

INTEGRATING FUNCTION AND ECOLOGY IN STUDIES OF ADAPTATION: Investigations of Locomotor Capacity as a Model System

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■ **Abstract** Understanding adaptation in morphological and physiological traits requires elucidation of how traits relate to whole-organism performance and how performance relates to fitness. A common assumption is that performance capacities are utilized by and important to organisms. For some systems, it is assumed that high levels of physical fitness, as indexed by measures of locomotor performance, lead to high fitness levels. Although biologists have appreciated this, little attention has been paid to quantifying how organisms use their performance capacities in nature. We argue that for the study of adaptation to proceed, greater integration of laboratory studies of performance and behavioral/ecological studies is needed, and we illustrate this approach by examining two questions. First, how does the environment affect locomotor function in nature? Second, what percentage of locomotor capacities do animals use in nature? A review of studies in several animal groups shows widespread effects of the environment on measures of locomotor function.

INTRODUCTION

Studies of locomotor function have contributed to our understanding of critical physiological issues, such as whether structure matches function and whether natural selection favors individuals with enhanced performance capacities (reviewed in Bennett & Huey 1990, Garland & Losos 1994, Gans et al. 1997, Boggs & Frappell 2000). Such studies have shown applications for the fields of conservation biology, evolutionary biology, and ecology (Miles 1994, Wainwright 1994, Turchin 1998). This synergy among fields is not surprising, as locomotor capacity is intimately associated with the ecology of animals, in part because the ability to move in a particular environment affects which portions of the habitat are accessible. Further, the modulation of locomotor speed determines the temporal component of how animals exploit space. Thus, understanding the locomotor capacities of organisms

sheds light on numerous issues relating to traditional ecological and evolutionary ideas.

Locomotor capacities have long intrigued biologists because of the assumption that they are critical to Darwinian fitness, although few studies have provided empirical evidence to support this assumption (Garland & Losos 1994). Arnold (1983) first codified a theoretical framework for relating variation among individuals in morphology, performance, and fitness. This "performance paradigm" assumes that variation in lower level morphological, physiological, and biochemical traits (subordinate traits) determines variation in some ecologically relevant performance capacity (e.g., sprint running speed). In turn, the performance measure may be correlated with Darwinian fitness (some measure of reproductive success in the wild, although precise empirical and theoretical definitions are complicated (e.g., see McGraw & Caswell 1996). In this manner, a direct link is created between morphology and fitness, but organismal performance forms the critical intermediate step between them. This paradigm has inspired numerous studies relating morphology to performance but a smaller number that relate performance to fitness (Pough 1989, Bennett & Huey 1990, Garland & Losos 1994).

Because of their presumed importance for Darwinian fitness, locomotor capacities have played a significant role in discussions of adaptation (Pough 1989, Bennett & Huey 1990, Garland & Losos 1994, Dickinson et al. 2000). However, relatively few studies have measured locomotor function in nature, particularly in comparison to laboratory studies (Wainwright 1994, Irschick & Losos 1998, 1999). Our goal is to review field studies that directly measure locomotor function in nature or that measure characteristics related to locomotion. We argue that any understanding of locomotor adaptation will be incomplete without data on how organisms function in nature.

We review four bodies of literature to demonstrate the diverse applicability of field studies for addressing physiological hypotheses: speed of birds, energetics and performance of lizards, diving physiology of marine mammals, and performance and kinematics of flying insects. Our criteria for inclusion in this review are that a paper (subsequent to 1950) provides quantitative data on locomotor performance in nature or contains quantitative data on some physiological function that is intimately related to locomotion in nature. We do not exclude papers using relatively simple methods of measurement. We include some studies that used trained marine mammals that were allowed to move unfettered in the ocean.

Although energetic efficiency is one aspect of locomotor performance, we do not consider the ecological cost of transport, i.e., the percentage of the total daily energy budget that is attributable to locomotor costs (Garland 1983). This measure is typically calculated by estimating the actual distance that animals walk in nature, then using laboratory data on the incremental cost of locomotion to estimate costs attributable to locomotion. This quantity can then be divided by an estimate of the total daily field energy expenditure. Recent work in this area has shown that larger animals tend to spend relatively more on locomotor costs, and lizards spend more than mammals (Goszczyński 1986, Kenagy & Hoyt 1989, Baudinette 1991,

Karasov 1992, Christian et al. 1997, Altmann 1998, Gorman et al. 1998, Drent et al. 1999, Steudel 2000, Girard 2001, T. Garland, unpublished observations).

Ecological Function

Central to any concept of ecologically relevant locomotor capacity is what we term "ecological function." A hypothetical example showcases the distinction between ecological function and traditional laboratory measures of function. Consider a biologist who studies the maximal sprinting capacities of two rodent species and finds that the maximal speed of both species under optimal laboratory conditions is 1 m/s. By optimal, we mean that the substrate provides good traction, etc., and that attempts have been made to motivate the animal to achieve maximal performance. In nature, the biologist finds that species A runs at about 0.9 m/s (90% of maximum) when escaping from a natural predator (a hawk), 0.7 m/s (70% maximum) when chasing insect prey, and 0.5 m/s (50% maximum) when chasing rival males from its territory. By contrast, species B runs at speeds of 1.5 m/s when escaping a hawk, 1 m/s when chasing prey, and 0.7 m/s when chasing rival males.

Thus, the speeds achieved by each species in the field form the ecological performance capacities of each species. This example is instructive in several ways. First, if the biologist found a positive correlation between laboratory maximal speed and survivorship in either species, then without quantification of ecological performance, one would have no understanding of why fitness is related to locomotor performance (see also Pough 1989). For the example given, though the positive correlation between Darwinian fitness and maximal speed consists of three components (escape from a predator, feeding, and chasing rival males), the field data suggest that the first is likely to be the most important because only during this activity do the animals run near their maximal abilities. Thus, laboratory studies alone, and correlational studies of natural selection alone, reveal little about the ecological reasons why selection favors high levels of performance. In addition, the above example illuminates that ecological performance may be greater than laboratory performance (species B in our example) if the animal is not actually maximally motivated in the laboratory, or if the animal's performance is constrained by the laboratory set-up (Irschick & Jayne 1999, Bonine & Garland 1999). Finally, studies of ecological function can be a rich source of information about organisms and may yield insights into their behavior that were not predicted by theory.

Two questions pervade this review. First, how does the environment affect ecological function? Second, what proportion of their maximal capacities do species use in nature during different behaviors? Understanding how the environment affects function has been a central goal of physiologists for many years (e.g., see Garland & Carter 1994, Feder et al. 1987, Feder et al. 2000), but most studies have examined this question under controlled circumstances in the laboratory. Understanding whether, and to what extent, species use their maximal locomotor capacities in nature is also important (Hertz et al. 1988), because if species never

use their maximal capacities, then selection cannot act directly on such traits as maximal sprint speed (Irschick & Losos 1998). Studies of ecological function can reveal the extent to which performance capacities are used in nature during different behaviors, and thus provide information on the potential for selection to act on a trait. Thus, Arnold's (1983) original paradigm has been expanded to include consideration of behavior as a potential "filter" between whole-organism performance and the direct effects of natural (or sexual) selection (Garland & Carter 1994, Garland & Losos 1994).

REVIEW OF LITERATURE

Speed of Birds

A substantial body of work has investigated how fast bird species fly in nature, using a variety of techniques (e.g., radar). The goals of these studies typically fall into several categories. Optimization tests compare competing hypotheses about which factors limit speeds used during migration and other activities. These studies test some optimization criterion under the assumption that birds either minimize or maximize some physiological quantity. Several reviews present details of these and other hypotheses (Welham 1994, Hedenstrom & Alerstam 1995, Pennycuik 1997). A smaller set of studies correlates variation in speeds to variation in habitat (e.g., movement over sea vs. land), variation in the technique of flying (e.g., cruising, soaring), or simply to describe the speeds that birds use. A third set of studies addresses whether species of special interest (e.g., the peregrine falcon) achieve the high levels of performance predicted by popular belief.

OPTIMIZATION TESTS OF FLIGHT One optimization hypothesis posits that birds will maximize the distance traveled per unit energy expended (termed the maximum range speed, V_{mr}), resulting in high ratios of speed to power. Several equations have been proposed for this optimization criterion (Welham 1994). Another hypothesis posits that birds will fly at speeds that minimize the amount of power they expend during flight (termed the minimum power speed, V_{mp}). In contrast to V_{mr} , V_{mp} should minimize the ratio of power to speed. Importantly, whether a bird is predicted to use V_{mr} or V_{mp} depends on both the ecological context (e.g., duration of flight, time of day) and the species involved (Norberg 1981). Because power or energy expenditure cannot be easily measured in free-flying birds, researchers have tested these hypotheses indirectly by measuring speeds of a variety of species during different activities (e.g., long-distance migration, feeding young). In addition to empirical studies, theoretical models of how fast birds should fly during different activities have been generated, usually based on V_{mr} and V_{mp} .

Birds may be engaged in multiple activities when speed is measured, and the predicted speeds can vary depending on the behavioral context (Hedenstrom &

Alerstam 1995). Several recent papers have reviewed studies of whether birds fly at predicted speeds (Hedenstrom & Alerstam 1995, Pennycuick 1997). We do not summarize how many studies support a particular hypothesis, but review studies of speed in birds by considering them in an ecological and behavioral context.

EFFECTS OF ENVIRONMENT ON SPEED

Activity Typically, researchers have examined flight performance during several activities: migration, movement between feeding sites and nests, and song flight. In addition, a number of studies have examined birds when their behavioral activity is unclear. Migration speeds are frequently double those during other activities (Hedenstrom & Alerstam 1992, 1994a, 1995), which may result in part from differences in flight behavior between migration and other activities (e.g., song flight). During migration, birds ascend to a preferred height and then fly level for long periods. By contrast, during song flight in skylarks (*Alauda arvensis*), individuals first climb to a culminating level flight where the bird flies against the wind and finally descends by parachuting, gliding, flapping flight, or occasionally a rapid dive (Hedenstrom & Alerstam 1992).

Migration speeds are not constant: Speeds over water are typically higher than over land (Alerstam 1975). This effect may be caused by rising thermals over land, resulting in soaring flight behavior, which is slower than steady-state flapping (Alerstam 1975, Pennycuick 1982a). Speeds of nonsoaring birds over land were similar to those observed over open water (Alerstam 1975). Although slope soaring had little overall effect on speed in the wandering albatross (*Diomedea exulans*) (Pennycuick 1982b), this species had a greater variance in speeds over land than sea. In a study of several species migrating across the English Channel, Parslow (1969) found that birds migrating in larger groups had higher speeds than did those in smaller groups, although Parslow (1969) attributed this effect to more favorable winds on nights with large groups of migrants. For 11 species of seabirds, airspeeds during nonforaging flights were higher than for foraging flights, although each was variable (Alerstam et al. 1993). Behavioral interactions also affect flight speed; when a pair of imperial shags (*Phalacrocorax alriceps*) were pursued and attacked by a south polar skua (*Catharacta maccormicki*), the skua accelerated rapidly from a speed of about 6 m/s to over 16 m/s, while the speeds of the Imperial shags remained almost constant (Alerstam et al. 1993).

Orientation The relationship between the orientation of flying (ascending, descending) and speed is unclear. For some bird species (e.g., skylarks), descending speeds tend to be the fastest and climbing speeds the slowest (Hedenstrom 1995), although for the Little blue heron, speeds are lower during descent than level flight (Tucker & Schmidt-Koeing 1971). However, in a variety of other species, speed and incline are unrelated (Tucker & Schmidt-Koeing 1971). Air speeds and climb rates were negatively related within migrating bird species (Piersma et al.

1997). Speeds can also vary dramatically as a function of the type of flight used. For instance, skylarks (*A. arvensis*) most often descend by parachuting at a mean sinking speed of 1.5 m/s, but occasionally dive 8.4 m/s, and flapping descent results in speeds of about 1.6 m/s (Hedenstrom 1995). Alerstam (1987a) found that when several bird species migrated across a strong magnetic anomaly (iron ore deposits), they tended to descend for about 2 minutes before leveling off, thus changing both their altitude and vertical speed.

Wind The available data support the notion that airspeeds are higher in headwinds than with tailwinds (Bellrose 1967, Able 1977, Larkin 1980, Larkin & Thompson 1980, Bloch & Bruderer 1982, Wege & Raveling 1984, McLaughlin & Montgomerie 1985, Gudmundsson et al. 1992, Wakeling & Hodgson 1992; see also Schnell 1965, Bruderer & Steidinger 1972, Tucker 1974, Schnell & Hellack 1979), although some studies are inconclusive (Blokpoel 1974, Tucker & Schmidt-Koeing 1971). Hedenstrom & Alerstam (1994b) argued that the climb rates of knots (*Calidris canutus*) and turnstones (*Arenaria interpes*) were enhanced by turbulent wind, such that the mean climb rate under conditions of no wind was 1.0 m/s, whereas under windy conditions it was 1.2 m/s (but see Piersma et al. 1997). At least one study (Able 1977) has also documented that birds alter their flight posture when flying into strong headwinds by flying at steep angles.

Body size Several studies have investigated both how body mass relates to observed speed and how closely observed speed matches predicted speeds based on theoretical models of how much power should be produced (i.e., V_{mp} or V_{mr}). Smaller birds tend to fly either consistently faster than, or equal to V_{mp} or V_{mr} , whereas larger birds tend to fly at speeds that are consistently lower than predicted estimates (Pennycuik 1982b, 1997, Hedenstrom & Alerstam 1992, 1994a, Welham 1994). Some authors have argued that the relatively slow speeds of larger birds result from the ability of small birds to extract power from their flight muscles to fly at any characteristic speed during level flight (Pennycuik 1997). Behavior may also be important: Some large species appear to have relatively slow speeds because they more frequently slope-soar than do smaller birds (Pennycuik 1997).

Diurnal and seasonal variation Relatively few studies have investigated systematically whether bird speeds change with either the time of year or time of day. In a survey of 12 species, undisturbed evening flight speeds were greater, although not substantially so, than midday flights (Evans & Drickamer 1994). In a massive survey of about 3500 individual birds (representing an unknown number of species) flying at night over southeastern New York, Larkin & Thompson (1980) found little seasonal variation in airspeed, with the exception that slightly more slow birds were detected during the fall. During the spring fast birds generally oriented northeast, whereas during the fall they oriented due west. By contrast, slow birds showed no obvious heading in either the spring or fall. These findings

show that performance can be affected by environmental factors not easily studied in the laboratory.

Type of flight Birds exhibit several kinds of flight, including gliding, flapping (Pennycuick 1987) and diving behavior in which the wings are folded into the body. Further, birds fly in a zig-zag pattern, which is associated with slope soaring along waves, (Pennycuick 1982a). In skylarks (Hedenstrom 1995), flapping flight is typically faster than parachuting or diving flight. Birds that rely on high-speed dives to capture prey modify their wing and body posture to alter their speed. For instance, gyrfalcons (*Falco rusticolus*) fold their wings as they accelerate during high-speed dives (Tucker et al. 1998). The kind of flight used, and consequently the airspeed, can be affected by wind and other conditions. For example, during calm conditions, albatrosses use swell soaring and turning within a width of about 300–500 m to travel about 10 m/s. Under windy conditions, they travel faster (about 22.5 m/s) by a combination of wave soaring and dynamic soaring (Alerstam et al. 1993). One group of barn swallows (*Hirundo rustica*) had low and straight flight paths (mean speed = 8.8 m/s), whereas another group used high and erratic flight behavior (mean speed = 6.8 m/s) during undisturbed activity (Blake et al. 1990).

Loading Pennycuick et al. (1994) trained falcons and hawks (six species) to fly 500 m to a lure and showed that only the gyrfalcon (*F. rusticolus*) had a lower air speed with a load (a transmitter) than without. Although these studies were not completed under natural conditions, they are a good first step for understanding the effects of loading on flight performance in unconstrained surroundings.

Effects of food availability Variation in speed relative to food availability tests the idea that birds are either maximizing the distance traveled per unit energy expended (foraging efficiency) or their overall rate of energy delivery. Lapland longspurs (*Calcarius lapponicus*) do not fly faster when food is more available, which is consistent with maximizing the distance traveled per unit energy expended (foraging efficiency) (McLaughlin & Montgomerie 1990).

WHAT PERCENTAGE OF MAXIMUM CAPACITY DO BIRDS USE DURING VARIOUS ACTIVITIES? Few studies have examined this issue, primarily because researchers have been more interested in testing whether birds moved at preferred speeds that matched theoretical optima. We address this issue in two ways. First, we review a small number of studies that have tested whether birds reach maximal speeds based on theoretical models of flight. Second, we describe some of the mean speeds that species use during migration (when speeds appear to be fastest) and consider these data in the absence of information on maximum capacities.

Because falcons are considered to be among the fastest animals, much effort has centered on both modeling and measuring the speeds they can achieve in nature. Mathematical models of an ideal peregrine falcon (*Falco peregrinus*) predict that

it should reach top speeds of 89–112 m/s for a vertical dive, the higher speed representing larger birds (Tucker 1998). If drag is considered, then top speeds could range from 138 to 174 m/s. This model further predicts that an ideal falcon diving at angles between 15 and 90°, with a body mass of 1 kg, reaches 95% of top speed after traveling about 1200 m (Tucker 1998).

In trials with a closely related species (a 1.02 kg gyrfalcon, *F. rusticolus*), during the first (acceleration) phase of the dive maximal speeds ranged from 52 to 58 m/s, which closely matched predicted speeds assuming minimum drag (Tucker et al. 1998). Falcons then began a constant-speed phase, which lasted no more than a few seconds, during which they increased the amount of drag and thus slowed considerably. Whereas these speeds are among the fastest reported, predicted speeds were much higher than actual speeds. This difference is attributable in part to the behavior of increasing drag after the initial acceleration phase, whereas Tucker's (1998) model assumes continued acceleration.

Alerstam (1987b) used tracking radar to detail diving behavior of two species known for their high-speed hunting dives, the peregrine falcon (*F. peregrinus*), and the goshawk (*Accipiter gentilis*). The initial portion of their dives consisted of flapping flight, during which birds accelerated along a level path. The next stage consisted of flapping flight and a gentle descent, followed quickly by diving at steep angles. After the strike animals leveled off. The falcons attained speeds ranging from 19 to 23 m/s during the initial period of vigorous flapping flight, which was nearly horizontal, but when they dived without wing beats, speeds approached 30 m/s. These observed speeds for shallow dives were similar to maximal speeds based on theoretical predictions (Pennycuick 1975). Theory predicts a positive curvilinear relationship between the angle of dive and velocity, but the observed relationship between these variables is nearly flat, suggesting that either the model is flawed or birds are adopting behaviors that affect diving speeds. One possibility is that birds use moderate stooping speeds to gain in hunting precision (Alerstam 1987b). This finding is intriguing in that it highlights how high levels of locomotor performance may not be desirable: Accuracy in locating prey may be more important than speed for some species.

In a review of undisturbed speeds of 36 species, Pennycuick (1997) listed mean speeds of 8.8–19.1 m/s. Given the maximal speeds of diving falcons and goshawks, which are presumably among the fastest of birds (Alerstam 1987b, Tucker et al. 1998), these estimates suggest that birds are using well over 50% of the maximal speeds during migration and likely are moving at speeds that are 70–90% of maximum capacity. For 48 species of birds (most of which were different from those in Pennycuick 1997), mean speeds ranged from 8.0–30.6 m/s during migration, although the average speeds for most species were approximately 11–13 m/s (Welham 1994). Thompson (1961) estimated the speed of a flying red-breasted merganser at 44 m/s, which would make it one of the fastest animals in the world. In short, the available data show that birds regularly move at extremely fast speeds during migration, suggesting that they are able to fly long distances at close to or maximal speeds.

Energetics of Lizards

Field studies of energetics in lizards are few and typically involve direct measurements of metabolic rates by use of doubly labeled water. Most studies have not directly measured speed during locomotor activity, but the papers reviewed here have attempted to quantify movement in relation to metabolic rates. Christian et al. (1997) and Nagy et al. (1999) have extensively reviewed the field energetics of lizards, and we examine a subset of those studies in the context of locomotion.

INTERSEXUAL DIFFERENCES Because males and females frequently differ in their energetic requirements, primarily owing to reproduction, one might expect sex differences in locomotor behavior that would also affect metabolic rates. Lichtenbelt et al. (1993) found that differences between male and female green iguanas (*Iguana iguana*) in average daily energy expenditure (DEE) were small, although males tended to have higher metabolic rates during the mating season, which is related to their higher levels of activity during this period.

In the temperate-zone lizard *Sceloporus virgatus* Merker & Nagy (1984) revealed an interesting interaction among activity levels, season, and sex. In the spring males had higher metabolic rates than females and were active for twice as long as females (7.6 vs. 3.6 h/day). Nevertheless, females had higher rates of energy intake than males (8.3 vs. 3.6 times resting metabolic rate), resulting in a weight loss for males. In the summer both sexes maintained constant body masses and similar energy budgets, but females were active for longer periods. This example shows how locomotor behavior is intimately related to many other factors in the environment, and further studies that quantify how fast and/or how often these lizards move would shed even more insight on the factors that affect field energetics.

TYPE OF ACTIVITY Behaviors often differ in their energetic costs. Lichtenbelt et al. (1993) found that climbing was about six times more energetically costly than movement on horizontal surfaces for green iguanas (*I. iguana*), which is consistent with laboratory studies in lizards that show movement up steep inclines is energetically expensive (Farley & Emshwiller 1996). Marine iguanas (*Amblyrhynchus cristatus*) forage in both the intertidal and subtidal zones, but total DEE apparently does not differ significantly between habitats (Drent et al. 1999).

Predatory lizards often differ in foraging behavior, with some lizards relying on infrequent, fast movements for capturing prey (sit-and-wait) and others moving actively in search of prey (actively-foraging) (see Perry 1999 for a recent review). A widely foraging lizard *Eremias lugubris* has a substantially higher metabolic rate than its close relative, *E. lineocellata*, despite the forager being active for shorter periods [2.75 h/day compared with 10.25 h/day, respectively (Nagy et al. 1984)]. A recent review of DEEs (Nagy et al. 1999) did not address whether such a correlation holds across all lizard species that have been studied, perhaps because of the scarcity of quantitative data on movement rates in the field (but see Garland 1993, Perry 1999).

INTERSEASONAL VARIATION Seasonal variation is typically associated with two key variables that influence locomotor behavior, temperature and reproduction. Varanid lizards are frequently inactive during the dry season, although this pattern can change depending on habitat type. During the dry season *Varanus panoptes* was largely inactive in woodland areas, whereas on floodplains, it often walked for 3.5 h/day, which is remarkably high for a reptile, and consequently led to high rates of energy expenditure (Christian et al. 1995). In the Galapagos islands marine iguanas, *A. cristatus*, were about three times as active during the warm than the cold season, resulting in substantially higher values of DEE for the former season (Drent et al. 1999).

Annual variation in energy allocation differed between male and female *I. iguana*, such that males primarily devoted energy on locomotion for social activities, whereas females devoted about 15% of their annual energy budget to the production of eggs (Lichtenbelt et al. 1993). Seasonal variation also affected activity levels, and hence the metabolic rates of male and female striped plateau lizards (*Sceloporus virgatus*), such that females were more active in the summer, whereas males were more active in the spring (Merker & Nagy 1984).

HABITAT DIFFERENCES The lizard *Cnemidophorus hyperythrus* exhibited higher DEE in woodland areas than in thorn scrub sites (330 J/g/day vs. 219 J/g/day), likely because woodland lizards were active most of the day (about 9 h), whereas lizards in thorn scrub habitat were active mostly in the morning (about 3.5 h/day) (Karasov & Anderson 1984).

Performance of Lizards

Lizards have long been used as a model for studies of both maximal locomotor performance (e.g., Garland & Losos 1994, Bonine & Garland 1999, Van Hooydonck et al. 2001) and ecology (Vitt & Pianka 1994). Until recently, however, relationships between performance and ecology were poorly understood (but see Aerts et al. 2000). A recent body of work on both terrestrial and arboreal lizards has shed considerable light on how ecological performance is affected by morphology, habitat use, and behavior (Irschick & Losos 1998, Jayne & Ellis 1998, Irschick 2000a,b, Irschick & Jayne 1998, 1999a,b, Jayne & Irschick 2000).

HOW DOES THE ENVIRONMENT AFFECT LOCOMOTION? Footprints of two species of lizard (*Callisaurus draconoides*, *Uma scoparia*) were studied in the soft sand of the Kelso dune system in southern California to examine how incline, vegetative cover, and other factors affected locomotion when lizards were escaping a threat (approach of a human) and when they moved undisturbed through the habitat (Jayne & Ellis 1998, Irschick & Jayne 1999a, Jayne & Irschick 2000). These two lizards are closely related, are morphologically and behaviorally different, yet occur sympatrically in various sand dune systems. From tracks left in the sand, one can gain accurate values of stride length, as well as determine the orientation of

paths relative to landmarks in the environment. Studies in the laboratory on sand show that both lizards exhibit a linear relationship between stride length and speed (Irschick & Jayne 1998, Jayne & Irschick 2000), which can be used to estimate speeds of movement in nature.

The fringe-toed lizard (*U. scoparia*) has several specializations for movement on sandy surfaces, such as laterally oriented toe fringes, a countersunk jaw, and smooth skin that facilitates burrowing into sand (Stebbins 1944). This lizard has a relatively stout body, short limbs, and a short tail and moves predominantly by quadrupedal locomotion. By contrast, the closely related zebra-tailed lizard (*C. draconoides*) is more specialized for movement on firm substrates and is considered a bipedal specialist (Irschick & Jayne 1998). Consequently, *Callisaurus* has several specializations for high-speed bipedal locomotion, including long hindlimbs, a long tail, and long distal elements (Snyder 1962, Bonine & Garland 1999).

Because moving up inclines is energetically more expensive than moving on level, or near-level surfaces (Taylor et al. 1972, Farley & Emshwiller 1996), one might predict that lizards will avoid moving on steep inclines, which on sand dunes reach as high as 32°. On the other hand, because incline does not affect maximal speed or acceleration as greatly in small animals as large animals (Huey & Hertz 1982, 1984), one might expect that lizards will preferentially flee uphill when escaping from a predator. Jayne & Ellis (1998) elicited escape locomotion of fringe-toed lizards by approaching the animals and measuring how speed (based on a stride-by-stride basis) and the orientation of escape paths were related to incline, angle of turning, and the location of nearby landmarks (vegetative cover, burrows, the steepest available incline). By comparing the frequency distributions of inclines used during escape with the inclines available in the habitat, they determined that *Uma* escaped randomly with respect to incline, but that maximal speeds were negatively affected both by running up steep hills and by large turn angles. Thus, running in a straight line on a level surface enhances maximal speed. Further, most *Uma* appeared to use a predetermined escape route (e.g., Stamps 1995), by which they ran toward and then down burrows (Jayne & Ellis 1998).

Bipedal locomotion has been cited as an important behavior that allows some lizards to move at faster speeds than strictly quadrupedal lizards, but few studies have examined how often lizards run bipedally in nature and whether speeds during bipedal locomotion are actually faster than for quadrupedal locomotion. Irschick & Jayne (1999a) examined the effects of incline and other habitat variables on the escape locomotion of *C. draconoides* and also measured whether each stride was bipedal or quadrupedal. Bipedal strides were, on average, 12% longer than quadrupedal strides, so if one assumes a similar stride frequency between the two modes, bipedal locomotion is significantly faster. Laboratory studies in *Callisaurus* for locomotion on a high-speed treadmill show a similar ratio of longer stride lengths for bipedal locomotion, suggesting that this result is robust (Irschick & Jayne 1999b). Another result in common between *U. scoparia* and *C. draconoides* was that maximal stride lengths were typically not achieved until several meters into the escape path, some of which were 30 m long (Irschick & Jayne 1999a).

Therefore, racetrack estimates of speed likely underestimate the maximal speeds of which both *Uma* and *Callisaurus* are capable, a problem that may be overcome by use of high-speed treadmills (Bonine & Garland 1999, Irschick & Jayne 1999b).

Callisaurus lizards exhibited an interesting threshold effect in regards to incline use. On shallow slopes ($<15^\circ$), over which most of the locomotion occurred, lizards moved randomly with respect to the incline. By contrast, lizards avoided moving directly up or down steep hills ($>15^\circ$), preferring to run horizontally across the hill (this cut-off value was found by evaluating movements on a variety of inclines). Thus, animals may have complex and often unpredictable behaviors regarding usage of habitats that pose functional challenges.

A field experiment was used to examine the effects of incline and vegetative cover on the undisturbed locomotion of *U. scoparia* (Jayne & Irschick 2000). Three 40×100 -m plots that differed in both incline and amount of vegetative cover were established. Before lizards were active each morning, all tracks were erased on the sand dunes, and paths were examined several hours later. Similar to escape locomotion, *U. scoparia* moved around the habitat randomly with respect to incline, but at two preferred speeds. Slow locomotion occurred near burrows and mounds of vegetation, which *Uma* used as retreats from both predators and high temperatures, whereas the high-speed movements (typically >2 m/s) generally occurred in open areas of the dune [undisturbed desert iguanas, *Dipsosaurus dorsalis*, have been observed to engage in a similar bimodality of speeds near Dale Dry Lake, San Bernardino County, California (T. Garland Jr., personal observations)].

Uma also tended to move more slowly on steep inclines and near vegetation, resulting in different locomotor behavior in different parts of the sand dune. On steep slopes with little vegetation the average speed was only 1.54 m/s, whereas on shallow slopes with more vegetation the average speed was 1.76 m/s. In addition, incline, speed, and orientation interacted for the undisturbed locomotion of *Uma*. On shallow inclines locomotion tended to be relatively fast and was distributed approximately equally on different inclines. On steep surfaces lizards favored direct uphill over downhill locomotion, and most locomotion was relatively slow. This research underscores several themes: (a) Environmental effects on locomotor performance are complex and interactive, (b) racetrack speeds may underestimate the true maximal speeds of lizards, and (c) species may exhibit threshold effects in terms of habitat use.

THE EVOLUTION OF ECOLOGICAL PERFORMANCE IN CARIBBEAN ANOLIS LIZARDS

An important, yet rarely addressed, issue in ecological and evolutionary physiology is whether performance capacity, as measured in the laboratory, and performance levels exhibited during natural behaviors have co-evolved. Several unresolved questions bear on this issue. First, is laboratory performance always maximal? Second, do species with low maximal capacities compensate for them by using a greater percentage of their performance capacities than species with high maximal capacities? These issues have been examined both across species and ontogenetically in Caribbean *Anolis* lizards (Irschick & Losos 1998, Irschick 2000a,b).

The ecology, morphology, and behavior of Caribbean *Anolis* lizards have been studied extensively (Williams 1972, Losos 1990a,b, Roughgarden 1995), but until recently the relationship between locomotion and habitat use has not been well understood. Within each of the Greater Antillean islands (e.g., Cuba, Hispaniola), largely independent radiations (Losos et al. 1998, Jackman et al. 1999) of *Anolis* have resulted in a series of ecologically and morphologically distinct forms, termed “ecomorphs” (trunk-ground, trunk-crown, twig, crown-giant, trunk, and grass-bush, named for the portion of the habitat they prefer) (Losos 1990a,b). For example, the trunk-ground ecomorph has long hindlimbs, a long tail, and tends to occupy broad tree trunks close to the ground (<1 m). By contrast, twig anoles have short hindlimbs, a short tail, and tend to occupy narrow surfaces higher in the canopy. Irschick & Losos (1998) and Irschick (2000a) focused on eight anole species that are similar in size yet represent three ecomorph types (Figure 1). The convergent evolution of ecomorphs provides enhanced statistical power for examining the evolution of ecological performance (e.g., see Van Hooydonck & Van Damme 1999).

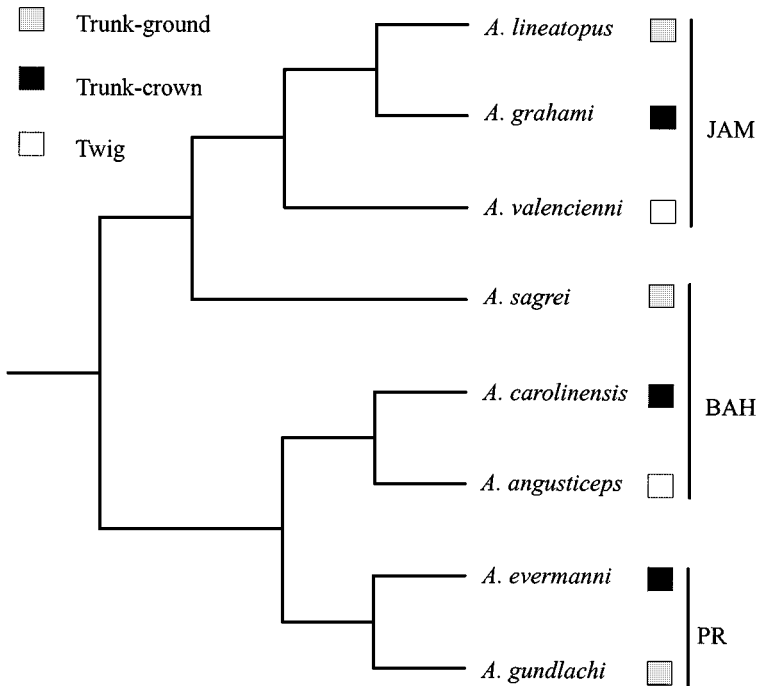


Figure 1 Phylogenetic tree for eight *Anolis* lizard species. Locality headings next to species names represent the Caribbean islands on which these species occur, although *A. carolinensis* was studied in Louisiana. JAM, Jamaica; PR, Puerto Rico; BAH, Bahamas. From Irschick & Losos (1998).

Irschick & Losos (1998) measured sprinting and jumping of all eight anoles during four behaviors, three in the field (escape from a threat, feeding, undisturbed locomotion) and one in the laboratory (maximal speed on a broad surface with sure footing). An initial test revealed that laboratory performance for both jumping and sprinting was significantly greater than for all three natural behaviors, with anoles using an average of about 90% of their maximal sprinting capacities during escape, 70% of maximum during feeding, and 33% during undisturbed locomotion. By contrast, the maximal jump distances in the field during feeding and undisturbed movements (the two activities in which they were most often used) were <40% of the maximum performance elicited in the lab. Therefore, two key factors, the ecological context and the kind of performance, both markedly affect the levels of performance. These results also show that if one were to conduct a study of natural selection on maximal jumping ability as measured in the laboratory, one likely would find no correlation with Darwinian fitness, because anoles do not use their maximum jumping capacities in nature. Phylogenetically informed, cross-species comparisons showed that for sprinting, performance capacity has evolved in positive correlation with both escape and feeding behavior; hence, performance capacity is a good predictor of performance in nature.

However, this finding does not address whether species with low performance capacities compensate by using a greater fraction of their capacities in the field. One possibility is that each species will use a similar fraction of its maximal abilities for a particular behavioral task. This possibility might be correct if successful escape from a predator is a direct function of absolute speed (but see Van Damme & Van Dooren 1999). Alternatively, a species with a lower capacity could compensate by using a greater fraction of its performance capacity for a given task as compared with species with a higher capacities. This possibility would be more likely if a particular absolute speed facilitated escape from predators. In other words, animals may perform only to the lowest level needed for successfully escaping a predator. This idea was tested both among species that vary in performance capacity (Irschick & Losos 1998) and for ontogenetic classes that also vary in performance capacity (Irschick 2000b).

For escape performance (elicited by human approach) among species, the hypothesis of compensation is supported (Irschick & Losos 1998), as species with low sprinting capacities, such as twig anoles, tended to use nearly all of their capacities, whereas the speedier trunk-ground anoles escaped by using as little of their performance capacities as possible (Figure 2). Irschick (2000b) studied maximal laboratory and field speeds during escape, feeding, and undisturbed locomotion for juveniles, adult females, and adult males of the trunk-ground anole *Anolis lineatopus*. Maximal speed is generally correlated with size in *Anolis* lizards, such that adult males are significantly faster than adult females, which, in turn, are significantly faster than juveniles (Macrini & Irschick 1998). In support of the hypothesis of compensation, juveniles used a greater fraction of their sprinting capacities in comparison with adult males and females during both escape and feeding. However, adult females did not use a significantly greater fraction of their sprinting

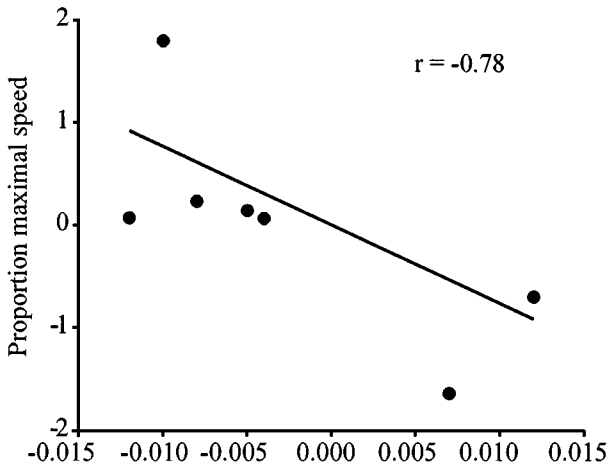


Figure 2 A plot of independent contrasts between maximal speed (x-axis) and proportion maximal speed used during escape (y-axis) for eight anole species $P < 0.05$. From Irschick & Losos (1998).

capacities than adult males during either escape or feeding, despite the females having, on average, an 11% lower sprinting capacity. Overall, the available data seem to support the notion that performance-limited lizard species or ontogenetic classes compensate by using a greater fraction of their performance capacities in nature (see also Clobert et al. 2000), but the hypothesis does not explain all the observed variation. One means of rigorously testing the hypothesis of compensation, and also determining which of the above metrics of performance [absolute speed, relative speed (see also Van Damme & Van Dooren 1999, Packard & Boardman 1999), percent maximal speed] is under selection would be to carry out a field study relating sprinting performance during different behaviors to Darwinian fitness among individuals of different sexes and sizes.

EVOLUTION OF PREFERRED SPEED IN ANOLIS LIZARDS Few studies have related the preferred speeds of animals in nature to their habitat conditions, particularly in a phylogenetic context. Arboreal animals, such as some lizards, are ideal for addressing this issue because they must move through environments that vary in incline and surface diameter, both of which affect locomotion (Taylor et al. 1972, Cartmill 1985, Losos & Sinervo 1989, Farley & Emshwiller 1996). For example, because of the negative effect of surface diameter on speed (Losos & Sinervo 1989, Macrini & Irschick 1998), arboreal lizards that frequently utilize narrow surfaces may move more slowly than lizards that typically utilize broad surfaces. Alternatively, if surface diameter does not pose a strong constraint on movement at slow speeds, then lizards that use broad surfaces may move at similar preferred speeds to those lizards that use narrow surfaces.

Irschick (2000a) examined the evolution of preferred speeds in the eight anoles mentioned above and tested the hypothesis that preferred speeds have co-adapted with habitat use. In contrast to *Uma*, the distributions of speed for all eight anoles were unimodal, with a preponderance of slow locomotion. Indeed, for all anoles, at least 75% of their movements were slower than 40% of each species' maximum speed. Comparative methods revealed that anole species that use narrow perches move at slower preferred speeds than species that use broader surfaces. Further, species with slow preferred speeds use a wider variety of surface diameters than species with high preferred speeds. This research demonstrates the usefulness of integrating ecological studies of habitat use and information on physiological data, such as preferred speed.

ARBOREAL VERSUS TERRESTRIAL HABITATS Arboreal habitats are characterized by discrete perches that vary in both incline and diameter and thus pose functional challenges for locomotion. Terrestrial habitats pose fewer constraints for locomotion. The habitat of *Uma* and *Callisaurus* consists of clumps of vegetation and burrows in an open terrestrial environment. Both lizards use these patches as retreats from predators and extreme temperatures. If one assumes that the threat of predation or overheating in open areas is higher than in retreats, then the high-speed movements in open areas may occur because the lizards perceive the open areas as dangerous (Lima & Dill 1990). The golden-mantled ground squirrel (*Spermophilus marmoratus*) primarily uses high-speed movements between retreats but slower movements when closer to retreats (Kenagy & Hoyt 1989). It also lives in a relatively open habitat interspersed with patches of vegetation.

At the other extreme, much of the undisturbed locomotion (jumping and running) of arboreal *Anolis* lizards is well below maximum capacity. Because of the characteristics of the discrete perches of arboreal anoles, much of their locomotion consists of short movements and is highly intermittent, which is an obvious constraint on achieving high speeds. Therefore, maximal speeds as measured under laboratory settings (broad diameter, long surface) are good approximations of their performance capacity. One difficulty is that *Uma* and *Callisaurus* are closely related, but anoles are distantly related to these species, and *Uma* and *Callisaurus* share many differences in morphology and behavior, which could confound terrestrial-arboreal comparisons. Thus, future comparisons would be most fruitful if they were to compare closely related species that differed in their degree of arboreality.

Diving Physiology of Marine Mammals

Common to all of the studies of ecological locomotor function in marine mammals is some test of actual versus predicted performance based on models of aerobic and anaerobic physiology. For example, the aerobic dive limit is the amount of time that an animal should be able to dive on a single breath of air and yet not suffer a substantial cost because of buildup of anaerobic waste products (e.g., lactate).

Consequently, the goal of many studies has been to test whether marine mammals exceed their aerobic dive limit, and if so, how often. Unlike terrestrial and arboreal habitats, aquatic systems are ideal for studies relating changes in physiology to locomotion. This is because most physiological variables will change in a regular manner with two related variables: dive depth and dive duration. Some of the relevant functional variables measured include speed, breathing and heart rates, levels of lactate before and after a dive, and levels of gases (O_2 and CO_2) in the blood. A few researchers (e.g., Kooyman et al. 1980) also measured additional aspects of blood chemistry (e.g., arterial hemoglobin concentrations), which will not be discussed here.

Some generalities have emerged in regard to the effects of depth on ecological locomotor function. As marine mammals dive, heart rate typically decreases (Fedak et al. 1988, Elsner et al. 1989, Andrews et al. 1997, Ponganis et al. 1997, Williams et al. 1999), in some cases as low as four beats per minute (Thompson & Fedak 1993). In many marine mammals heart rate decreases during the descent and subsequently increases during the ascent, with a noticeable tachycardia just prior to surfacing (Fedak et al. 1988, Elsner et al. 1989, Thompson & Fedak 1993, Andrews et al. 1997, Williams et al. 1999). Once the animal surfaces, heart rate increases, presumably to increase blood flow to oxygen-starved tissues (Thompson & Fedak 1993, Andrews et al. 1997, Williams et al. 1999). The amount of lactate in tissues increases with dive time (Kooyman et al. 1983, Ponganis et al. 1997, Shaffer et al. 1997, Williams et al. 1999), but for some marine mammals, lactic acid concentrations were not different from resting levels unless the dive was quite long (e.g., >20 min) [Weddell seals (Kooyman et al. 1983)].

How deep marine mammals dive, and the characteristic speeds and behaviors during dives, also shows some trends. The typical pattern is that marine mammals dive to a certain depth, spend a brief time moving horizontally, and then ascend to the surface [Weddell seals (Kooyman et al. 1980), sea lions (Feldkamp et al. 1989), narwhals (Martin et al. 1994), white whales (Shaffer et al. 1997)]. Some marine mammals, however, move for relatively long periods both slowly and horizontally at the bottom of their dives, resulting in some cases in a dramatically decreased metabolic rate [some gray seals (Thompson & Fedak 1993), elephant seals (Andrews et al. 1997)]. In elephant seals the amount of time spent moving horizontally along the bottom is substantial (Hindell et al. 1992), although males appear to have more flat-bottomed dives than females (Le Boeuf et al. 1988, 1996). For gray seals, Thompson & Fedak (1993) hypothesized that this horizontal movement is part of a sit-and-wait strategy in which the animal moves slowly along the bottom in hopes of finding passing prey. More research into what behaviors (e.g., feeding) are used during diving (possibly through the use of video cameras) could provide more information as to the reasons for long dives.

Average transit times are generally higher during deep than shallow dives [humpback whales during ascent (Dolphin 1987a,b), elephant seals (Hindell et al. 1992), harp seals (Lydersen & Kovacs 1993), narwhals (Martin et al. 1994), white whales (Shaffer et al. 1997)], which is consistent with the notion that marine

mammals can spend only a limited amount of time under water. In bottlenose dolphins, however, speeds for both ascent and descent are similar for dives to 60 m and 210 m (Williams et al. 1999). Speeds tend to be faster during ascent (when presumably the cost of lactate build-up is at its greatest) than descent [humpback whales (Dolphin 1987a,b), elephant seals (Le Boeuf et al. 1988), white whales (Shaffer et al. 1997), bottlenose dolphins (Williams et al. 1999)], although in some marine mammals there appear to be few differences in speed between ascent and descent [harp seals (Lydersen & Kovacs 1993), narwhals (Martin et al. 1994), white whales (but see below) (Ridgway et al. 1984)]. The former pattern suggests that marine mammals are conserving oxygen at the beginning of a dive. In a study of four species of otariids, Ponganis et al. (1990) found that speeds when moving along the surface were similar to diving speeds for species that ranged in size from 30 to 130 kg.

Descent and ascent rates in some marine mammals are related to the depth of the dive. The relationship between descent and ascent rate and depth is curvilinear in some cases, such that on deep dives, the speeds of both ascent and descent are relatively slow compared with shallower dives [narwhals (Martin et al. 1994)]. For greater dives (≥ 20 m in depth), both the average and maximum rates of ascent and descent were positively related to the maximum depth of diving in narwhals. However, for dives ≥ 20 m in depth and lasting >10 minutes, there were negative relationships between the average rates of descent and ascent, and the durations of diving. In brief, during extremely long dives, narwhals moved more slowly as the duration of the dive increased. In white whales speeds during ascent and descent were similar during shallow dives (<200 m), but for deep dives ascent speeds were significantly faster than descent speeds (Ridgway et al. 1984). These findings suggest complicated relationships between the environment and performance and also show the value of a comparative approach, as not all species react to the environment in the same manner.

Do marine mammals travel at the predicted speeds that would minimize their energetic cost of transport? Gray whales that migrate southwards move at speeds predicted to minimize the cost of transport (Rice & Wolman 1971, Sumich 1983), as do fur seals, Galapagos sea lions, and Galapagos fur seals (Ponganis et al. 1990), but such is not the case for Hooker's sea lions (Ponganis et al. 1990), narwhals (Martin et al. 1994), and bottlenose dolphins (Williams et al. 1999). The direction of migration may also affect average speed, as northbound gray whales migrate about half as fast as southbound gray whales (Pike 1962). More data on the frequency distributions of speed are needed to evaluate this question to provide a point of comparison with birds, in which migration also occurs.

Respiratory rate decreases with speed in white whales (Shaffer et al. 1997), in contrast to the pattern in other animal groups (Taylor et al. 1987). This pattern may be related to surface/submergence patterns, rather than coupling between respiratory patterns and locomotor movements. In some marine mammals, such as gray whales (*Eschrichtius robustus*) (Sumich 1983), this pattern is reversed. Some studies have measured blood gas levels in diving marine mammals and

have generally found a substantial decrease in the partial pressure of oxygen after animals have been diving for extended periods [Weddell seals (Kooyman et al. 1980), white whales (Shaffer et al. 1997), bottlenose dolphins (Williams et al. 1999)].

Seasonal and diel variation may affect how long animals dive, potentially because of variation in prey availability. For instance, in 1983 the Southern Californian Bight experienced a major influx of warm water, which correlated with a 20-fold reduction in zooplankton biomass and a marked decrease in commercial catches of squid, salmon, and other fish (McGowan 1984). Sea lions dove more often and for significantly longer periods than prior to the reduction in food, which Feldkamp et al. (1989) suggested was compensation for a reduced prey encounter rate. It would be interesting to know whether the speeds and durations of dives during periods of low food availability differ from those during periods of greater food abundance.

Numerous studies have addressed whether marine mammals dive for time periods that break the predicted aerobic dive limit (ADL), and if so, why [e.g., Weddell seals (Kooyman et al. 1980, 1983), humpback whales (Dolphin 1987a,b), sea lions (Feldkamp et al. 1989), harp seals (Lydersen & Kovacs 1993), elephant seals (Hindell et al. 1992), bottlenose dolphins (Williams et al. 1999)]. ADLs are calculated from estimated speeds of movement, metabolic rates, and the amount of oxygen stores in the animal prior to diving. From these values, aerobic dive limits are calculated as the amount of time an animal can spend underwater before oxygen stores are depleted and anaerobic waste products begin to increase. Consequently, estimated ADLs can change depending on the values input to the equation. The presumed cost of such a lactate build-up is that the marine mammal would have to spend additional surface time to rid the body of the anaerobic waste products. Most marine mammals dive for periods shorter than their ADLs [Weddell seals (Kooyman et al. 1983), humpback whales (Dolphin 1987a,b), sea lions (Feldkamp et al. 1989), harp seals (Lydersen & Kovacs 1993), narwhals (Martin et al. 1994), bottlenose dolphins (Williams et al. 1999)]. However, for some marine mammals, some individuals substantially exceeded the estimated ADLs [gray seals (Thompson & Fedak 1993), elephant seals (Hindell et al. 1992, Andrews et al. 1997, Williams et al. 1999)]. For instance, some bottlenose dolphins dive for over 243 s, which exceeds their predicted oxygen stores by 28%, yet they do not incur the predicted anaerobic costs (Williams et al. 1999).

Why can some of these marine mammals break the rules? Part of the answer may lie in their locomotor behavior. An implicit assumption in calculations of ADL is that marine mammals are moving continuously, but the intermittent locomotion of some marine mammals appears to violate this assumption. During ascent, when oxygen stores are presumably at their lowest, dolphins and other marine mammals use burst-and-glide locomotion in which they glide for extended periods following active propulsion (Williams et al. 1999). This behavior is especially interesting because it is rarely observed in marine mammals in captivity, in part because tanks are too small. Other factors also may play a role in increasing dive times without

incurring substantial costs. Ridgway et al. (1969) found that bottlenose dolphins swimming horizontally at depths <25 m had lower pulmonary oxygen reserves (and therefore greater metabolic demands) than the same individuals diving to 200 m, and lung compression and changes in the mode of swimming may have enhanced these energy savings. Thus, calculations of aerobic time limits may, in some cases, overestimate the energetic costs of locomotion under water (Williams et al. 1999). Finally, marine mammals such as elephant seals may substantially decrease their metabolic rates when diving, which would lead to incorrect values of ADL (see Hindell et al. 1992). The common thread to all three of these factors is that animals can alter their behavior in such a way as to violate the basic assumptions of physiological models, such as calculations of ADL. ADL is also an example of a physiological hypothesis that can only be tested in the field.

Performance and Kinematics of Flying Insects

A small body of work has measured ecological locomotor function in flying insects, typically their speeds of movement and kinematics. Two kinds of studies are apparent. First, studies on migratory locusts (*Locusta*) have yielded important insights into differences in performance and kinematics between field and laboratory settings. Second, work on Neotropical butterflies has documented interesting relationships between morphology, behavior, and performance in nature.

Locust flight has been studied extensively in the laboratory (see Baker et al. 1981 for references), but only a few studies have measured kinematics or flight speeds in nature. By filming swarms of migrating locusts (*Locusta migratoria*), Baker et al. (1981) found that both wing-beat frequencies and flight speeds were higher in the field than in the laboratory. For instance, the mean wing-beat frequency of locusts under tethered flight was 19.8 Hz, compared with 22.9 Hz during natural free flight. Similarly, mean speeds were 40% greater in the field than for tethered flight (Baker et al. 1981), but the linear relationship between flight speed and wing-beat-frequency was similar between free and tethered flight. Kinematic analyses of the wing motions of individuals within swarms show that a variety of parameters (e.g., ratio of upstroke to downstroke, stroke angles) are more variable in nature than during tethered laboratory flight (Baker & Cooter 1979). Other studies have shown that natural flight speed in locusts increases with air temperature (Waloff 1972, range 22–33°C), a result that also differs from laboratory studies, which have found flight speed to be temperature independent (Weis-Fogh 1956), despite a similar range of temperatures tested in the laboratory (range 25–35°C). These studies support the notion that certain aspects of tethered flight may be ecologically unrealistic, although such laboratory studies have clearly contributed to our understanding of insect flight.

In an elegant group of studies Dudley and his colleagues examined the natural (undisturbed) airspeeds of dozens of Neotropical butterfly species by following them across Lake Gutan in Panama. They were able to correlate these airspeeds to the morphological and behavioral characteristics of different species. In a study of 27 genera of Neotropical butterflies Srygley & Dudley (1993) found that palatable

butterflies fly at faster natural speeds and are better able to avoid predators in a small cage, primarily owing to their center of mass being positioned near their wing base. By contrast, unpalatable butterflies fly at relatively slow natural speeds and are less effective at eluding predators, likely as a consequence of their posterior position of their center of mass. The natural airspeeds of the butterflies that were studied were 2–6 times faster than ground speeds obtained from the same genera in insectaries (Srygley & Dudley 1993). Data on natural airspeeds in habitats other than a large lake are needed to verify the generality of these findings.

In another comparative study of 62 Neotropical butterfly species, natural airspeed was positively correlated with body mass, thoracic mass, and wing loading (Dudley & Srygley 1994). Once body mass was controlled statistically, higher wing loadings were correlated with increased flight speed, but flight speed and wing aspect ratio were negatively correlated. These results suggest that butterfly airspeeds under natural conditions can reasonably be predicted from morphometric measurements (Dudley & Srygley 1994).

Studies of natural flight within butterfly species have also generated important insights into the biomechanics of insect flight. Dudley & DeVries (1990) found that certain aspects of their flight for the moth *Urania fulgens* consisted of unsteady aerodynamic movements because of the relatively large lift coefficients (between 2 and 3). For most flight sequences, however, lift coefficients were closer to 1.0 or were substantially less, suggesting quasi-steady aerodynamic mechanisms (Dudley & DeVries 1990). Verification of whether organisms use fundamentally similar flight mechanics in the field and in nature is important for understanding the generality of basic models of insect flight.

Intersexual differences in flight physiology were also studied for *U. fulgens*. DeVries & Dudley (1990) studied the effect of internal (thoracic) and ambient temperature, as well as morphology, on the airspeeds of both sexes. Airspeeds generally increased with increased thoracic temperature but did not change with ambient temperatures. Males and females differed significantly in external morphology but not airspeeds or thoracic temperatures, suggesting that neither ambient temperatures nor morphology greatly affect the natural flight speeds of this moth.

Srygley et al. (1996) examined natural airspeeds, wind speeds, and headings of two migrating butterflies and one moth over Lake Gutan in Panama. The Pierid *Aphrissa statira* and the nymphalid *Marpesia chiron* were capable of wind-drift compensation during migration, whereas the moth *U. fulgens* was not. Thus, information on how fast free-living animals move in nature provides interesting clues to many aspects of their biology, including migration behavior, which could have important implications for the conservation of these species.

CONCLUSIONS AND PROSPECTUS FOR THE FUTURE

An emerging theme from this review is the complex manner in which behavior and habitat interact to affect ecological locomotor function. This theme reinforces the suggestion that the “performance paradigm” (Arnold 1983, Wainwright 1994)

must be expanded to include behavior (see Garland & Losos 1994, Garland & Carter 1994).

Several trends are noteworthy. First, levels of performance or relationships between environmental variables and function can be dissimilar between the field and laboratory. Laboratory studies indicate that flight speed is independent of temperature in locusts, whereas field studies show that flight speeds increase with temperature (Weis-Fogh 1956, Waloff 1972). In some cases the difference may be methodological; the slower speeds of the fringe-toed lizard (*U. scoparia*) in the laboratory relative to the field may be a consequence of using a racetrack (Jayne & Ellis 1998, Bonine & Garland 1999). Second, many species show seasonal variation in locomotor behavior. Studies of the field metabolic rates of lizards show that they vary their activity levels seasonally, resulting in different energetic requirements. Especially interesting would be studies that combine energetic information with more exact data on speeds.

Birds and marine mammals dominate the literature on ecological locomotor function; more data are needed for terrestrial organisms. The different results from studies of preferred speed in terrestrial *Uma* lizards and arboreal *Anolis* lizards show that generalities about ecological function are difficult to establish when there are substantial differences in habitat and behavior. For instance, do arboreal animals always move at slow preferred speeds? Do animals that occur in open habitats with patchily distributed retreats typically exhibit bimodal distributions of speed? Further, despite the impressive amount of data for some animal groups, certain key issues remain unresolved. First, few studies have used an evolutionary approach for investigating ecological function. The amount of data required for evolutionary comparisons would be prohibitive for certain physiological measurements, but comparative data can yield insights that would not be possible from studies on single species. For instance, comparative studies of ecological performance in *Anolis* lizards revealed that low-performance species compensate for their poor sprinting capacities by using a greater fraction of their capacities when fleeing from a threat. Other questions pertaining to the co-adaptation of physiology and behavior could also be addressed. Has maximum speed (Djawdan & Garland 1988) or evasiveness (Djawdan 1993) of rodents co-adapted with how fast they move when escaping a natural predator? Do species that gain an energetic advantage from intermittent locomotion also use the mode of locomotion more often in nature?

Few studies have developed methods for quantifying intermittent locomotion in nature. Recent laboratory studies have shown that terrestrial animals experience enhanced distance-running capacity if they move intermittently (Full & Weinstein 1992, Weinstein & Full 1992, 2000, Adamczewska & Morris 1998), but quantifying intermittent locomotion is a challenge. Unlike steady-speed locomotion, intermittent locomotion is characterized by three variables: the durations of movements, the durations of the pauses of movements, and the speed of movements. Several questions remain unanswered. Do the lengths of pauses among movements in nature correspond to pauses that minimize the energetic cost of transport, or are species using pauses that are not energetically efficient but instead enhance

some other physiological or behavioral function, such as lactate clearance or vigilance? Do species switch between intermittent and steady-speed locomotion in nature depending on the ecological context? A recent experiment with laboratory mice found that lines selectively bred for high levels of voluntary wheel running (Koteja et al. 1999) also exhibit more intermittent locomotion, as compared with unselected (random bred) control lines (Girard et al. 2001).

Most glaringly, no studies have examined the relationship between fitness and ecological function, despite the importance of this issue for evolutionary theory. For example, one could examine the relationships of laboratory performance, field performance, and fitness. The difficulties for these studies are measuring performance on the same individuals over time and accurately determining the fitness of free-living animals. It would be interesting to examine sympatric species that vary in the degree to which they use a performance capacity for a given task. One might predict that in the species that uses the performance capacity to the greatest extent, fitness is most closely correlated with performance, whereas in the species in which only a small fraction of their capacity is used, fitness will be unrelated to performance. However, empirical complications may occur if individuals with low performance abilities compensate for those low abilities, or if high performance has both positive and negative consequences. For example, a recent study of the lizard *Lacerta vivipara* found that individuals with low stamina, as measured in the lab at birth, tended to exhibit reduced activity in the field, lower growth rate, and higher parasite load, but apparently lower predation risk as assessed by tail losses (Clobert et al. 2000). Individuals with high stamina showed higher rates of activity in the field, higher growth rates, and lower parasite loads, but higher incidence of broken tails. Across all individuals, stamina at birth did not predict survivorship to the age of sexual maturity.

With the exception of those on diving physiology, few studies have followed the movement of individual animals over time and published complete histograms for whole-organism performance variables. Such histograms are invaluable because they provide a baseline for comparison to less common kinds of performance, such as when animals use locomotion to capture prey. Most studies provide only point estimates in which a performance variable is measured at a single point in time. This limitation results in part from the methods used to measure performance, such as radar guns for measuring speeds.

Finally, a potentially fruitful source of data is artificial enclosures, which provide much of the complexity of natural habitats, yet are simple enough that certain variables can be controlled (Watkins 1996, Losos et al. 2000). For instance, one might design an enclosure with artificial dowels of different diameters and inclines to investigate how these variables affect the speed of arboreal lizards. A crucial issue for such experiments is accurate replication of the scale and complexity of natural habitats, which is especially problematic for large animals that move long distances (e.g., many marine mammals). Consequently, these techniques will probably be most useful for small organisms that move short distances. Especially useful would be studies that combine data from artificial manipulations with field data on how natural environmental variation affects locomotor function.

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