

Integrated Studies of Locomotor Performance

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Abstract. Locomotion is an organismal level phenomenon, but it has its basis in structural and functional properties at all lower levels of biological organization. It also has important consequences for behavioral capacity and function and evolution in natural environments. All these topics are important areas for biological research, which will proceed most rapidly through integrated, cooperative studies by biologists of different specializations. The approach suggested involves the measurement of the locomotor performance space of an animal, that is, an analysis of the limits of its behavioral repertoire, with subsequent analyses of the structural and functional bases and the ecological and evolutionary importance of those limits.

INTRODUCTION

Biologists are usually content to specialize their studies at one functional level of organization (e.g., molecular biology, organ morphology, population biology). They seek the bases for the phenomena they study at one level removed from their expertise and are generally satisfied with explanations at those levels. Organisms, in contrast, are integrated units that encompass all levels of biological organization. They do not make distinctions between such properties as morphology, physiology, and behavior nor do they develop those properties in isolation from all the other traits they possess. Individual traits do not evolve independently, rather they evolve only in the context of a complete, functioning organism.

For a biologist to understand a complex organismal phenomenon such as locomotion, including its structural and physiological basis and its ecological implications, a broader perspective is required than is normally employed. Such an integrated study must begin with an analysis of locomotor performance of an animal and proceed in both directions of the biological hierarchy. On one hand, the basis of locomotor performance may be sought

within muscular and nervous morphology and physiology and at lower levels of cell and molecular biology. On the other hand, the ecological consequences and evolutionary implications of locomotor performance must also be examined and studied. This paper will outline some approaches that have currently been taken in these types of analyses and point to areas requiring further research and collaboration among biologists of different disciplinary backgrounds.

ORGANISMAL STUDIES OF LOCOMOTOR PERFORMANCE

The point of departure for locomotor studies must be the performance of the organism itself. It has been emphasized that organisms are constrained by compromises among the functional capacities of their interacting systems (Bartholomew 1986). Locomotion is one of those organismal properties that emerge only from the coordinated function of many organ systems acting in concert. The unique combinations of structural and functional properties of each individual and of each species will determine locomotor properties, which may emerge in nonobvious ways from their component parts. Locomotor performance capacities are difficult to predict *a priori* and must therefore be studied directly.

Most animals have a great repertoire of potential locomotor movements, ranging from very slow and sustained activity to rapid bursts of intense exertion. What is the best way to study this potential range of locomotor behavior? I suggest that a fruitful approach is to measure the limits of different sorts of locomotor modes, that is, to define the locomotor capacities of an individual species (for instance, its maximal speed). These capacities set boundary conditions within which all locomotor behaviors must, by definition, be undertaken. An animal, for instance, may run at slower speeds but cannot exceed its maximal speed; greater speeds are not part of its potential behavior. Taken together, measurements on the limits of locomotor performance define a volume (here designated as the locomotor performance space) that encompasses the entire locomotor repertoire of an animal. Such a volume is potentially *n*-dimensional. As a first approximation, one can define this space by the measurement of three variables: speed, maximal exertion, and endurance. Speed (or burst speed) may be considered the fastest movement over a short distance of which the animal is capable in a second or two. It is measured as absolute distance travelled per unit time. Maximal exertion is the locomotor effort expended during intense activity culminating in exhaustion within a minute or two. It can be measured directly as the total distance travelled under pursuit to exhaustion. Endurance is the capacity to sustain activity for longer periods, such as ten minutes or more. It can be measured directly as the highest average speed that an animal can sustain for this time period. Taken together, these three

locomotor measurements define a performance space in the shape of a rectangular prism (see Fig. 1). Any point within this volume is a potential choice of behaviors that an animal may exercise. It can travel at its maximal speed or any slower speed or can exercise all of its endurance capacity or only a fraction of it. These three measurements are proposed because they encompass all the levels of effort that organisms display and probably reflect independent functional and structural characteristics (see next section). In addition, they are relatively easy to define and to measure. Depending on the type of animal studied, other factors might be added to or substituted for these, such as maximal jump distance for a saltatory animal, maximal climbing speed for an arboreal species, or turning angle during evasion for a terrestrial runner.

What is the utility of knowing the performance space of an animal? The performance space, properly measured, is an envelope within which all normal activities must occur. As it expands or contracts, locomotor options enlarge or shrink. Consider, for instance, the effect of such ecologically relevant conditions as body temperature, parasitic infection, level of

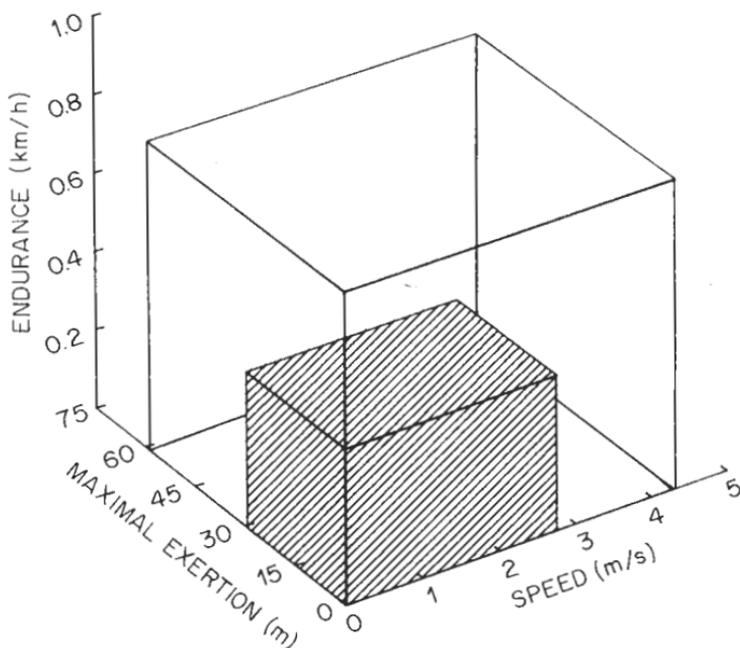


Fig. 1—Locomotor performance space of the lizard *Dipsosaurus dorsalis* at body temperatures of 25°C (hatched figure) and 40°C (open figure). Speed is the fastest velocity observed over 0.5 m (Marsh and Bennett 1985); maximal exertion is the distance run under pursuit in 2 min (Bennett 1980); endurance is the maximal speed sustained for 15 min on a motor-driven treadmill (John-Alder and Bennett 1981).

hydration, or reproductive state (e.g., pregnancy). We can examine the effects of each of these factors, singly or in combination, on performance space. We can determine whether all types of locomotion are similarly affected or whether only one or two are influenced by the condition. For example, locomotor performance space is very sensitive to body temperature in ectothermic animals. In the lizard *Dipsosaurus dorsalis*, performance space at 25°C is only 14% that at 40°C (Fig. 1). All locomotor variables are thermally sensitive, but endurance is most affected by temperature ($Q_{10} = 1.9$); speed is less affected ($Q_{10} = 1.3$). Clearly, at cold temperatures locomotor capacity is greatly constrained in this species; many behaviors that are possible at higher body temperatures are not available to colder animals, with obvious ecological consequences. The advantage of examining performance space in this manner is that it gives a comprehensive picture of a physiological or environmental variable on the entire behavioral repertoire of an animal.

Furthermore, measurement of performance space facilitates comparison of locomotor repertoires among species or among individuals. Performance space can be highly variable even among animals of the same population, and these differences can be both heritable and stable ontogenetically (Bennett 1987). Consequently, we can ask whether there are necessary trade-offs in specialization of locomotor function: does an individual or a species of high endurance have a low speed capacity or are these independent factors or are they positively related? We can also examine ontogenetic trajectories of locomotor capacity. How does locomotor performance capacity and hence the potential range of possible behaviors expand as animals grow?

Measurement of the performance space leads naturally to two different sorts of questions and approaches. First, we can ask what are the underlying bases of the performance limits observed. What makes a fast animal or species fast or gives it a greater capacity for maximal exertion? What are the morphological and physiological bases for the differences observed? This exploration may proceed from the organismal level down to the molecular level. Second, one may ask about the ecological and evolutionary consequences of the performance space of individuals or species. In which portion of the performance space do most natural activities occur? Do performance limits establish important constraints on such critical activities as feeding, courtship, or predator avoidance? Both approaches are biologically interesting and important. They reflect the approaches suggested by Arnold (1983) regarding the analysis of the ecological and evolutionary consequences of morphological and physiological features. Specifically, the relationship between these features and organismal performance ("the performance gradient") is analyzed separately from the correspondence between performance and fitness ("the fitness gradient"). The separation of these relationships facilitates their analysis and interpretation. Different approaches to these analyses are discussed in the following sections.

THE PHYSIOLOGICAL AND MORPHOLOGICAL BASIS OF LOCOMOTOR PERFORMANCE CAPACITY

What limits locomotor performance? What is there about some individuals or species that makes them faster, more enduring, or capable of greater bursts of activity than others? This is a poorly investigated interface of morphology, physiology, and behavior, but one that is crucial to our understanding of how locomotor systems are structured. We may make several a priori predictions, based on our knowledge of activity physiology, about the significance of various systems in limiting different types of locomotor performance (Table 1). We can predict that no single factor will limit locomotion at all speeds, but rather that different factors will limit performance at different levels of locomotor intensity. At very low speeds which can be sustained indefinitely, physiological and structural factors will all be permissive to continued locomotion. It is motivation and ultimately fuel exhaustion that will constrain continued activity. As speed increases, locomotor ability will first become limited by aerobic capacity: the ability of the animal to sustain activity will be set by its maximal oxygen consumption. At higher (but still submaximal) speeds, locomotor intensity and duration will be limited by the ability to produce energy anaerobically and/or to tolerate the effects of anaerobiosis (e.g., lactic acid production). At maximal burst speeds, structural and/or functional factors, such as muscle contractile speed or limb biomechanics, will limit performance. The absolute levels of locomotor output and the transitions between them figured in Table 1 are highly dependent upon such factors as taxon, body size, physical medium, and cost of locomotion. Nevertheless, we might expect to find the same hierarchical sequence of factors limiting to locomotion to be found within any single organism.

Before briefly examining the evidence for these asserted limitations, it is appropriate to present a general design principle that has been applied to describe the functional capacities of interacting morphological and physiological systems. This is the principle of symmorphosis, proposed by

TABLE 1 A hierarchy of factors anticipated to limit locomotion at different levels of locomotor intensity.

Speed	Limiting Factor
Slow sustainable speed	Motivation, ultimately fuel
Fast sustainable speed (endurance)	Maximal oxygen consumption
Fast nonsustainable speed (maximal exertion)	Anaerobic metabolism
Maximal burst speed	Structure/function of musculoskeletal complex

Taylor and Weibel (1981), which states that animals are composed of structural elements designed ". . . to satisfy but not exceed the requirements of the functional system." It holds that no element within a system has excess capacity: all elements will reach their functional limitations at similar levels of performance. From this design perspective, single controlling or limiting factors are not anticipated. According to this principle, adaptation will result in the optimization of structural design (for further discussion see Linstedt and Jones 1987). Symmorphosis is a useful first hypothesis for the examination of the structure of functional systems, as it makes explicit falsifiable predictions about animal design. It has, however, some conceptual difficulties, including a definitive stipulation of a functional system and the purpose for which it was designed, problems of conflicting selection pressure on single morphological elements, and the failure to recognize historical or developmental constraints on adaptation. Empirically, some systems analyzed apparently conform to symmorphosis and others do not (see Linstedt and Jones 1987). Ultimately, it will probably be more useful as a heuristic hypothesis rather than as a description of how systems actually are built and function. A contrasting view, predicting excess construction in many morphological systems, is presented by Gans (1979).

Of all the locomotor performance capacities, the determinants of endurance are best understood. Endurance is very tightly linked to the maximal capacities of an animal for aerobic metabolism (maximal oxygen consumption [see Bennett 1985]). As locomotor speed increases, oxygen consumption rises in all locomotor modes (e.g., swimming, flying, running). Over this range of speeds, locomotion is sustainable indefinitely. At the maximal aerobic speed, maximal oxygen consumption is reached and activity is not sustainable at greater speeds. Endurance is tightly linked both intra- and interspecifically with maximal oxygen consumption. In ectotherms, decreased body temperature restricts both in concert. With the establishment of this linkage, attention has turned to analyzing the components that may limit maximal oxygen consumption, specifically the pulmonary, cardiovascular, or skeletal muscular systems. Symmorphosis maintains that none of these is specifically limiting but that all have similar capacities for oxygen transport; however, empirical data do not support this view. For a variety of reasons, pulmonary oxygen uptake capacity is not thought to be limiting in most animals (Weibel et al. 1981; Mitchell et al. 1981; Withers and Hillman 1988; but see Carrier 1987). The capacity of the muscle system to use oxygen is very difficult to assess directly and its role as a limiting factor must be considered undetermined at this time. Several lines of evidence suggest that the capacity of the cardiovascular system may be a limitation to oxygen delivery, at least in some animals (Withers and Hillman 1988). Studies concentrating on the determinates of endurance behavior might therefore begin by concentrating on cardiovascular and muscular morphology and physiology.

Limiting factors of maximal exertion, intense bursts of activity to exhaustion, are poorly understood. They are undoubtedly correlated to anaerobic metabolism, which in vertebrates involves the formation of lactic acid by the skeletal muscles. Animals capable of great bursts of activity have large anaerobic capacities (Bennett 1978). However, the causal factors of exhaustion are not known and might involve many different factors, such as muscle acidity, muscle glycogen depletion, depletion of neurotransmitter, or a combination of these. More work is necessary in this area, however the limiting factors will probably be found to be internal to the skeletal musculature itself.

Maximal locomotor speed in some animals is directly limited by the contractile kinetics of the skeletal musculature. Twitch duration is the minimal response time for muscle contraction; twitch kinetics of locomotor muscles apparently limit locomotor speed *in vivo* in fish (Wardle 1975) and lizards (Marsh and Bennett 1985), at least at lower body temperatures. Muscle fiber morphology and activities of metabolic enzymes correlate with individual differences in sprint speeds in the lizard *Dipsosaurus dorsalis* (Gleeson and Harrison 1988), and many other physiological and morphological variables do not correlate with speed (Garland 1984). The role that muscles actually play during locomotion, along with their time of contraction and force production, is poorly known and represents an area rich in potential for elucidating ultimate limitations on locomotor speed.

The approaches cited above examine locomotor performance at one or two functional levels below that of the integrated organism. A few studies have pursued these problems to the level of molecular biology, specifically, the locomotor consequences of genetic polymorphisms in metabolic enzymes in natural populations. Different isozymes of lactic dehydrogenase are associated with differences in blood oxygen transport and endurance in the fish *Fundulus heteroclitus* (Powers 1987), and flight capacity is correlated with polymorphisms in alpha-glycerophosphate dehydrogenase in *Drosophila* (Barnes and Laurie-Ahlberg 1986) and in phosphoglucose isomerase in *Colias* butterflies (Watt 1985). These are exemplary studies in the breadth of the investigations undertaken and in their reductionist approach to locomotor studies. However, the extent to which differences in locomotor performance space of other organisms have identifiable bases at the level of single gene loci remains to be determined. This will certainly be an area of intense investigation and of considerable promise in the future.

It should be apparent from the foregoing that, apart from the well-established linkage between endurance and maximal oxygen consumption, the empirical basis of our knowledge of the determinants of locomotor performance capacity is very fragmentary. Thus, the hierarchical relationships of limiting factors hypothesized in Table 1 remain largely untested. This condition results not so much from the difficulty of the problems but from the absence of investigation. We are not particularly lacking in analytical

capacity for approaching such studies. Even such techniques as regression of performance on morphological and physiological variables can reveal interesting correlations for further study. For instance, 89% of the size-corrected interindividual variability in endurance in the lizard *Ctenosaura similis* is correlated with only four morphological and physiological variables (leg and heart muscle mass, maximal oxygen consumption, and hepatic aerobic enzyme activity), while 58% of the variability in maximal exertion is associated with only two such factors (maximal carbon dioxide production and muscle glycolytic enzyme activity [Garland 1984]). I expect that progress will be made soon in elucidating the basis of locomotor performance at the physiological, morphological, and biochemical levels. This is an area in which progress will be more rapid and more synthetic if cooperative studies are undertaken jointly by teams of morphologists, physiologists, and molecular biologists working together.

THE ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF LOCOMOTOR PERFORMANCE CAPACITY

Locomotor systems of animals are ultimately shaped by natural selection operating in a particular environmental context. They must be examined within that context if we are to achieve a comprehensive and integrated view of locomotor performance. A number of questions arise concerning the ecological role of locomotor behavior. For example, what is the significance of locomotor performance capacity to animals in nature? What part of their performance space do they use routinely? Does the portion of performance space utilized change during ontogeny? Do animals regularly or ever approach their performance limits? Is, for example, speed or maximal exertion important in predator avoidance or prey capture? Is maximal exertion used in courtship encounters or territorial defense? How is endurance related to distance travel?

These and related questions are not conceptually complex but are practically very challenging to investigate under natural conditions. It is technically difficult to undertake the observations required. It is generally impossible to monitor locomotor movement continually under field conditions throughout the entire life span of an animal. Such observations would probably show that most animals spend most of their time sitting still or moving slowly. However, the importance of such crucial activities as predation, predator avoidance, and courtship to survivorship and fitness is completely disproportionate to their fraction of an animal's time budget. Even if they are very infrequent and of short duration, the animal may die without reproducing if performance is inadequate. Performance under these situations is particularly critical, and it would be especially difficult to observe and to measure this performance under natural conditions. Under

certain favorable circumstances, it might be possible to stage such activity under field conditions, such as by introducing a conspecific animal or a predator into an animal's territory or providing a receptive mate and monitoring the response of the resident. It may also be feasible to stage such encounters under laboratory conditions (Bennett 1986). For instance, Feder and Arnold (1982) staged predatory encounters of snakes on salamanders in the laboratory and found that the salamanders used their maximal exertion capacities (judged by lactic acid formation) in attempting to escape from the snakes. As longtime monitoring of field activity is impractical, these more experimental approaches both in the field and laboratory hold more promise in indicating to what extent locomotor performance capacities may be used naturally.

Is differential locomotor performance capacity directly related to survival and hence to fitness? Is it important for animals to be fast or strong, or are the principal sources of mortality related to factors extraneous to locomotor performance? These questions grow logically out of those previously addressed but relate more directly to the microevolutionary significance of locomotion. It is relatively easy to build convincing hypothetical arguments for either its importance or its insignificance. Only empirical observations on natural populations will tell us whether locomotor capacity is in fact an important attribute in enhancing survival and fitness.

Such studies are not easy, but they are feasible in some kinds of animals. They require securing large numbers (hundreds) of animals immediately after birth or hatching and measurement of their performance space. For selection to operate on the components of this space, locomotor performance must be variable among individuals, heritable, and repeatable; that is, fast animals, for example, must remain relatively fast during ontogeny. The animals must be marked for individual identification and released into their natural population. The population must then be sampled subsequently over the lifespan of the animals released and the differential appearance of animals of different locomotor performance space determined. Two such studies have been undertaken. The study on the fence lizard *Sceloporus occidentalis* by R. Huey and co-workers (personal communication) failed to detect differential survivorship according to size-corrected capacity of speed or endurance. The other study on locomotor performance in the garter snake *Thamnophis sirtalis fitchi* is currently in progress by our research group. We have monitored a cohort of 275 snakes born in our laboratory in 1985 and released directly into their natural population. Their size-corrected locomotor performance for each locomotor trait was found to be highly variable, heritable, and repeatable, even from year to year under field conditions. Correlations among locomotor traits are low. We have followed the survival of these individuals and other animals in the population during subsequent years. We have tested for the correlation between

survivorship and size-corrected locomotor performance by determining whether the survivors were randomly distributed in their original age class with respect to their locomotor capacity. The probability of such random distribution of locomotor traits is reported in Table 2. Size-corrected locomotor capacities are not apparently related to survivorship during the first year of life in these snakes, but rather during the next year, yearling animals with greater performance capacities survive differentially. Data on older animals suggest that speed remains an important correlate of survivorship. Since these snakes do not reproduce until four to five years of age, differential locomotor performance ability at younger ages is consequently also correlated with differential fitness. These observations do not demonstrate the direct operation of natural selection on locomotor performance characteristics; perhaps selection occurs on other characters correlated with locomotor performance (although the removal of body size as a confounding variable may also be expected to reduce nonspecific correlations). The relationships demonstrated in this study, however, are consistent with the potential selective importance of locomotor capacity.

Field studies on the ecological and evolutionary importance of locomotor capacity are thus seen to be feasible. They are both a reasonable and desirable extension of laboratory studies on locomotion and form the ultimate context of its importance to animals. Their design, execution, and interpretation will be greatly facilitated by structuring cooperative studies with ecologists and evolutionary biologists.

THE IMPORTANCE OF INTEGRATED STUDIES

Locomotor ability is a vital part of the biology of most animals. It gives rise to their enormously varied and rich behavioral repertoire, and it is rooted deeply in their structure and functional capacities. Because it

TABLE 2 The effect of locomotor performance capacity on survivorship in a natural population of garter snakes (*Thamnophis sirtalis*). Values reported are probabilities generated by a randomization procedure that animals surviving to the next year are randomly distributed with respect to their size-corrected performance in the original group of released animals. Hence, a low probability indicates a significant (nonrandom) association between the variable and survivorship. Age classes are: neonates = year 0 to year 1, yearlings = year 1 to year 2, older snakes = year 2+ to the following year.

	Neonates	Yearlings	Older Snakes
Speed residual	.28-.75	.04	.002
Maximal exertion residual	.17-.45	.01	.11
Endurance residual	.12-.24	.06	.22

encompasses so many levels of biological organization, a comprehensive examination of locomotion is a topic that would benefit particularly from synthetic, cooperative studies by biologists with different interests and expertise. Understanding how limbs are used during locomotion, for instance, can best be achieved by interactive research involving functional morphologists, muscle physiologists, and neurophysiologists. Field studies on locomotor performance would be greatly facilitated if undertaken jointly by functional biologists, behaviorists, and ecologists. Such integrated studies on locomotion have a great potential to produce a more rapid understanding of the phenomenon than if individual practitioners work in isolation. They also can serve to unify different groups of organismal biologists and to remind us that we are studying organisms, and not just their parts.

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