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ANIMAL ATHLETES

An ecological and evolutionary approach

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Foreword

This book examines how animal athletes have evolved. While many of us might normally think of the activities associated with "athletes" as consisting of only running and jumping, we set out to show that animals perform many tasks to an amazing degree of accomplishment. Some of the examples might seem obscure at first—for example, how can the rattling tail of a rattlesnake be considered an "athletic feat"? Once one realizes that the snakes vibrate their tail at 90 Hz for over an hour, then one's view changes. If you don't believe us, try shaking your hand as quickly as you can for an hour! In other words, the mundane world of animals is filled with extraordinary accomplishments, and our book sets out to celebrate this wonderful diversity by focusing not just on spectacular feats of running and jumping but also on feeding, vocalization, diving, flying, and many other feats. Each of these facets operates in a larger evolutionary and ecological context, and therefore we wanted to examine not only the "how" of amazing animal athletic feats but also the "why." Why do seals dive so deep? Why do some lizards live on twigs? Why do frogs vocalize for long periods of time when, in so doing, they expend a tremendous amount of energy? Our belief is that only in the broader context of ecology and evolution can these questions be answered and the broader pattern of animal athletic traits be understood.

Therefore we delve into many areas—such as, for example, how natural selection and sexual selection operate on performance traits, the musculoskeletal basis of these traits, and how such traits vary in different geographical or evolutionary settings. Our examples are wide-ranging and are drawn from a range of invertebrates and vertebrates, including frogs, lizards, sharks, rodents, bats, birds, insects, spiders, and more! Our goal was not to be comprehensive in our analysis of different systems, and therefore our approach is exemplary rather than exhaustive. We took this approach to enhance readability, and readers are recommended to read many of the cited papers and books to learn more on a certain topic. Our language was intended to be simple, and therefore not every study is covered in the exhaustive detail one might expect to find in a typical academic paper. Our book was hopefully written so that many could access it, but we include enough detail that (we hope) will please specialists. We sincerely hope that this book inspires a new way of thinking about animal athletics and spurs new research into the integrative biology of complex functional traits.

This book could not have been written without the assistance of many individuals. A number of individuals read key chapters and provided invaluable assistance. These individuals include Anthony Herrel, Scott Kelly, Rodger Kram, Henry Astley, Kiisa Nishikawa, William Hopkins, Jerry Husak, Jonathan Losos, Daniel Moen, Jennifer Grindstaff, Simon Lailvaux, Sheila Patek, Raoul Van Damme, Roberto Nespolo, and others. Several discussions with members of the Irschick and Higham lab groups solidified some ideas regarding performance as well as helped identify idiosyncrasies that frequently arise in science. Our editors Lucy Nash and Ian Sherman were especially helpful in guiding us throughout the book-writing process by keeping us on schedule and providing invaluable assistance in the editing process. Their patience during the ten (!) years of writing and during our many twists and turns is greatly appreciated. Finally, we could not have written this book without the support of our families. Specifically, Duncan Irschick thanks Jitnapa Suthikant, as well as Darwin and Calder Irschick for their support and patience. Tim Higham would like to thank Melissa, Daphne, Iris, and Violet for their encouragement, enthusiasm, and endless support.

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1 Animal performance

An overview

1.1 Why study performance?

What is performance ability? If one were to ask this question in any classroom or lecture hall (and we have!), one would immediately be greeted by a showing of hands, followed by a variety of different opinions. In the common vernacular, good "performance" can mean almost anything, such as how well one dances, sings, or even earns money. Simply put, "performance" can mean many things to many people, but a concept is only as useful as it is specific and explanatory. An overly broad use of the term "performance" is meaningless unless it allows us to examine a common body of knowledge. Fortunately, in the world of functional morphology and evolution, this term has enjoyed a more specific meaning that we will focus on throughout this book: performance capacity is any quantitative measure of how well an organism performs an ecologically relevant task that is vital for survival. As explained below, there are some more stringent assumptions behind this definition, but let's put that aside for now. Some classic examples include how fast an animal can run, jump, bite, fly, or perform nearly any athletic feat. You could even think of animal performance as being analogous to the human Olympics, although in the nonhuman animal world, the consequences of a bad day at the track are far more dire than any for even the most heartbroken athlete who has lost his or her event. Indeed, one of the hallmarks of animal performance is that nonhuman animals can place themselves at tremendous risk when performing "animal Olympics"; a cheetah or lion running after its prey can have its jaw dislocated if it miscalculates during the closing phase, and a miscalculated bite on a hard object can irreversibly damage a dog's jaws. One could speculate about the level of performance we might see at the human Olympics if lions were chasing those sprinters!

A study we had each heard of when we were graduate students crystallizes the difference between nonhuman animal and human performance. In a study in the 1980s, the physiologist Todd Gleeson performed a simple experiment with two groups of fence lizards (*Sceloporus;* a lizard commonly seen basking on trees, fences, and rocks in the western United States). For the "control" group, he allowed the lizards to stay in their small cages for about 6 weeks (Gleeson 1979). For the "experimental" group, he induced them to perform aerobic exercise on a treadmill in a training regimen for the same length of time. After 6 weeks had passed, he compared the aerobic capacities of both groups (the control and experimental) and found, much to his surprise, that the two groups did not differ! Obviously, if one performed the same experiments with humans, one would find that the group that had been trained would not only have superior aerobic capacities compared to the control group but also possess several physiological differences, such as increased capillary networks adjacent to large skeletal muscles, increased maximum aerobic capacity, improved blood pressure, and so forth. While not every animal shows this lack of a response to exercise (see chapter 11), for those species that do, it signifies the profound divide between human and nonhuman animal physiology. *Sceloporus* lizards rely on both burst speed and aerobic capacity to elude predators, capture prey, and defend territories, and the relentless pressure of natural selection over millions of years has not only removed many of the "weakest" individuals, it has done so to such an extent that natural selection has a far more limited menu to choose from. In other words, performance capacity is life and death for animals and has shaped their morphology, behavior, and physiology over vast stretches of evolutionary time.

The concept of performance also holds a key place in the human consciousness, both in terms of our own lives and for the natural world around us. Much of our obsession with performance dates to Charles Darwin and his synthetic theory of natural selection. A central thrust of his theory of natural selection is that some organisms will be more fit than others, and one of the main reasons for this variation in fitness is the ability of animals to perform such feats as running, jumping, biting, and so forth. Consequently, one implication of his theory is that some organisms are better performers than others and that this variation is vitally important to survival. His theory has also been extrapolated to include social aspects of human behavior—"Darwinism" or the "survival of the fittest," the idea that only the strong survive—an appealing, though somewhat misguided, view of human culture. Nonetheless, the idea of performance capacity as an arbiter of who lives or dies, or reproduces or not, has percolated in our collective consciousness and has been a spur for biological research into the process of adaptation.

We are fascinated with the traces that, in our everyday lives, reflect our obsession with performance. Each year, people lose millions of dollars betting on which dog or horse will be the winner at the racetrack, and entire countries have been known to explosively celebrate or fall into despair at the success or defeat of their favorite athletes at the Olympics. It is performance that drives almost 200,000 people to attend a single football (termed "soccer" in North America) match in Brazil. At such events, one can clearly see the range of performance abilities in nonhuman animals and humans; while some horses or humans are superior runners, others lag behind. But the artificial world of nonhuman animal and human athletics is not the only window into the mysteries of animal performance, as the natural world offers many strange and wonderful examples of the extremes to which animals have evolved various kinds of performance traits. Even the most jaded observer is fascinated when watching a small frog, only as small as a thumbnail, emit a piercing call that echoes over great distances. Most of us marvel at the rapid speeds of cheetahs when watching them chase their prey on the African plains. We are often caught pointing up in the air as hummingbirds zip by on a nice spring day, saying, "Wow, look at that!" Even in the mundane setting of our homes, the powerful crunch of a dog's jaw on a bone is a reminder of the extreme biting capacities of man's best friend. Evolution has seemingly endowed animals with amazing abilities that can exceed the limitations of animal morphology.

This book examines the broad scope of animal performance and integrates information on morphology, behavior, ecology, and evolution to understand the significance of performance in the lives of animals. We have two primary goals: first, to provide a perspective on the range of performance capacities present in nature; and, second, to understand the ecological and evolutionary context in which these performance capacities have evolved. To address these broad goals, we will explore how five factors, namely, behavioral, ecological, evolutionary, morphological, and physiological, act as innovators and constraints for generating diversity in animal performance. These factors allow us to identify how different parts of an animal work in concert to execute behaviors. It is during this behavior that we can define the kind of performance we are interested in. One theme we will explore is the underlying complexity of animal performance. One cannot fully comprehend the diversity of animal performance either by reducing an animal to its parts (reductionism) or by focusing solely on each factor (behavioral, ecological, evolutionary, morphological, and physiological) without considering interactions among these parts and how the whole organism behaves in nature. This integrative approach is important because performance capacities emerge from the whole organism, not from individual parts, and it is the whole animal that lives and dies and that passes on its genes (or not) to the next generation.

On the other hand, there is much to be learned by studying a few components in detail; but the important point is that reductionist studies are only pertinent when we also understand how the whole organism functions.

Beyond the aesthetic pleasure one derives from watching animals run, swim, jump, or fly, why should biologists study animal performance and how will such a focus provide insights into the broader fields of evolution and ecology? To address this, let's consider how natural selection works. Within any animal population over a span of time, individuals will either live or die, and some of those individuals will reproduce, while others will not. For the most part, factors that cause death or that influence the probability of reproduction, such as temperature, food, predators, and so forth, act on the whole organism. Let's consider an example that explains this point. Imagine a male frog calling on a summer night. The main reason that male frogs call is to attract mates. For most frogs, males that call the loudest and the longest are most likely to attract female frogs (Wells and Taigen 1989) and hence are more likely to reproduce and increase their overall fitness. Based on this line of logic, it seems reasonable that every male should have evolved the ability to call both loudly and for long periods; however, an inspection of both variables (call loudness and call duration) shows this not to be the case. As with many biological systems, there is tremendous variation in both traits, with some males being able to call both louder and longer than other males, often by large margins. The reason for this inequality is that calling in frogs is energetically expensive (fig. 1.1) and requires substantial aerobic investment, which is driven by muscles that are specialized for long-duration aerobic movements (Wells and Taigen 1989). Further, frog vocalization is a complex process, involving both a variety of muscle groups and complex behaviors, such as extension of the throat sac. However, because females choose males on the basis of call loudness and call duration, natural selection will operate *primarily* on these aspects of male performance (in this case, a specific form of natural selection called "sexual selection") and only *secondarily* on other aspects of this complex system. In other words, one can state with certainty that "natural selection favors frogs with large aerobic muscles" for long bouts of calling, but in fact selection favors individual frogs that can call for long durations. Female frogs care nothing for the muscles involved in calling. That feature is favored by natural selection only because it is necessary for frogs to call for long periods of time. In short, performance abilities are the "face" that animals put forth in the natural world, with many other supporting features "hidden" in the organism (although in some cases, natural selection does act directly on morphology or behavior alone). This example underscores how one cannot understand the evolution of unique morphological traits (i.e., the throat sac and the specialized muscle groups) or behavior (i.e., vocalization) without understanding the resultant performance capacity (call intensity and duration) or vice versa.

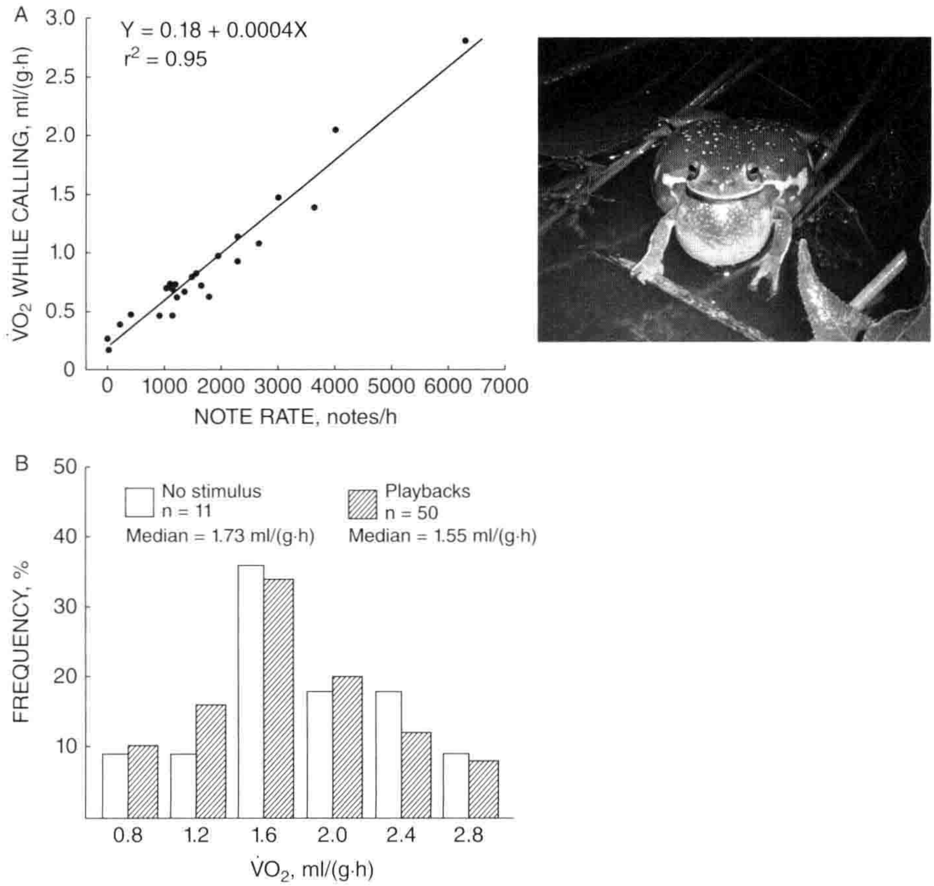

Fig. 1.1 *A*, A plot showing the relationship between note rate and the rate of oxygen consumption for the frog *Hyla microcephala* during vocalization. *B*, A frequency distribution of different oxygen consumption rates (VO_2) for the frog *Hyla microcephala* during vocalization. The open and filled bars indicate vocalizations in response to playback or without a stimulus, respectively. Note that, in *A*, the higher the note rate, the higher the rate of oxygen consumption. Redrawn from Wells and Taigen (1989) with permission from Springer publishing. Image is from Wikimedia Commons

Now let's examine a common predator-prey scenario that reveals both the importance and subtlety of animal performance for survival. Small fish often elude predators (e.g., a larger fish) by using rapid bursts of acceleration (Webb 1976), often in the stereotyped form of a C-start, a circular escape motion in which the fish swims off in the opposite direction from which it was first stimulated (by, for example, a touch on the tail, or the sensation of water pushing up against its tail). The salient point is that predators only have a very brief period of time to capture their prey, given this mode of rapid escape, and this time is usually on the order of milliseconds (a millisecond is one thousandth of a second). Whether the predator successfully captures the prey or, from the prey's point of view, whether the prey lives to see another day depends on many factors, including the initial attack distance and accuracy of the predator, the relative sizes of the predator and prey, and the relative performance capacities of each (i.e., how fast each can accelerate). Clearly, both predator and prey in such circumstances would evolve many specializations for maximizing their chances of success (capturing prey or eluding capture, respectively), but one of the most prominent specializations is the ability to accelerate quickly either to capture an evasive prey or to evade a quick predator. In other words, we can think of this simple yet ubiquitous dynamic as a coevolutionary arms race between contestants for performance supremacy. Performance often comes at a cost, so it isn't surprising to see this high level of performance relaxed when competition is absent. Indeed, if you find a lake where fish live without looming predators, their ability to accelerate could be reduced, as should the size of the anatomical parts that contribute to acceleration.

1.2 Definitions of performance

Before proceeding further, let's revisit the definition of performance capacity and flesh out some of the underlying assumptions. The ability to *quantify* a task is essential and distinguishes performance from other characteristics: one can measure how hard a dog can bite, count the number of seconds a frog will croak, measure the adhesive ability of geckos to cling to a surface, and quantify how long it takes Usain Bolt to run 100 m. This ability to quantify performance is essential for comparing different individuals, or comparing the same individuals at different times. However, based on this simple definition, many other kinds of performance can be defined, including how quickly an animal can digest food, how many offspring a female mammal can raise in a year, and so forth. In other words, "performance," if not carefully defined, can be extrapolated to a myriad of seemingly disconnected actions. From an evolutionary perspective, whole-organism performance holds little meaning if we attempt to compare "apples and oranges," such as comparing the maximum sprinting speed of a cheetah to the maximum book-reading performance of a teenage boy. In the former case, the task is essential for survival and pushes the entire physiological and muscular system to its limits whereas, in the latter case, extreme book-reading performance may be simply a function of a few heightened senses (e.g., eye coordination) and can hardly be considered as essential to survival (although we heartily advocate reading).

Because the goal of this book is to examine comparable kinds of performance that have significance in the lives of animals, we adopt a dynamic, functional, and whole-organism view of animal performance; such a view has been the center of conceptually related studies over the past several decades. The utility of this seemingly narrow definition can be understood by considering our own human Olympics, which measures human performance at a myriad of tasks, including sprinting, weightlifting, rowing, and so forth. However, the human Olympics do not measure many other potentially valid measures of performance, such as how many books an individual can read in a year or how much money a person can earn in a year. Similarly, this above definition of performance precludes suborganismal measures of performance, such as biochemical and physiological functions within organisms; these measures might include aspects such as the ability of enzymes to catalyze reactions, for example. A dynamic view of performance necessarily emphasizes movement, such as vocalization, locomotion, feeding. By contrast, aspects of performance such as digestion, metabolism, and other such measures are not considered here. In addition, we as humans intuitively consider performance to be a factor that can be increased with training, which would typically preclude things like digestion.

The logic behind this emphasis on the whole organism relates to the hierarchical nature of biological systems. Animals exhibit behaviors and functional capacities that are "emergent" properties at the organism level and cannot be fully understood by only examining individual components (fig. 1.2). Moreover, as noted above, it is the whole organism that is visible to the environmental forces that dictate life or death. Therefore, although understanding how an individual enzyme's function may provide some insight into a larger physiological process, it is the functioning of the larger system (e.g., the organism) that is of paramount importance for evolution. A final criterion is best illustrated by the Castanza family from the TV comedy "Seinfeld." Instead of celebrating Christmas, they celebrate "Festivus" in which "feats of strength" take place (alongside the presence of a bare iron rod). In other words, an important aspect

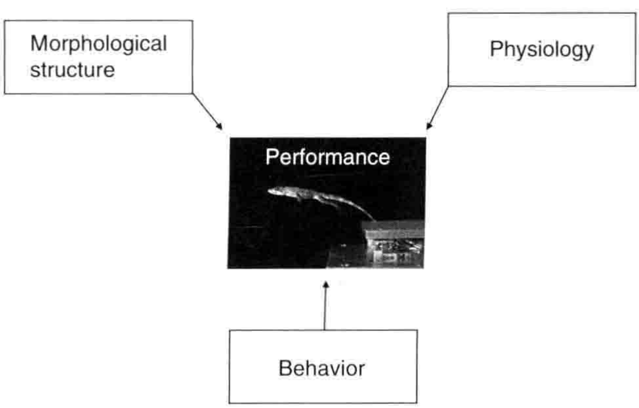

Fig. 1.2 A heuristic diagram showing the interrelationships between morphological structures, physiology, and behavior for influencing performance in animals. The image of the jumping lizard *Anolis valencienni* was taken by Esteban Toro with permission.