sexual selection for territorial defense by males increases their vulnerability to predation, leading to selection for longer limbs and greater speed. Alternatively, but not exclusively, the shorter limbs and slower speeds of the females may relate to biomechanical requirements associated with carrying heavy egg burdens.

This eclectic set of comparative studies suggests that locomotor capacity often reflects the behavioral ecology of a species, population or even sex. They are thus consistent with the hypothesis that maximal locomotor

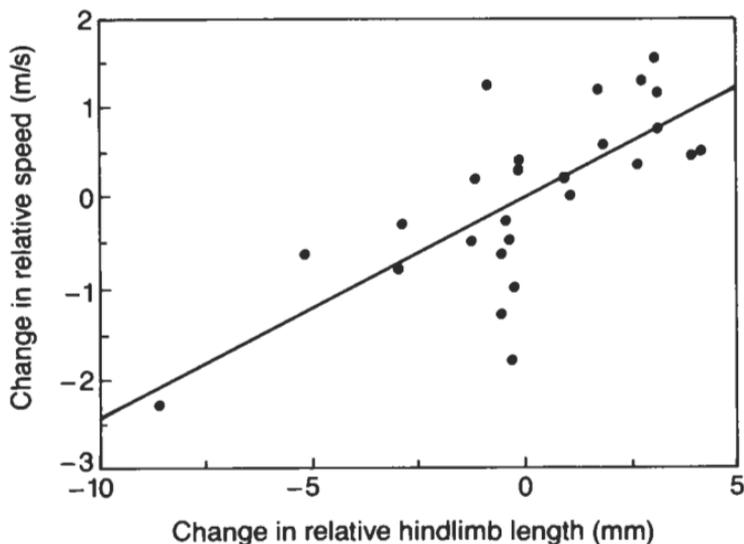


Fig. 4. A phylogenetic analysis of different species of *Anolis* lizards from the Caribbean showing that evolutionary changes in relative hindlimb length are correlated with evolutionary changes in relative speed. The effects of body size have been removed by regressing the variable against snout-vent length. Reprinted from Losos (1990a) with permission.

performance is evolutionarily important. Nevertheless, comparative studies show that reduced locomotor capacity can sometimes evolve (Huey and Bennett 1987; Huey *et al.* 1989).

7. CONCLUSIONS AND FUTURE DIRECTIONS

We have examined here a physiological character, specifically maximal locomotor capacity, from a variety of distinct but complementary evolutionary perspectives. We chose locomotor capacity because of its presumed ecological significance and the relative availability of information on the topic, but at least theoretically nearly any functional character could be subjected to a similar analysis. Because we are still developing and applying our approach, our chapter should be considered a progress report. To date we have found that locomotor capacity is highly variable among individuals, that this variability is stable through time, and that it has a genetic component. Therefore, the potential exists for studying the dynamics of selection on the character in real time and for detecting responses to selection over evolutionary time. Intrapopulation studies of phenotypic selection, which examine the process of evolution, yielded conflicting results: one study found directional selection on locomotor performance in certain age classes, yet two others failed to detect such selection. Interspecific, interpopulation and intersexual comparative patterns, which document the results or the patterns of evolutionary change, generally suggest that maximal performance correlates with the behavior and ecology of reptiles in nature, thereby suggesting that maximal performance is important over evolutionary time-scales.

We believe that the integrative, multi-approach type of study that we have described here has potential not only to enrich physiological ecology and evolutionary biology, but also to promote interaction between them. For example, this approach can yield insights into the evolution of complex organismal functions, such as energy exchange, activity and growth. These sorts of characters are generally speculated to be of biological and evolutionary importance but are often too complex and environmentally dependent to be analyzed profitably in experimental laboratory systems or by traditional physiological or genetic techniques. Moreover, such studies have the promise of freeing physiological ecology from an implicit adaptationist program (cf. Gould and Lewontin 1979; Feder 1987; Pough 1989) by turning attention to the process of adaptation, rather than its simple assumption. These protocols also open hosts of new and interesting questions and firmly embed studies within the natural environments, demography and ecology of the organisms investigated.

The general approach outlined here is not the only one likely to generate novel insights into the evolution of physiology. Several 'gene to perform-

ance' studies (Arnold 1987) have been remarkably successful (Watt 1985; Koehn 1987; Powers 1987). Moreover, considerable potential exists for using selection experiments (Service 1987; Rose and Graves 1989; Hoffman and Parsons 1989; Huey and Kingsolver 1989; Bennett *et al.* 1990; Huey *et al.*, in press; Garland, personal communication), 'allometric' engineering (Sinervo 1990; Sinervo and Huey 1990) and genetic engineering (Powers 1987) as manipulative tools to probe the evolution of physiological performance.

Because new directions in evolutionary physiology are rapidly being developed, we expect a much broader dialogue among organismal biologists and evolutionary biologists than has occurred in the recent past. We expect to see many more explicit interactions between evolutionary geneticists and physiological ecologists and much more sophisticated analyses of the genetic contribution to observed character variation. We encourage a greater concentration on the examination of performance during the entire life-cycle of organisms, rather than a concentration just on a single stage (e.g. neonates, or adults only during breeding). Studies – descriptive and manipulative – that investigate the selection of complex organismal functions in natural populations have only just begun. Similarly, physiological ecologists are only beginning to take advantage of phylogenetic techniques to study comparative patterns of trait evolution. Wide open are opportunities to use selection experiments and related techniques to study the microevolution of physiological traits in the laboratory. If these new approaches are integrated with the powerful ones traditionally used by physiological ecologists to dissect the mechanistic bases of trait variation, the field of evolutionary physiological ecology will have an exciting future.

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