

Measuring Performance in Nature: Implications for Studies of Fitness Within Populations¹

DUNCAN J. IRSCHICK²

Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana 70118

SYNOPSIS. Significant relationships among morphology, behavior, performance and fitness have long served as *bona fide* evidence for the role of selection in shaping natural populations. Here, I discuss how studies of ecological performance, or how organisms perform in nature, provide an ecological context for such selection studies. Laboratory studies assume that the level of performance expressed under “optimal” conditions accurately reflects the level of performance used in nature, but I show here that this assumption is not always borne out. A review of how various factors affect ecological performance (ontogeny, microhabitat, and macrohabitat) show that animals often express very different levels of movement speed both among different tasks, and when comparing laboratory *versus* field performance. Thus, a failure to take this variation into account could lead to negative, or even misleading significant fitness-character correlations. While laboratory performance studies should continue to play a key role in studies of selection, recent technological (*i.e.*, portable high-speed cameras) and methodological developments should enable researchers to measure performance in nature to high degrees of accuracy. Thus, I encourage researchers to measure performance both in the laboratory and in the field, and thus expand the traditional paradigm of morphology → performance → fitness to morphology → ecological performance → fitness.

INTRODUCTION

A central theme within ecological and evolutionary physiology is the extent to which variation in physiology and morphology affects performance and fitness (Hertz *et al.*, 1988; Pough, 1989; Bennett and Huey, 1990; Garland and Losos, 1994; Aerts *et al.*, 2000; Irschick and Garland, 2001). Many biologists consider performance to be a key intermediary link between the phenotype and fitness (Bartholomew and Tucker, 1963, 1964; Huey, 1983), and consequently biologists have studied performance under laboratory settings, particularly locomotor performance, in a variety of different species (see references above). However, despite the importance of this paradigm, two key problems plague studies of performance and fitness. First, few studies have attempted to determine whether individuals with high levels of performance enjoy high fitness in nature (Hertz *et al.*, 1988; Kingsolver *et al.*, 2001). Indeed, far more studies have examined the relationship between morphology and performance than between performance and fitness. Second, little information is available on the ecological context in which selection occurs (Bennett and Huey, 1990; Irschick and Losos, 1998; Irschick and Garland, 2001; Kingsolver *et al.*, 2001). For example, until recently, little was understood concerning how many animal species use their maximum sprinting capacities regularly in nature (here referred to as “ecological performance” *sensu* Irschick and Garland, 2001; see also Hertz *et al.*, 1988).

The implications of studying ecological performance for within-species selection studies are profound. The oft-cited paradigm linking morphology, performance and fitness within a population (Arnold,

1983) to understand the dynamics of selection, and hence, adaptation relies on the assumption that performance as measured under laboratory settings accurately reflects how animals perform in nature. A recent review of field studies of ecological performance shows that this assumption is frequently violated (Irschick and Garland, 2001). Further, animals often exhibit behaviors in laboratory situations that they might not in the wild (see *e.g.*, Hertz *et al.*, 1982). Thus, if performance in the lab does not accurately reflect ecological performance, then selection coefficients could be inaccurate, or even misleading. Perhaps even more importantly, studies of ecological performance enable biologists to interpret correlations between laboratory measures of performance, morphology and fitness. In this paper, I aim to show that (1) one can accurately measure locomotor performance in nature, (2) that ecological performance frequently differs from laboratory performance, and (3) this disparity could potentially affect interpretation of selection coefficients. I argue that biologists should find ways to measure performance for their respective organisms under more natural settings, and that they adopt the inclusive paradigm outlined in Figure 1 by measuring performance in both the laboratory and in the field. I demonstrate the above three points by discussing how various factors affect ecological performance in lizards.

Two key factors that could influence the level of ecological performance expressed within or among populations are ontogeny, and variation in habitat use. Numerous studies have examined how habitat use, performance, and even morphological shape change across ontogeny in animal and plant species (*e.g.*, see reviews by Werner and Gillam, 1984; Carrier, 1996, see also Warner and Andrews, 2002 for a recent example). A recurring finding from this body of work is that changes in both age and size (which are often linked) affect a broad range of ecological, physiolog-

¹ From the Symposium *Selection and Evolution of Performance in Nature* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 4–8 January 2003, at Toronto, Canada.

² E-mail: Irschick@tulane.edu

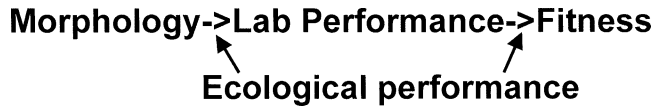


FIG. 1. The traditional paradigm for understanding the adaptive value of a morphological trait by relating morphological variation to performance variation and fitness. Included is the term "ecological performance," which is how animals perform in nature.

ical, and behavioral characteristics. For example, previous studies have examined how both maximum speed and endurance change ontogenetically (see reviews by Garland and Losos, 1994; Carrier, 1996), and a general finding is that larger, and hence older, individuals tend to have greater locomotor capacities relative to smaller individuals. Thus, differences in size have potentially profound implications for the ecology and fitness of large and small animals (e.g., Huey and Hertz, 1984; Martin and Lopez, 1995; Van Damme and Van Doreen, 1999). If fitness is positively related to absolute levels of performance, then larger individuals should enjoy higher levels of fitness compared to smaller animals. However, if fitness is more closely tied to relative (*i.e.*, size-adjusted) performance capacities, then smaller individuals may actually enjoy higher fitness relative to larger individuals (Van Damme and Van Doreen, 1999). One way for smaller animals to compensate for their poor performance is to run at higher levels of maximum performance in nature when doing different tasks, such as capturing prey or escaping predators. Of course, this assumes that adult animals will not run at their highest levels of performance capacity in nature, which has proven to be correct in a few cases (Irschick and Losos, 1998), but why this is true is not completely clear. Another way for performance-impaired animals to compensate is for them to adopt escape behaviors that minimize the importance of speed, such as female lizards adopting more cryptic habits when gravid (Bauwens and Thoen, 1981). If one found a general trend that performance-impaired animals moved to higher levels of maximum capacity in nature, then this would suggest that such animals are under intense selection to overcome these constraints (the hypothesis of compensation, Irschick, 2000a). However, to address this issue, one needs information not only on how maximal speed changes with age, but also on the actual speeds used by animals while performing different behavioral tasks in nature.

Both micro- and macrohabitat variation can also affect ecological performance, and consequently, fitness. Consider, for example, two populations of the same species that occur in different habitats. One population occupies a habitat characterized by steep inclines, such as a sand dune with an undulating series of hills, while the other population occupies a generally flat area. Because of the effects of incline on maximum speed and acceleration (Huey and Hertz, 1982, 1984), the dynamics of predator escape and locomotor performance in these two areas are likely to differ substantially. For example, the population that occupies the habitat with

steep hills may prefer to escape predators by running directly uphill, which would diminish the animals speed, but not to the same extent as the larger predators (Huey and Hertz, 1984). By contrast, animals within the second population may run randomly with respect to incline, because running uphill provides no true advantage. Thus, in both populations, maximum speed may show a significant relationship with fitness, but the context in which performance is important for predator evasion differs. Thus, habitat variation, both within and among populations, has potentially profound consequences for how selection favors individuals with different performance capacities.

Here, I discuss recent studies examining how both variation in ontogeny and macro- and microhabitat use affects ecological performance in lizards and also discuss the implications of these studies for studies of fitness. I then provide some conclusions for how future research could integrate studies of fitness and ecological performance.

ONTOGENETIC EFFECTS ON ECOLOGICAL PERFORMANCE

To illustrate the effects of ontogeny on ecological performance, I discuss studies of how different age and sex classes differ in ecological performance during several key tasks (escape from a threat, capturing a prey item, and undisturbed movement) within a single arboreal lizard species (*Anolis lineatopus*) from Jamaica (Irschick, 2000a). *Anolis lineatopus* is a small, semi-arboreal lizard (about 5 g in mass) that is common throughout lowland habitats of Jamaica. More exact details of this work can be found in Irschick (2000a). Briefly, the maximum sprint speeds of adult males, adult females and juveniles (juveniles could not be sexed reliably) were examined both in nature during the three above-mentioned tasks, and in the laboratory during locomotion under presumably optimal conditions, which for anoles consists of broad (>5 cm diameter) surfaces inclined at 45°. This convention is used because anoles typically jump on flat or near-flat surfaces, and they rarely run on flat surfaces in nature (Irschick and Losos, 1999). Thus, a broad, inclined surface presents an optimal or near-optimal setting for measuring maximum speed in these lizards. I then used measure of maximum speed under optimal laboratory conditions as a measure of performance capacity, and scaled the measures of ecological performance to them (see below). A recurring issue when examining locomotion is which aspect of locomotion is important when comparing animals of different sizes (Van Damme and Van Dooren, 1999). Thus, I calculated three metrics of performance (absolute speed, relative speed [absolute speed divided by body length], and speed as a percentage of maximum).

During escape trials, lizards were filmed when approached by a threat (another person approaching at a constant pace), and the maximum speed used by each individual lizard (filmed at 30 frames/s) was used as the estimate of maximum speed for that individual. For feeding trials, lizards were carefully approached and

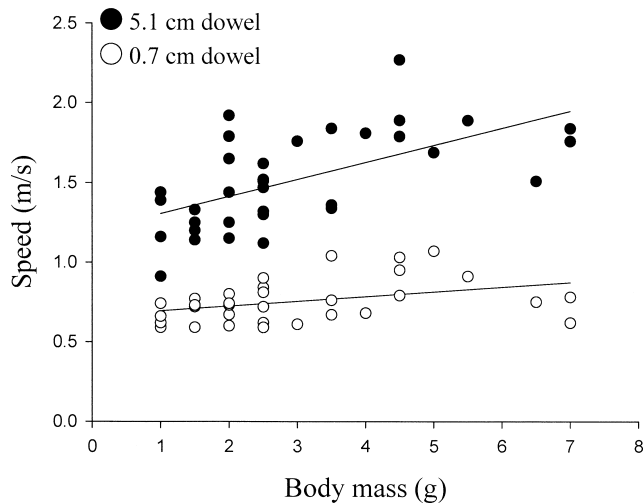


FIG. 2. A plot of speed in the laboratory vs. body mass for 34 adult male, adult female, and juvenile *A. lineatopus* lizards for both 5.1 cm and 0.7 cm dowels. Each point is an individual. Regression lines are least-squares. Both regressions are statistically significant ($P < 0.05$). Taken from Macrini and Irschick (1998).

an artificial fly resembling a mosquito was placed about 1 m from the lizard to elicit a feeding reaction, which consisted of the lizard chasing the prey item. The maximum speed used by each individual when capturing the prey item (lizards almost always ran after and bit the prey item) was used as the estimate of maximum speed for feeding. Finally, lizards were filmed when moving undisturbed through their habitats with a video camera, and the speeds and distances of all movements were recorded. Quantifying undisturbed locomotion provides an important “baseline” comparison to more typically “maximal” events, such as predator escape or feeding (Irschick, 2000b). This is because one cannot determine whether performance during “rare” events (*i.e.*, capturing prey, escaping predators, Hertz *et al.*, 1988) is unusually high or low without comparison to movements that the animal conducts on a daily basis. Because gravity may affect sprint performance and behavior (*e.g.*, Bauwens and Thoen, 1981), none of the anole females were gravid.

Primary findings and analysis

Maximum speed in the laboratory scaled positively with size within *A. lineatopus* (Fig. 2). The mechanism of this increase in speed with size is not entirely understood, but likely relates to the greater stride lengths of larger lizards, which is commonly observed (see *e.g.*, Bonine and Garland, 1999). Thus, if absolute speed is important for avoiding predators or capturing prey, one would predict that smaller lizards would try to compensate for their poor absolute speeds by moving at either higher relative speeds, or at a higher percentage of maximum capacity when feeding or escaping a threat. I used one-way ANOVAS comparing different age/sex classes for different kinds of performance (see Table 2 of Irschick, 2000a). I could not examine interactions of behavior (*e.g.*, escape *versus*

feeding) because different sets of individuals were examined for each behavior. Likewise, because the smaller adult females run at slower absolute speeds than adult males, then one would also predict that adult females would run at relatively faster speeds compared to adult males, but not compared to juveniles. Inspection of the data provides only partial support for this hypothesis.

In terms of absolute speed, juveniles did not differ significantly in either escape or feeding speed compared to adult males and females (Fig. 3). When expressed as relative speed (SVL/s), juveniles were significantly better performers than adult males and adult females during both escape and feeding. When expressed as a percentage of maximal speed, juveniles were significantly better performers than adult females during escape, and adult males and adult females during feeding. Thus, by any measure, juveniles are generally equal or better performers than the two larger intraspecific classes that have higher absolute maximum speeds. However, adult females were not significantly better performers than adult males during either escape or feeding using either relative speed or percent maximal speed, despite the females having, on average, an 11% lower sprinting capacity than adult males (Macrini and Irschick, 1998).

The implications of these findings for the fitness of different age and sex classes within *A. lineatopus* is an area of current investigation. All studies of natural selection on performance to date have focused on absolute speed, or perhaps size-adjusted speed as a metric upon which selection should act (Jayne and Bennett, 1990; Kingsolver *et al.*, 2001), but no study has examined the relationship between the percentage of maximum speed used in nature during different behavioral tasks and fitness. Several authors have previously suggested that selection on locomotor performance is particularly strong during the juvenile stages because many predators feed on young organisms (Bennett and Huey, 1990; Jayne and Bennett, 1990). The fact that juvenile *A. lineatopus* move at very high percentages of maximum speed in nature when both escaping a threat and when capturing a prey item is suggestive that they are under intense pressure to both capture prey and escape predators. In this manner, juveniles appear to be using behavior as an intermediary to improve their performance (Garland and Losos, 1994). Of course, the above data beg the question as to why adult male lizards do not run at faster speeds in nature, of which they are capable. In this regard, it could be that lizards only run as fast as necessary to capture prey, or avoid being eaten. Thus, excess performance capacity may be used more rarely than previously thought. A direct test of this hypothesis would be to carry out fitness studies examining the survivorship of these different age classes, as well as examining the link between maximum speed, ecological performance and fitness. Completing the last portion would be time-consuming, as one would have to film individual lizards in nature, mark them, and then fol-

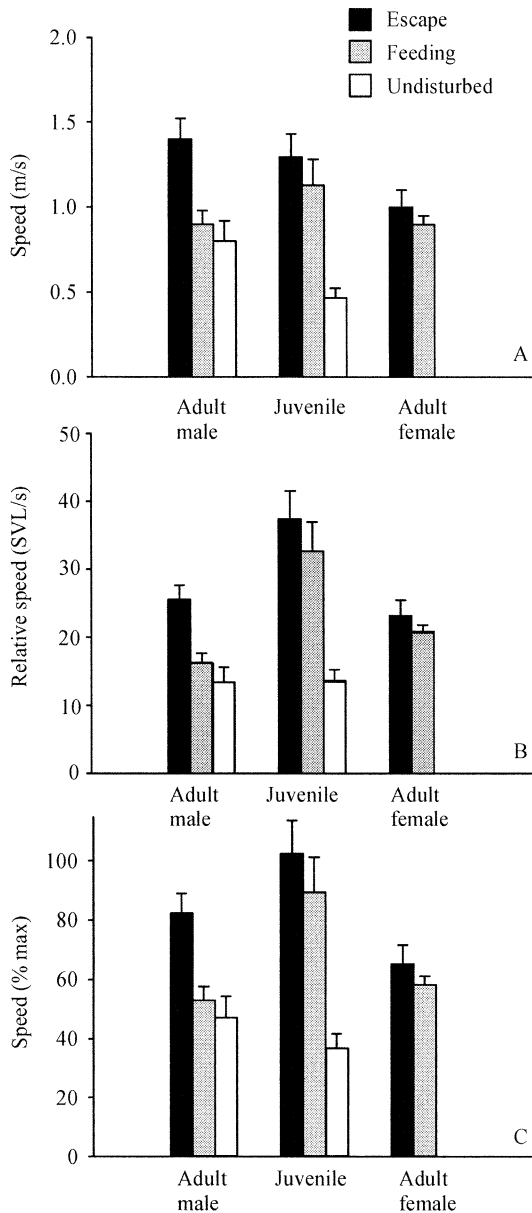


FIG. 3. Mean (+1 SE) values for absolute speed (A), relative speed (B), and percent maximal speed (C) for different behaviors for adult males, juveniles and adult female lizards of the species *A. lineatopus*. Sample sizes (numbers of individuals sampled) are as follows: Adult males (taken from Irschick and Losos, 1998): escape (20), feeding (17), undisturbed (18), Juveniles; escape (12), feeding (15), undisturbed (17), adult females; escape (14), feeding (14). Note that no undisturbed data are available for adult females. Taken from Irschick (2000a).

low these individuals across time. However, this project would be feasible for species such as *A. lineatopus*, for which individuals are fairly easy to recapture in certain habitats.

EFFECTS OF MACROHABITAT VARIATION ON ECOLOGICAL PERFORMANCE

Movement in arboreal and terrestrial environments presents very different functional challenges for lo-

comotion. This transition actually forms a continuum, ranging from highly arboreal environments (*e.g.*, forest canopies) to semi-arboreal environments (*e.g.*, rocks), to fully terrestrial habitats (*e.g.*, flat ground) (see *e.g.*, studies of rock-dwelling lizards by Herrel *et al.*, 2001, 2002). When moving on narrow surfaces, which are frequently encountered in arboreal habitats, animals must contend with the problem of balancing their body mass over the perch to avoid toppling, which can be accomplished by either using a stiff, slow walk with erect limbs raised over the surface (as found in chameleons), or by adopting a body posture very close to the branch surface, which allows the center of mass to be positioned near the substrate (Moermond, 1979; Pounds, 1988; Losos and Sinervo, 1989; Losos, 1990). Similarly, movement up steep inclines, which are often present in arboreal environments, poses both energetic and mechanical challenges for locomotion (Taylor *et al.*, 1972; Reichman and Aitchison, 1981; Farley and Emshwiller, 1996), as moving upwards increases the amount of work needed to move a given distance relative to a flat surface, and this increased energetic cost increases with animal size. Further, a relatively unexplored area of functional research concerns the interactive effects of these different variables. Thus, a relevant question is how animals cope with these environmental challenges in nature. Here, I contrast the results from distantly related lizard taxa (the terrestrial fringe-toed lizard, *Uma scoparia*, and the arboreal *Anolis* lizards). Because this comparison is completed on different lizard taxa differing greatly in phylogenetic affinity, interpretations of any differences must be done with caution. Ideally, the issue of how species adapt to arboreal and terrestrial environments might be more profitably examined in a single species that occurs over a wide range of habitats, such as *Sceloporus* or *Urosaurus* (see below for more discussion of some recent work on this latter species).

PRIMARY FINDINGS AND ANALYSIS

Fortunately, comparative data on how arboreal and terrestrial animals move in nature is available. Data on the undisturbed speeds of a small terrestrial desert lizard (*Uma scoparia*) on their sand dune habitat (Jayne and Irschick, 2000) showed that their locomotion consisted of long bouts of relatively high-speed locomotion broken with short intervals of relatively low-speed locomotion. This species is a sand-dune specialist that has specialized morphological features for moving on loose sand, and uses bushes or clumps of vegetation as escape retreats (Stebbins, 1944). Jayne and Irschick (2000) estimated these speeds by examining tracks in the sand, and calculating stride lengths, which are closely related to speed (Alexander, 1989; Bonine and Garland, 1999; Irschick and Jayne, 1999). The high speeds used by *Uma* were note-worthy, as a closer inspection shows a bimodal distribution of speeds in which the higher data grouping consisted of high-speed running (average of this group = 75% of maximum) between patches of vegetation, and a lower

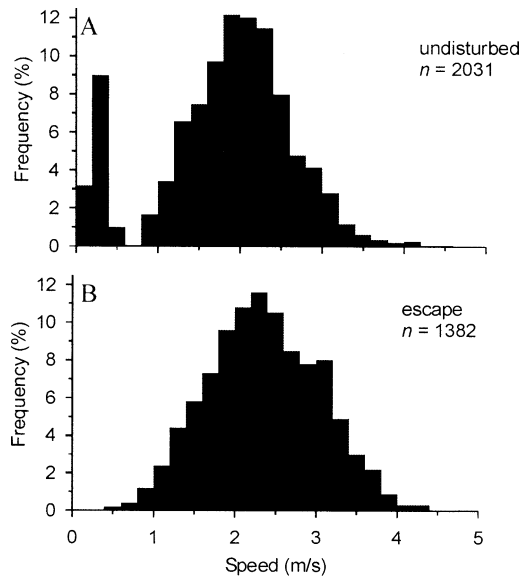


FIG. 4. Frequency distributions of speed per stride for the undisturbed (A) and escape (B) locomotion of the fringe-toed lizard *Uma scoparia* in the Kelso dunes. The undisturbed locomotion is from one of several plots in the sand dune, and the escape data from Jayne and Ellis (1998) were re-analyzed to facilitate direct comparisons with undisturbed locomotion. See Jayne and Irschick (2000) for more detail.

bin, which consists of slow-walking near patches of vegetation (Fig. 4A). Indeed, the undisturbed speeds of *Uma* were similar to those used during escape in the same habitat (Fig. 4B). The sand-dune landscape in which *Uma* occurs consists of clumps of scrubby vegetation that *Uma* and other animals use as retreats, either in the form of the bush itself, or in burrows that lie at their bases. The reason for the high-frequency of high-speed running in *Uma* is puzzling, but likely is related to two factors: the risk of overheating due to high temperatures, and the risk of predation. The Kelso sand dune surface can reach temperatures of up to 50°C during summer months, which is about 10 degrees higher than the preferred body temperature of *Uma*, and would likely be fatal to the lizard (Jayne and Irschick, 2000). Thus, one possibility is that lizards move quickly across open sand dune areas to avoid exposure to the sun and unshaded sand. A non-exclusive possibility is that *Uma* moved quickly among different patches of vegetation to avoid predators. Data on the maximum speeds of *Uma* in nature when escaping predators shows that these lizards reach substantially higher top speeds in nature compared to the laboratory, which is likely a consequence of the relatively short racetracks used to measure maximum speed (Jayne and Ellis, 1998).

A comparison with several arboreal species of *Anolis* lizards shows a very different pattern. Irschick (2000b) filmed eight arboreal *Anolis* lizard species when moving undisturbed through their habitats and quantified the speeds and distances of all movements. Several patterns were apparent from these data. First, the distributions of undisturbed speeds for all the eight

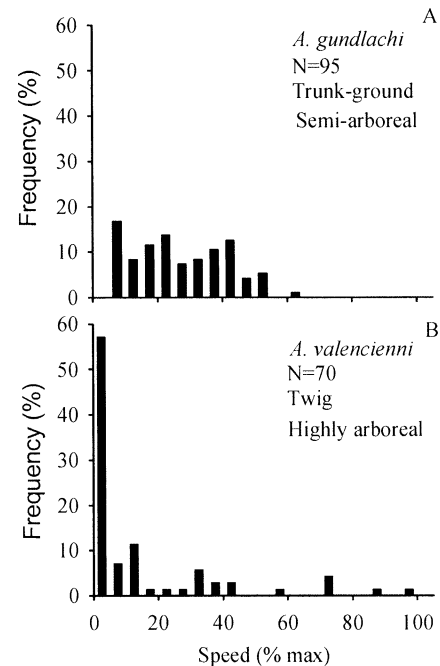


FIG. 5. The frequency distributions of field undisturbed speeds per move for two different *Anolis* lizard species, of which *A. gundlachi* is relatively terrestrial, and *A. valencienni* is highly arboreal. See Irschick (2000b) for more details.

species were unimodal, and consisted of relatively slow locomotion, typically averaging 10–20% of maximum speed (Fig. 5). By contrast, maximum speeds during predator escape and prey capture averaged about 90% and 70% of maximum speed (among species), respectively (Irschick and Losos, 1998). Nevertheless, laboratory measures of maximum speed were good approximations of the maximum speeds of which *Anolis* lizards were capable. A second pattern was that more terrestrial *Anolis* species moved at generally higher speeds than more arboreal anole species. For example, the trunk-ground Puerto Rican anole *A. gundlachi* moved at speeds ranging from 25–40% of maximum speed, whereas the twig *A. valencienni* moved at significantly slower speeds (5–20% maximum speed). Thus, while both species move slowly when undisturbed, the species that occurs on broader and lower perches (*A. gundlachi*) generally moves at faster undisturbed speeds, which may result from its more conspicuous and territorial habits. By contrast, the twig anole *A. valencienni* moves on surfaces on which rapid locomotion is difficult (narrow twigs), and thus this species relies on being cryptic (by moving slowly) to avoid predators. This pattern was also manifested in the maximum speeds observed during predator escape and feeding (Irschick and Losos, 1998). Another notable difference in comparison to *Uma* was the very short distances moved by *Anolis* lizards during undisturbed movements, escape, and feeding. *Anolis* lizards typically moved only 50–100 cm at most when capturing prey or escaping a threat, in comparison to escape paths of up to 30 m for *Uma scoparia* (Jayne and

Ellis, 1998). During undisturbed locomotion, *Anolis* lizards took only short moves of 5–10 cm, on average, while *Uma scoparia* traveled long distances (>10 m) unbroken by pauses (Jayne and Irschick, 2000).

Which factors could explain these differences in the patterns of undisturbed and maximum escape speeds for the terrestrial *Uma* species and arboreal *Anolis* lizards? First, one must be cognizant of the fact that one is comparing lizards from two different families, which is concomitant with various morphological, behavioral, and physiological differences (e.g., Perry, 1999; McBryder and Reilly, 2002). Only a greater amount of comparative data, preferably from different clades that have independently invaded arboreal and terrestrial habitats, will enable us to determine if these findings are general. Second, the physical structure of the sand dune and arboreal habitat may explain some of these differences. The arboreal habitats of anoles are composed primarily of short perches separated in space. Consequently, the movements of all eight anole species, during undisturbed, escape, and feeding locomotion, were extremely short, which places a severe constraint on the speed of locomotion. By contrast, the open habitat of the Kelso sand dune system enables lizards to move much longer distances. This difference in escape distances is important because *Uma* achieve their top speeds after about 2 m of running, whereas *Anolis* lizards rarely run continuously for more than about 1 m. Thus, *Anolis* lizards may never achieve their top speeds in either nature or in the laboratory due to their pattern of moving intermittently. Finally, the structure of escape retreats may also play a key role in how *Uma* and *Anolis* lizards modulate speed. *Uma* will frequently run long distances when escaping a predator to reach their escape retreats, which are typically bushes or clumps of vegetation. By contrast, when disturbed, *Anolis* lizards typically only moved long enough to outrun the immediate threat, and they did not appear to use obvious escape retreats. Lastly, one must be aware that while I have only discussed running or walking in anoles, many of their movements consist of jumps between adjacent perches (Moermond, 1979; Irschick and Losos, 1998), a behavior not observed in most terrestrial lizards. Thus, more detailed studies on how anoles jump in different behavioral contexts would be welcome.

A key lesson from the above comparison is that different species will adapt their locomotor behaviors for occupying habitats with different structures. In general, biologists have neglected the role of macro-variation in habitat use in terms of the influence on locomotion. Future studies could extend these studies by examining locomotion in nature in different environmental circumstances, such as when lizards occupy completely vertical surfaces (e.g., geckos), or subterranean habitats (i.e., legless lizards). Comparative studies of lizards have shown that lizards adopt a wider array of escape behaviors in regions with more predators (Schall and Pianka, 1980), so one must also be cognizant of geographic variation in such aspects. Ma-

nipulative studies of the effects of habitat use on natural locomotion would be useful, particularly if they could alter natural features of the environment. For example, one could manipulate the inclines of terrestrial habitats, or the surface diameters of arboreal habitats and then use a comparative approach to determine how different species respond to this imposed environmental heterogeneity (e.g., Pounds, 1988). These kinds of studies would provide a more experimental component to the descriptive studies already published.

EFFECTS OF MICROHABITAT STRUCTURE ON ECOLOGICAL PERFORMANCE IN DESERT LIZARDS

The habitat of any animal species is composed of a mosaic of different environmental features (e.g., Ender, 1993). For example, arboreal animals regularly encounter a variety of handholds that they must successfully navigate to move through their environment (Moermond, 1979; Cartmill, 1985). Ecologists have largely focused on quantifying those aspects of habitat use that they have considered to be important for resource partitioning, such as prey type, or where the animal occurs in the forest canopy. By contrast, many aspects of the environment that are important for animals functionally have rarely been quantified comprehensively, and even fewer studies have related variation in these variables to micro-variation in ecological locomotor performance. An exception to this generalization is spatial and temporal variation in temperature, as physiological ecologists have devoted considerable time and effort to quantify temperature in nature, as well as its effects on many aspects of animal physiology in the laboratory (e.g., Huey, 1974; Huey and Stevenson, 1979; Bennett, 1984; Bakken, 1989; Adolph, 1990; Hertz, 1992a, b; Adolph and Porter, 1993; Angilletta *et al.*, 2000). It would also be interesting to understand the relationship between body temperatures in the field and ecological locomotor performance. However, with this exception, most ecological or evolutionary physiologists have little understanding of the distribution of environmental variables that bear a direct relationship to functional capacities. This statement is particularly true for environmental variables important for locomotion, but movement is a key ecological variable that is critical for animals to access different parts of their habitat.

A hypothetical example highlights the importance of both quantifying habitat use in detail, and measuring how that variation affects ecological performance. Consider an arboreal animal species that moves on a matrix of branches (e.g., Moermond, 1979). The ability of that animal species to successfully move through its habitat is in large part determined by their choice of perches. For example, if an individual animal tends to move only on perches on which it runs quickly, then that individual may have enhanced success at capturing prey and avoiding predators. If one assumes that every individual is making choices to move as effectively as possible, then every individual within a spe-

cies would only choose those branches that optimize their ability to move quickly or efficiently, but other behavioral or ecological factors may preclude them from doing so. For example, in many animal species, subadults are confined to suboptimal habitats that are less beneficial for finding food. Thus, if an individual within this hypothetical animal species is constrained to only use habitats that are suboptimal for climbing, then one might predict that this individual might have a lower fitness than individuals that occupy more favorable habitats. As a first step in addressing this issue, one must quantify the range of environmental variables used by individuals of differing ages and sexes within a population, and then examine how this variation affects ecological performance. A logical second step would be to relate variation in fitness among different individuals to variation in habitat preference. Here, I discuss these issues by describing recent field studies examining relationships among ecological performance, incline use, and the amount of vegetation within a terrestrial lizard (the zebra-tailed lizard, *Callisaurus draconoides*) (Irschick and Jayne, 1999).

Inclines can profoundly affect the dynamics of predator-prey interactions. For example, large animals cannot accelerate up steep inclines to the same extent as for small animals. Thus, one potential strategy for relatively small animals in an environment that varies in incline is to escape by preferentially running up steep inclines (Huey and Hertz, 1984). However, this issue has rarely been examined via detailed field studies. In addition to incline, the amount of vegetation in a habitat can also influence the dynamics of predator-prey interactions. In a terrestrial habitat, many animals use clumps of vegetation as escape retreats (see *e.g.*, Kenagy and Hoyt, 1989). Thus, an animal in a terrestrial habitat that varies both in incline and the amount of vegetation cover faces a choice when faced with a predator in terms of where to run. To comprehensively address this issue, one needs to first assess the availability of habitat variables in the habitat, and then examine how animals modulate their escape behavior relative to these variables.

PRIMARY FINDINGS AND ANALYSIS

Irschick and Jayne (1999) examined this issue for the escape locomotion of the zebra-tailed lizard (*Callisaurus draconoides*). They measured the escapes of 30 individual lizards and determined both the availability of inclines in their habitat, as well as the inclines used during escapes. Further, they examined how these lizards modulated speed in the field, and how they changed their escape behavior as a consequence of the surrounding vegetation and inclines. Zebra-tailed lizards are common, small terrestrial lizards that typically occur in open desert habitats throughout the Mojave and Sonoran deserts; they show a distinct preference for sandy, or loose-grained soils (Hasson *et al.*, 1989). In the Kelso sand dunes of Southern California, these lizards occupy the edges of sand dunes, and thus all of the movements of this species are on

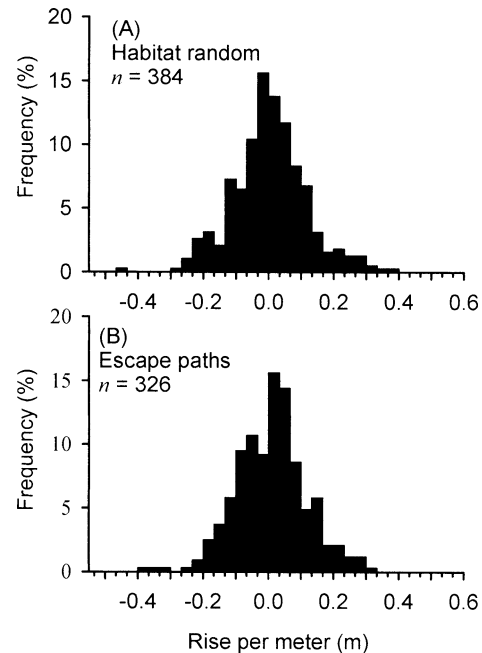


FIG. 6. The frequency distributions of random and actual inclines in the Kelso sand dune system. Actual inclines were gathered from 30 escape paths of the zebra-tailed lizard *Callisaurus draconoides*, and are based on meter by meter measurements. See Irschick and Jayne (1998) for more details.

fine wind-blown sand, on which their footprints are faithfully preserved. This provides an excellent opportunity to quantify speed in nature during different activities, which can be accomplished by measuring stride length, which in most vertebrate tetrapods, is closely linked with speed (Irschick and Jayne, 1999). Of course, this method ignores stride frequency, but laboratory studies with the closely related fringe-toed lizard (*Uma scoparia*) show that stride length is an excellent surrogate for speed (Jayne and Ellis, 1998). Escapes were elicited by approaching the lizard until they fled. Further, Irschick and Jayne (1999) noted whether the lizard escaped by running to nearby vegetation, or up the steepest incline. They also determined whether each stride was bipedal or quadrupedal, which is especially important for this species because they are known to run bipedally.

The Kelso sand dune habitat is composed of a continuum of inclines, that vary from flat (0°) to steep (up to 32° , which is the angle of repose for fine sand). Thus, zebra-tailed lizards encounter many different inclines on which they can potentially escape. The distribution of available inclines shows that the majority of inclines are shallow, and the actual data from escapes show that zebra-tailed lizards tend to escape by running up inclines at random (Fig. 6). In fact, zebra-tailed lizards showed a marked preference for running directly towards the nearest vegetative cover, regardless of the incline encountered, which suggests that they do not use inclines purposefully during their escape behavior. Interestingly, despite this willingness to

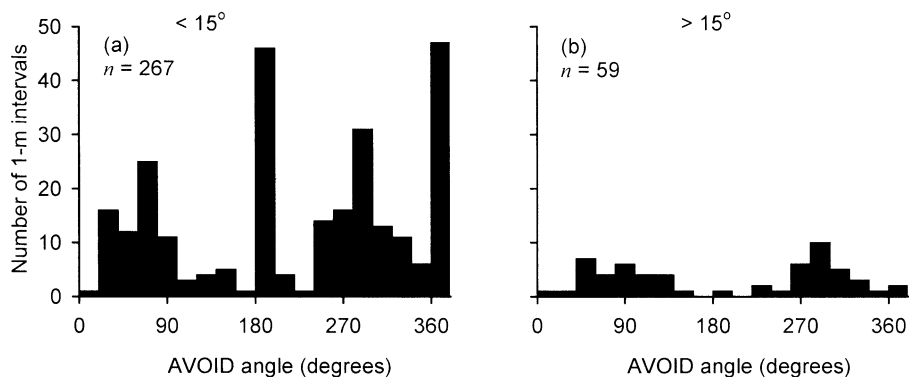


FIG. 7. The frequency distributions of field escapes on “shallow” (A) and “steep” (B) inclines for the zebra-tailed lizard, *Callisaurus draconoides*. 90° and 270° represent running horizontally, and 0° and 180° represent running directly uphill and downhill, respectively. Note the scarcity of running directly uphill or downhill on steep inclines. Taken from Irschick and Jayne (1999).

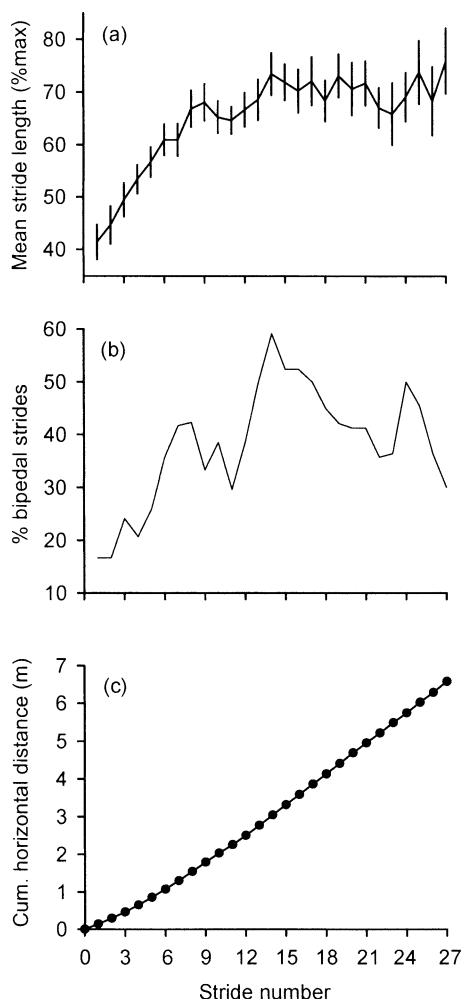


FIG. 8. (A) Mean (± 1 SE) relative stride length (% maximum), and (B) % bipedal strides versus stride number for data pooled across all field escape paths of the zebra-tailed lizard *Callisaurus draconoides*. Sample size for the first stride was 30, and declined to 10 for stride 27 as a result of different lengths of escape paths. (C) Mean cumulative distance traveled during escape paths versus stride number. Note the correlated increases in relative stride length and the proportion of strides that were bipedal as lizards initially accelerated from a standstill. Taken from Irschick and Jayne (1999).

escape up inclines at random, incline nevertheless exerted a significant negative effect on maximum escape speed. However, lizards may alter their behavior on inclines of different slopes. Indeed, closer inspection of the data reveal an interesting twist to the escape data. When the escape paths are divided into “steep” ($>15^\circ$), or “shallow” ($<15^\circ$) inclines (inspections of other inclines showed no such threshold), zebra-tailed lizards on shallow slopes escape randomly with respect to incline, but on steep surfaces, they avoid running directly uphill or downhill, and instead show a marked preference for running horizontally, or alongside the hill (Fig. 7). Observations of these lizards support this trend, as several lizards escaped by first running up a hill for a short distance, and then proceeded to run alongside the hill for the remainder of the escape run. Why zebra-tailed lizards should run horizontally along the hill is not obvious, but this behavior may enable these lizards to run faster than if they ran directly up the hill. The reason for the 15° threshold is unclear, but seems analogous to the gait changes of mammals (*i.e.*, trot-gallop transition, Hoyt and Taylor, 1981). An interesting study would be to conduct more detailed behavioral studies of lizards on inclines bordering this threshold. Thus, in sum, zebra-tailed lizards appear to run primarily in the direction of the nearest vegetation, and if they encounter a steep incline, they typically choose to run alongside the hill, not up or down it.

Another notable feature of the escape locomotion of zebra-tailed lizards was the high incidence of bipedalism, particularly as lizards accelerated from a standstill. Indeed, increases in velocity and the incidence of bipedalism were strongly correlated within escape paths (Fig. 8). Unfortunately, determining whether bipedalism was the cause of increased velocity, or simply a behavioral by-product (Aerts *et al.*, 2003), is difficult, as bipedality increased with stride number. Inspection of all strides showed, however, that bipedal strides were about 12% longer (Fig. 9), on average, than quadrupedal strides, which, assuming a similar stride frequency, suggests that bipedalism provides a performance advantage for this species. Laboratory studies

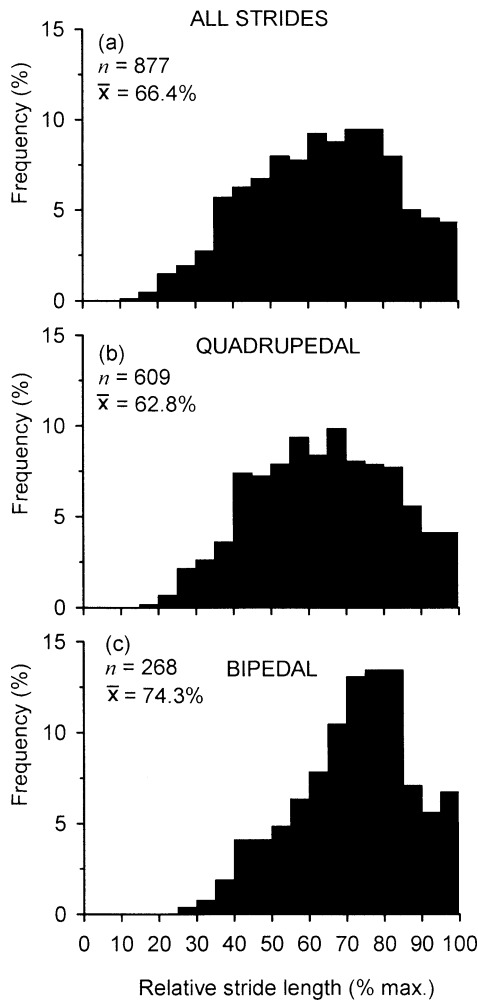


FIG. 9. Frequency distributions for relative (% maximum) stride lengths for a) all strides, b) quadrupedal strides only, and c) bipedal strides only from 30 escape paths of *Callisaurus draconoides*. Compared to quadrupedal strides, bipedal strides had a more distinct mode which was at a higher % maximum stride length.

show that speed during bipedal running increases in a similar manner with stride length as for quadrupedal locomotion (Irschick and Jayne, 1998, 1999). Whether this 12% difference is biologically significant is unclear, however. Another distinctive feature was the remarkably long escape paths of zebra-tailed lizards, which ranged from 2–30 m. In this regard, the maximum speeds of these lizards were typically not achieved until well into the escape path, typically not before 3-m, which is usually longer than racetracks used in the laboratory. These data underscore the importance of quantifying ecological performance, and not assuming that performance under optimal laboratory conditions will be an estimate of maximal capacity in all circumstances.

Overall, these data show that the escape responses of zebra-tailed lizards are remarkably fine-tuned to micro-habitat variation in inclines and vegetation. Zebra-tailed lizards changed the direction of movement, as well as their escape performance as incline increases,

and this behavioral shift typically occurred at inclines of about 15°. This form of ecological or behavioral threshold seems relatively rare, at least for studies of locomotion. Thus, future studies should consider the possibility that animals may exhibit subtle responses in their locomotor behavior as a response to environmental heterogeneity. Consequently, detailed measurements of environmental variables may be necessary to fully understand how animals modulate speed in natural habitats.

DISCUSSION AND CONCLUSIONS

Ecologists have long been interested in mapping environmental variation in great detail, but although physiologists have employed these kinds of techniques for analyzing temperature, and several other key variables, they have generally not applied the same set of techniques to study locomotion. However, because of its inherently ecological nature, a complete understanding of locomotion requires an ecological approach (Huey and Hertz, 1984; Dickinson *et al.*, 2000; Irschick and Garland, 2001; Biewener, 2002). Fortunately, new technology now allows researchers to literally take the “laboratory” into the field. Field-portable accelerometers (Harper and Blake, 1989, 1990) enable researchers to measure acceleration in nature, and the new field-portable Redlake motionmeter enables one to film locomotion in nature at high framing rates (up to 1,000 f/s), which is a dramatic improvement over standard field-portable video cameras (30 f/s). Further, the quantitative techniques discussed in this chapter and in other papers should allow for increasingly detailed analyses of locomotion in nature.

About 15 years ago, Hertz *et al.* (1988) and Pough (1989) made a plea for more field studies that examine performance in nature, particularly for locomotor performance (see also Wainwright, 1994). While we are far from achieving the same level of detail for locomotion as known from laboratory studies, enough studies have been completed to make some generalizations regarding how animals perform in nature relative to optimal laboratory conditions (*e.g.*, see Irschick and Garland, 2001). Despite these new studies, no studies have examined how ecological performance is related to fitness. Doing so would require working with animals that can be easily tracked in nature, and are also highly abundant. For example, one could examine the relationship between maximum speed in nature and fitness, or perhaps the relationship between percent maximum speed used during escape (which would require data on maximum speeds under optimal conditions) and fitness. The danger of ignoring ecological performance is that optimal performance as observed in the laboratory does not always translate into how animals perform in nature (Irschick and Garland, 2001), which could lead to negative results, or even misleading selection coefficients. Biologists should be aware that performance could be maximal in either the field or the lab, and should not assume that lab conditions are always optimal.

Another problem with ignoring ecological performance is that even if selection is detected on some characters, the ecological reason for why this selection is occurring may be unclear. Most studies of selection examine only morphological characters (Kingsolver *et al.*, 2001), and in many of these cases, the reason for why the morphological variable is under selection is not well-understood. Thus, even if researchers are unable to directly relate ecological performance to fitness for a species, one could at least examine ecological performance for a subset of animals during different tasks to gain an understanding of how that animal responds to a given pressure in a natural setting. Doing so might shed light on the adaptive significance of trait variation and selection on these traits. Another promising ecological area of research for locomotion involves the integration of energetic considerations into more natural measures of locomotion. For example, recent studies (*e.g.*, Hancock and Gleeson, 2002) have shown that much of the energetic expenditure of lizards occurs after they have stopped moving. Such factors could prove a powerful constraining factor on how fast or how far animals move in nature.

As a further extension, an unresolved question in evolutionary physiology concerns how survivorship is modulated by multiple aspects of performance (*e.g.*, Phillips and Arnold, 1989), which few, if any, researchers have investigated (Kingsolver *et al.*, 2001). This trend likely occurs because of the logistical difficulties of measuring performance on a large group of animals, particularly for more than one performance variable simultaneously. However, the fitness of any organism is likely an interaction between multiple aspects of performance that may evolve independently of one another. For example, for arboreal lizards, the ability to jump far or run quickly may be important for escaping predators, whereas the ability to cling well may be particularly important for escaping the clutches of a predator. Finally, the ability of lizards to bite may be valuable for defending against predators, intruders, and may also be important for consuming prey. However, because these different performance abilities are functionally related to different aspects of morphology (*i.e.*, jumping to hindlimb length, clinging to toepad area, and bite force to head dimensions), then evolution of these different characters may be largely independent, but the fitness of a lizard is likely influenced by all factors.

Recently, several collaborators and I (Bieke Van-Hooydonck, Anthony Herrel, and Jay Meyers) began to address this issue by establishing a marked population of the green anole (*Anolis carolinensis*) in St. Charles, Parish in southern Louisiana. Over a period of 4 weeks during September of 2002, we surveyed each day a 755 m long \times 12 m linear transect for any lizards, including adult males and females, and juveniles. The transect is a rarely used dirt access road with about 4 m of vegetation on each side of the road. Lizards cannot easily move out of the transect because a large open swamp bordered either side of the vegeta-

tion. A total of 405 lizards were captured, measured for morphology, performance (jumping, clinging, and bite force), diet, and habitat use, and released at their original point of capture. The ultimate aim is to attempt to recapture individual lizards yearly over the next 5–10 years to examine whether survivorship is significantly related to any specific kind of performance, or perhaps a combination of different kinds of performance. This kind of study would be a natural extension of previous studies of selection on single performance variables, such as maximum speed in snakes or lizards. The addition of measurements of ecological performance could also shed light on how evolution proceeds on multiple characters.

ACKNOWLEDGMENTS

I thank the organizers of this symposium (Dr. Ray Huey and Dr. Joel Kingsolver) for inviting me to participate. Special thanks to G. Perry, S. Adolph, R. Huey, and an anonymous reviewer for helpful comments on previous versions of this paper. This paper was supported by an NSF grant to D. Irschick (IBN 9983003).

REFERENCES

- Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71:315–327.
- Adolph, S. C. and W. P. Porter. 1993. Temperature, activity, and lizard life histories. *Am. Nat.* 142:273–295.
- Aerts, P., R. Van Damme, B. Van Hooydonck, A. Zaaf, and A. Herrel. 2000. Lizard locomotion: How morphology meets ecology. *Netherlands J. Zool.* 50:261–277.
- Aerts, P., R. Van Damme, K. D'Août, and B. Van Hooydonck. 2003. Bipedalism in lizards: Whole-body modelling reveals a possible spandrel. *Phil. Trans. Roy. Soc. Lond.* 358:1525–1533.
- Alexander, R. McN. 1989. Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* 69:1199–1227.
- Angilletta, M. J., Jr., R. S. Winters, and A. E. Dunham. 2000. Thermal effects on the energetics of lizard embryos: Implications for hatchling phenotypes. *Ecology* 81:12–17.
- Arnold, S. J. 1983. Morphology, performance and fitness. *Amer. Zool.* 23:347–361.
- Bakken, G. S. 1989. Arboreal perch properties and the operative temperature experienced by small animals. *Ecology* 70:922–930.
- Bartholomew, G. A. and V. A. Tucker. 1963. Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. *Physiol. Zool.* 36:199–218.
- Bartholomew, G. A. and V. A. Tucker. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiol. Zool.* 37:341–354.
- Bauwens, D. and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecology* 50:733–743.
- Bennett, A. F. 1984. Thermal dependence of muscle function. *Am. J. Physiol.* 247:R217–R229.
- Bennett, A. F. and R. B. Huey. 1990. Studying the evolution of physiological performance. *Oxford. Surv. Evol. Biol.* 7:251–284.
- Biewener, A. 2002. Future directions for the analysis of musculoskeletal design and locomotor performance. *J. Morph.* 252:38–51.
- Bonine, K. E. and T. Garland, Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J. Zool. London* 248:255–265.
- Carrier, D. 1996. Ontogenetic limits on locomotor performance. *Phys. Zool.* 69:467–488.

- Cartmill, M. 1985. Climbing. In M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake (eds.), *Functional vertebrate morphology*, pp. 73–88. Belknap Press, Cambridge.
- Dickinson, M. H., C. T. Farley, R. J. Full, M. R. Koehl, R. Kram, and S. Lehman. 2000. How animals move: An integrative view. *Science* 288:100–106.
- Endler, J. A. 1993. The color of light in forests and its implications. *Ecol. Mon.* 63:1–27.
- Farley, C. T. and M. Emshwiller. 1996. Efficiency of uphill locomotion in nocturnal and diurnal lizards. *J. Exp. Biol.* 199:587–592.
- Garland, T., Jr. and J. B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. In P. Wainwright and S. M. Reilly (eds.), *Ecological morphology: Integrative organismal biology*, pp. 240–302. University of Chicago Press, Chicago.
- Hancock, T. V. and T. T. Gleeson. 2002. Metabolic recovery in the Desert Iguana (*Dipsosaurus dorsalis*) following activities of varied intensity and duration. *Func. Ecol.* 16:40–48.
- Harper, D. G. and R. W. Blake. 1989. On the error involved in high-speed film when used to evaluate maximum accelerations of fish. *Can. J. Zool.* 67:1929–1936.
- Harper, D. G. and R. W. Blake. 1990. Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *J. Exp. Biol.* 150:321–342.
- Hasson, O., R. Hibbard, and G. Ceballos. 1989. The pursuit deterrent function of tail-wagging in the zebra-tailed lizard (*Callisaurus draconoides*). *Can. J. Zool.* 67:1203–1209.
- Herrel, A., J. J. Meyers, and B. Vanhooydonck. 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): A population-level analysis. *Biol. J. Linn. Soc.* 74:305–314.
- Herrel, A., J. J. Meyers, and B. Vanhooydonck. 2002. Relations between microhabitat use and limb shape in phrynosomatid lizards. *Biol. J. Linn. Soc.* 77:149–163.
- Hertz, P. E. 1992a. Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: A field test using null hypotheses. *Oecologia* 90:127–136.
- Hertz, P. E. 1992b. Temperature regulation in Puerto Rican *Anolis* lizards: A field test using null hypotheses. *Ecology* 73:1405–1417.
- Hertz, P. F., R. B. Huey, and T. Garland, Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: Are reptiles Olympians or Boy Scouts? *Am. Zool.* 28:927–938.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1982. Fight versus flight: Body temperature influences defensive responses of lizards. *Anim. Behav.* 30:676–679.
- Hoyt, D. F. and R. C. Taylor. 1981. Gait and the energetics of locomotion in horses. *Nature* 292:239–240.
- Huey, R. B. 1974. Behavioral thermoregulation in lizards: Importance of associated costs. *Science* 184:1001–1003.
- Huey, R. B. 1983. Temperature, physiology, and the ecology of reptiles. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 12, Physiology (C), pp. 25–91. Academic Press, London.
- Huey, R. B. and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Amer. Zool.* 19:357–366.
- Huey, R. B. and P. E. Hertz. 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *J. Exp. Biol.* 97:401–409.
- Huey, R. B. and P. E. Hertz. 1984. Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.* 110:113–123.
- Irschick, D. J. 2000a. Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. *Func. Ecol.* 14:438–444.
- Irschick, D. J. 2000b. Comparative and behavioral analyses of preferred speed: *Anolis* lizards as a model system. *Phys. And Biochem. Zool.* 73:428–437.
- Irschick, D. J. and T. Garland, Jr. 2001. Integrating function and ecology in studies of adaptation: Investigations of locomotor capacity as a model system. *Ann. Rev. Ecol. and Syst.* 32:367–396.
- Irschick, D. J. and B. C. Jayne. 1998. Effects of incline, acceleration, body posture, and hindlimb kinematics in two species of lizard, *Callisaurus draconoides* and *Uma scoparia*. *J. Exp. Biol.* 201:273–287.
- Irschick, D. J. and B. C. Jayne. 1999. A field study of the effects of inclines on the escape locomotion of a bipedal lizard. *Phys. And Biochem. Zool.* 72:44–56.
- Irschick, D. J. and J. B. Losos. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* 52:219–226.
- Irschick, D. J. and J. B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.* 154:293–305.
- Jayne, B. C. and A. F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204–1229.
- Jayne, B. C. and R. V. Ellis. 1998. How inclines affect the escape behaviour of a dune dwelling lizard, *Uma scoparia*. *Anim. Behav.* 55:1115–1130.
- Jayne, B. C. and D. J. Irschick. 2000. A field study of incline use and preferred speeds for the locomotion of lizards. *Ecology* 81:2969–2983.
- Kenagy, G. J. and D. F. Hoyt. 1989. Speed and time-energy budget for locomotion in golden-mantled ground squirrels. *Ecology* 70:1834–1839.
- Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.* 157:245–261.
- Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: An evolutionary analysis. *Ecological Monographs* 60:369–388.
- Losos, J. B. and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* 145:23–30.
- Macrini, T. E. and D. J. Irschick. 1998. An intraspecific analysis of trade-offs in sprinting performance in a West Indian Lizard (*Anolis lineatopus*). *Biol. J. Linn. Soc.* 63:579–591.
- Martin, J. and P. Lopez. 1995. Escape behaviour of juvenile *Pseudommodromus algirus* lizards: Constraint of or compensation for limitations in body size? *Behaviour* 132:181–192.
- McBryder, L. D. and S. M. Reilly. 2002. Prey processing in lizards: Behavioral variation in sit-and-wait and widely foraging taxa. *Can. J. Zool.* 80:882–892.
- Moermond, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* 60:152–164.
- Perry, G. 1999. The evolution of search modes: Ecological versus phylogenetic perspectives. *Am. Nat.* 153:98–109.
- Phillips, P. C. and S. J. Arnold. 1989. Visualizing multivariate selection. *Evolution* 43:1209–1222.
- Pough, F. H. 1989. Organismal performance and Darwinian fitness: Approaches and interpretations. *Phys. Zool.* 62:199–236.
- Pounds, A. J. 1988. Ecomorphology, locomotion, and microhabitat structure: Patterns in a tropical mainland *Anolis* community. *Ecol. Mon.* 58:299–320.
- Reichman, O. J. and S. Aitchison. 1981. Mammal trails on mountain slopes-optimal paths in relation to slope angle and body weight. *Am. Nat.* 117:416–420.
- Schall, J. S. and E. R. Pianka. 1980. Evolution of escape behavior diversity. *Am. Nat.* 115:551–566.
- Stebbins, R. C. 1944. Some aspects of the ecology of the iguana genus *Uma*. *Ecol. Mon.* 14:313–332.
- Taylor, C. R., S. L. Caldwell, and V. J. Rowntree. 1972. Running up and down hills: Some consequences of size. *Science* 178:1096–1097.
- Thompson, D. B. 1990. Different scales of adaptation in the climbing behavior of *Peromyscus maniculatus*: Geographic variation, natural selection, and gene flow. *Evolution* 44:952–965.
- Van Damme, R., and J. M. Van Dooren. 1999. Absolute versus per unit body length speed of prey as an estimator of vulnerability to predation. *Anim. Behav.* 57:347–352.

- Wainwright, P. C. 1994. Functional morphology as a tool in ecological research. In P. C. Wainwright and S. M. Reilly (eds.), *Ecological morphology: Integrative organismal biology*, pp. 42–59. University of Chicago Press, Chicago.
- Warner, D. A. and R. M. Andrews. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biol. J. Linn. Soc.* 76:105–124.
- Werner, E. E. and J. F. Gillam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15:393–425.