SYMPOSIUM

Terrestrial Locomotion—Where Do We Stand, Where Are We Going? An Introduction to the Symposium

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Synopsis Locomotion is fundamental to the survival of many animal species, and terrestrial environments are one of the primary habitats through which a wide range of animals (including humans) must move. Many recent efforts have been made to broaden the approaches and systems used to understand how terrestrial locomotion is executed and modulated. This symposium highlights these efforts and seeks to identify new directions for the study of this diverse behavior. Studies focusing on the structural and functional foundations of terrestrial locomotion, terrestrial locomotor dynamics, and terrestrial locomotor diversity point toward several promising areas for future work. These include: the development, application, and refinement of computational and robotic models; the integration of approaches to clarify which of multiple layers of selection and biological organization influence locomotor performance; increasing the taxonomic, environmental, and behavioral range of study systems to promote new research syntheses and questions; and expansion of studies from laboratory settings to examinations in the field and in the context of ontogenetic and evolutionary time. With new, integrative data from diverse systems in natural settings, new opportunities will emerge for understanding how locomotion contributes to the survival and fitness of terrestrial animals.

Introduction

Locomotion is fundamental to the survival of an enormous range of animal species (Alexander 2003; Biewener 2003). One of the single greatest factors affecting the mechanics and performance of locomotion is the environment in which locomotor behaviors are executed (Gillis and Blob 2001). At a basic level, locomotor environments can be categorized as aquatic, terrestrial, or aerial, with each of these environments placing distinct demands on the animals that move through them (Dejours et al. 1987; Denny 1993; Vogel 1994; Ashley-Ross et al. 2013). Several technological and analytical advances in recent years have enabled novel approaches and new questions in studies of locomotion and, for aquatic and aerial locomotion in particular, many of these have been highlighted through SICB symposia (Lauder and Long 1996; Blob and Rivera 2008; Dudley and Yanoviak 2011; Miller et al. 2012). Studies of locomotion over land have also benefited from the

advent of new technologies and new perspectives in recent years, providing an opportunity for a complementary consideration of locomotion in terrestrial environments. The goal of this symposium is outlined in its title: to highlight recent efforts to broaden the approaches and systems used to understand how terrestrial locomotion is executed and modulated (i.e., Where Do We Stand?), and to use these efforts to forecast the next steps in our study of this diverse behavior (i.e., Where Are We Going?)

A long tradition of research on terrestrial locomotion focused on laboratory studies of physiological performance while traversing level ground. More recently, however, research examining terrestrial locomotion from an ecological or evolutionary perspective has emphasized the need for studies of a greater breadth of behaviors, conditions, and model taxa to understand how animals move through, and interact with, the environment (Biewener 2002). This outlook has been mirrored

by growing interest in biomimetics and the construction of freely moving terrestrial robots (Flammang and Porter 2011; Lee and Biewener 2011; Lin et al. 2011), which must ultimately accommodate natural conditions and could draw from a wide range of models in order to do so. Thus, to better understand the demands of variable terrestrial locomotor conditions, an increased breadth of study-systems and circumstances may need to be matched by the coordination of a breadth of disciplines, spanning from morphology, physiology, ecology, and evolutionary biology to physics and engineering. Through such efforts to expand understanding of how land-based locomotion is executed, reciprocal insights across fields not only should broaden the potential for biomimeticists to draw on more diverse systems for inspiration, but also improve the foundation for studies of locomotion to give insight into organismal adaptation to heterogeneous environments and, potentially, into organismal responses to environmental change.

To highlight recent efforts in these regards, symposium presentations were grouped into three broad categories. The first group, titled "Structural and Functional Foundations," included studies examining fundamental building blocks of locomotor behavior and performance, including skeletal load-bearing (Blob et al. 2014) neuromuscular recruitment and muscle force (Biewener et al. 2014), and metabolic costs (Arellano and Kram 2014). The second group, titled "Terrestrial Locomotor Dynamics," examined a diversity of factors affecting the regulation of propulsive forces across systems ranging from steady (Lee et al. 2014) and unsteady (Qiao and Jindrich 2014) locomotion in limbed vertebrates to the locomotion of soft-bodied invertebrates (Trimmer and Lin 2014). The third group, titled "Terrestrial Locomotor Diversity," used examinations of distinctive exemplar taxa and locomotor environments as a source of insights and directions for future study, including studies of toads landing from jumps (Gillis et al. 2014); arboreal leaping and bipedally galloping sifakas (Wunderlich et al. 2014); and locomotion on inclines (Birn-Jeffrey and Higham 2014).

Structural and functional foundations

A common theme emerging from the studies on foundational locomotor systems that were presented in this symposium was that many current questions require data that are either exceptionally difficult, or impossible, to measure directly. Reasons for such challenges are numerous. In some cases, anatomical structures do not lend themselves to established

experimental techniques, e.g., *in vivo* measurements of force from proximal limb muscles (Biewener et al. 2014). In others, taxa from which direct physiological measurements would be required are extinct, e.g., patterns of loading from limb bones of the first terrestrial tetrapods (Blob et al. 2014). For such questions, modeling approaches have become a productive strategy. In their broadest application, such models can seek to provide a comprehensive explanation for a body of observations, e.g., the spring–mass model of human running (McMahon et al. 1987; Blickhan 1989; Arellano and Kram 2014; Lee et al. 2014). In other cases, models can allow the calculation of specific values of interest from a given set of parameters, such as the use of representative force-length and force-velocity properties of muscles to estimate output of force in Hill-type models (Biewener et al. 2014), or the integration of phylogenetic data with locomotor measurements from a diversity of taxa to produce reconstructions of ancestral states in traits such as limb-bone safety factors (Blob et al. 2014).

The output of such models can provide significant direction to new lines of study. For example, models of the evolution of limb-bone safety factors for terrestrial locomotion indicate higher values in the first tetrapods than in modern birds and mammals, which independently diverged to lower values (Blob et al. 2014). This result indicates that the evolutionary novelties requiring explanation are within mammals and birds, rather than in earlier lineages such as amphibians. However, the simplifications of such models often leave major phenomena unexplained. Identification of such gaps can, by itself, spark new study efforts. For example, simplified task-by-task models of the metabolic cost of human running produced results that summed to overestimate costs by more than 30% (Arellano and Kram 2014). These results motivated Arellano and Kram (2014) to develop a more refined approach that accounted for synergies among tasks and left only 11% of the cost of running unexplained. Similarly, knowledge that the differing contractile properties of slow and fast muscle fibers were not adequately considered in standard one-element Hill-type models of the production of force by muscles motivated Biewener et al. (2014) to develop a more refined, two-element Hill-type model to account for these properties.

Validation is key to evaluating the merit of such refinements and the more general success of such models (Arellano and Kram 2014; Biewener et al. 2014). For example, comparisons of *in vivo* measurements of force from the lateral and medial gastrocnemius of goats, to estimates from multiple Hill-type

models, showed that under most gait conditions a two-element model predicts forces more accurately (Biewener et al. 2014). However, an even broader significance of the study by Biewener et al. is that it represents the first effort to validate a Hill-type model of muscles in comparison with directly measured *in vivo* forces, and that it found the encouraging result that one-element and two-element models both produced generally accurate estimates of the magnitude and timing of forces.

Primary motivations for the refinement and validation of models are to assess the generality of findings and explore their underlying mechanisms. Even for fundamental systems and functions such as the skeleton, muscles, and energetics, diversifying the sample of empirical data available is crucial to such efforts. This can include expanding the range of behaviors that are considered (e.g., walking versus trotting versus galloping), as well as expanding the functional variety of muscular (Arellano and Kram 2014; Biewener et al. 2014) and skeletal (Blob et al. 2014) units that are examined. For example, Blob et al. (2014) compared safety factors between the femur and humerus in alligators, and found higher values in the humerus that were consistent with potential advantages of such intraskeletal variation proposed by Alexander (1997). Such efforts can also include diversification of sampled taxa. Such taxa provide rewarding opportunities to test hypotheses under novel conditions (e.g., ectothermic versus endothermic physiology) and to facilitate insights from an evolutionary context (Blob et al. 2014).

Terrestrial locomotor dynamics

Models have also proven critical for understanding the dynamics of terrestrial locomotion (i.e., regulation of the forces and moments affecting movement over land). One example, for animals with jointed legs, is the spring-loaded inverted pendulum (or SLIP) referenced previously which, with a minimal number of parameters, provides a reasonable representation of locomotion at a constant average velocity (Lee et al. 2014; Qiao and Jindrich 2014). Such models can facilitate a wide range of functional studies (e.g., Full and Koditschek 1999). However, the attractive simplicity of such models carries assumptions that may warrant investigation. For example, in typical applications of SLIP, stiffness of the leg is evaluated by a parameter k_{leg} that is derived from a virtual representation of the leg as a spring between the animal's center of mass and the substrate (Lee et al. 2014). Studies have found k_{leg} to scale as the two-thirds power of body mass (Farley et al. 1993),

agreeing with predictions of dynamic similarity (Alexander and Jayes 1983) that maximum locomotor forces at equivalent dimensionless speeds should scale directly with body mass. However, this result is not independent because changes in deflection of the leg that reflect its stiffness are estimated from the leg's initial length, which can strongly direct the scaling relationship through isometric scaling of length of the leg with body mass (Lee et al. 2014). This difficulty led Lee et al. (2014) to develop an alternative spring constant, k_{rad}, that reflects the force and deflection of the actual leg at every instant of stance (rather than just maximum force and initial length), and can account for asymmetrical dynamics exhibited by real limbs. Measurements of k_{rad} across mammals from a broad range of sizes also produced scaling relationships consistent with dynamic similarity, independently verifying this pattern. However, k_{rad} was consistently one-third stiffer than k_{leg} at any body mass, which may reflect the prevention of excessive leg deflection and facilitate performance of unsteady movements (Lee et al. 2014).

Models of locomotion may also need to be modified to account for circumstances outside those for which the models were derived (Qiao and Jindrich 2014). For example, the SLIP model was developed to characterize steady terrestrial locomotion, but movement through real, complex environments often requires unsteady behaviors such as maneuvers and the maintenance of stability against perturbations (Lee et al. 2014; Qiao and Jindrich 2014). Qiao and Jindrich (2014) found that human maneuvering turns, beyond the SLIP template, require feedback control of foot placement and hip moments for translational speed and upright orientation to be maintained. Stabilizing responses to perturbations, however, might involve different movement strategies than would maneuvers because the former typically are reactive, rather than anticipated (Qiao and Jindrich 2014). In studies of human responses to impulsive mediolateral perturbations, Qiao and Jindrich (2014) found that the center of mass displaced less during walking than during running, but that despite the faster speed of running there was no significant difference (compared with walking) in the time or number of steps required to recover. The ability to execute compensation to perturbation based on feedback may be limited, such that some recovery can be initiated during a perturbed step, but step-transitions may be necessary to allow the modulation of foot-placement and other conditions of stance needed for full recovery (Qiao and Jindrich 2014).

Divergent body designs can lead to divergent dynamics or locomotor patterns compared with expectations from models. For example, although both ostriches and humans are bipeds, differences in body design allow ostriches to exert smaller braking forces than humans during turns (Qiao and Jindrich 2014). In addition, goats exhibit stiffer limbs than other mammals of similar size (e.g., dogs), potentially through reductions in joint moments and differences in the cross-sectional areas of the tendons of limb muscles (Lee et al. 2014). In concert with such potential variation, the complexity of locomotion, based on the integration of many component systems in the context of environmental conditions, frequently requires parallel examination of many levels of biological organization (Qiao and Jindrich 2014; Trimmer and Lin 2014). Studies of terrestrial locomotion in soft-bodied insect larvae presented by Trimmer and Lin (2014) provide an outstanding example of such an effort. A substantial body of work on the locomotor biomechanics of soft-bodied animals has focused on taxa exploiting hydrostatic mechanisms that, despite their different organization, exhibit important functional parallels to the operation of jointed animals. These include the use of constant-volume tissues to allow the predictable transfer of force and displacement, and the distribution of circumferential and longitudinal muscles to provide antagonist functions (Trimmer and Lin 2014). In contrast, insect larvae have compressible internal air tubes and muscles in multiple planes that prevent straightforward application of such parallels. Although caterpillars can pressurize their hemocoel, they do not use such changes in pressure to drive locomotion and, instead, remain soft and conform to substrates (Trimmer and Lin 2014). Waves of motion pass anteriorly along the body, lifting the prolegs by dorsal flexion of the body before placing them back on the substrate (Trimmer and Lin 2014). Measurements from force plates show that these patterns correspond to the prolegs imposing drag on the body, rather than imparting thrust as in limbed vertebrates (Trimmer and Lin 2014). Novel approaches also have been used to assess the patterns of muscle activity and work-loops of caterpillars. With such data providing a foundation, robots have been constructed from soft materials, using shape–memory alloys as actuators (Trimmer and Lin 2014). With the flexibility to design robots with different parameters and apply a range of commands, this approach provides a new opportunity to explore the distinctive dynamics and control of the soft-bodied locomotion found in a substantial number of insect species representing a major portion of insect (and animal) diversity.

Terrestrial locomotor diversity

The diversity of subjects for studies of terrestrial locomotion can be expanded along a variety of axes, each of which has the potential to garner novel insights into the understanding of this behavior. Broadening of comparative data across species is among the most intuitive of these axes, and the potential for such efforts to generate evolutionary insights into patterns of diversity has already been highlighted (Blob et al. 2014). However, our symposium identified additional benefits to increasing taxonomic sampling. One benefit is that the study of distinctive taxa may allow the examination of novel locomotor behaviors that expand understanding of the limits of locomotor performance, or provide advantageous models for investigating specific questions. For example, examination of the unique, bipedal mode of galloping by Verreaux's sifaka may provide insight into the origin of novel locomotor behaviors, by evaluating whether distinctive features reflect constraints imposed by other modes of locomotion (e.g., holdovers from vertical arboreal leaping), or advantageous features that potentially arose as novel adaptations (Wunderlich et al. 2014). Even more standard jumping is, by itself, a distinctive behavior, and Gillis et al. (2014) used the demands imposed, in particular, during landing in toads to test which sensory inputs are required for the successful execution of locomotion. Although vestibular or proprioceptive input acquired during takeoff may be sufficient to allow controlled landing, vestibular and visual input gained during the aerial phase can also be utilized (Gillis et al. 2014). Examinations of jumping are also well suited to studies of coordination across locomotor structures. For example, toads can modulate the kinematics and motor recruitment of forelimb muscles to promote stable landings with a reduced chance of injury, and can modulate the aerial movement of the hind limbs to increase stability (Gillis et al. 2014). In sufficiently long jumps, such modulations allow placement of the foot for the following takeoff (Gillis et al. 2014). Coordination of locomotion across sequential jumps may have significant advantages; as illustrated by sifakas, data on accelerations of the body suggest that strides of bipedal galloping that are part of sequential series may be less costly than strides executed as a single event (Wunderlich et al. 2014).

Increasing the breadth of taxa from which data on terrestrial locomotion are available can also facilitate

scaling analyses of locomotor parameters across significant ranges of body size (Birn-Jeffrey and Higham 2014). Although there is a long tradition of locomotor analyses from the perspective of scaling (e.g., Biewener 1989), the range of terrestrial locomotor conditions for which such analyses have been conducted is limited. Thus, comparative data and analyses are needed from a broader range of locomotor environments. To begin such an effort, Birn-Jeffrey and Higham (2014) conducted scaling analyses of speed, duty factor, and length of stride during locomotion up and down terrestrial slopes. Even within just this range of additional habitats, the predictability of scaling patterns differed, with uphill locomotion showing more consistent patterns across species than did downhill locomotion (e.g., small species use short strides on declines relative to level ground, whereas large species use longer strides).

Studies of diverse species also present new opportunities, and motivations, to study terrestrial locomotion directly in its ecological context, rather than in strict laboratory settings. For example, the sporadic locomotor habits of sifakas motivated Wunderlich et al. (2014) to pursue techniques such as body-mounted accelerometers to gain a better understanding of how bipedal galloping was used in the field, given its potentially high energetic cost. In addition, having determined that small and large species may be affected differently when running down slopes, Birn-Jeffrey and Higham (2014) advocated new efforts to identify the range of inclines that animals actually use in nature. This could provide relevant insights for a range of ecological interactions, such as predator–prey encounters, in which animals often are of different sizes, and trajectories of pursuit or escape could incorporate heterogeneous environments (Birn-Jeffrey and Higham 2014).

Presentations from the symposium also called for further studies of terrestrial locomotor diversity from an ontogenetic perspective. Frogs present an intriguing subject for such work, given their transition to terrestrial locomotion after metamorphic acquisition of the limbs (Gillis et al. 2014). However, understanding of unique behaviors such as galloping by sifakas (Wunderlich et al. 2014) could also benefit from studies of their development, and Birn-Jeffrey and Higham (2014) noted the limited number of studies examining the ontogeny of locomotion on inclines (e.g., Shapiro et al. 2014). Although such efforts can be complicated, ontogenetic investigations have the potential to allow significant integration across biomechanical, ecological, and evolutionary perspectives (e.g., use of wing-assisted incline running by juvenile birds; Dial 2003).

Perspectives and directions for future research

As highlighted by the presentations in this symposium, terrestrial locomotion is being investigated with increasingly creative approaches that forecast an exciting future for the study of this behavior. Four major themes draw together some of the most promising directions for future work.

First are the development, application, and refinement of models. The use of mathematical models in studies of terrestrial locomotor physiology has a long history (Arellano and Kram 2014; Biewener et al. 2014; Lee et al. 2014; Qiao and Jindrich 2014), and the application of phylogenetic models to examine the evolution of locomotion has grown considerably in recent years (Blob et al. 2014). Some of the most recent advances have included computational models to assess the performance of extinct taxa (e.g., Blob 2001; Hutchinson and Garcia 2002; Gatesy et al. 2009; Pierce et al. 2012), and increasingly sophisticated biomimetic robots (Trimmer and Lin 2014) with a capacity for parameter-manipulation that provides a powerful new tool for testing the mechanisms underlying locomotor phenomena (Mazouchova et al. 2013). But even for well-established modeling approaches, continued refinement facilitates new insights with the potential to lead to new lines of inquiry (Miler et al. 2012; Arellano and Kram 2014; Biewener et al. 2014; Lee et al. 2014).

Second is integration across approaches of study. Research on terrestrial locomotion is certainly not unique in this regard, but the potential for complexity in the execution of locomotion, a behavior depending on multiple inputs, component systems, and environmental interactions, places a premium on an integrative perspective. Integration can be pursued in a variety of ways, through the study of different component systems in the examination of a particular behavior (Gillis et al. 2014; Trimmer and Lin 2014), or through the application of techniques from distinct fields, e.g., phylogenetics with biomechanics (Blob et al. 2014), and neuromechanics with robotics (Trimmer and Lin 2014). In addition, the integration of the locomotor system with other behaviors may result in trade-offs, depending on the task (Higham 2007). Thus, studies of the integration of locomotion with other behaviors, such as feeding, can provide insight into the multiple layers of selection that act on the locomotor system (Higham 2007). The combination of such approaches

improves the potential to understand how multiple levels of biological organization influence locomotor performance (Schoenfuss et al. 2013).

Third is the importance of increasing the diversity of study subjects. Studies of a broader range of taxa, environments, and terrestrial locomotor behaviors open opportunities for new syntheses and the identification of new questions. The explosion of detailed phylogenies that have been published in recent years provides a new opportunity to understand how locomotor systems evolve (Lauder 1991, 2003). For many aspects of terrestrial locomotion, however, basic data from a diversity of species that could enable such analyses are still lacking (Kawano and Blob 2013; Birn-Jeffrey and Higham 2014; Blob et al. 2014; Lee et al. 2014; Qiao and Jindrich 2014). Efforts to expand the range of behaviors and environments under which terrestrial locomotion is studied are also an important focus for the future (Birn-Jeffrey and Higham 2014; Gillis et al. 2014; Pace and Gibb 2014; Trimmer and Lin 2014; Wunderlich et al. 2014). In some cases, new possibilities for such studies are now possible through the advent of new technologies, e.g., XROMM visualization of the rotation of limb bones during running maneuvers (Kambic et al. 2014), and the recognition of understudied habitats, e.g., granular media (Li et al. 2013). Studies of novel systems also can allow fields of inquiry to be connected in new ways, e.g., studies of waterfall-climbing fishes ascending vertical substrates have shown that differences in locomotor mechanics can lead to different modes of evolutionary selection (Kawano et al. 2013).

Fourth is the placement of studies in a ''real world'' context. Laboratory studies have long provided a foundation for research in terrestrial locomotion (Biewener 2002), and many aspects of locomotor performance remain most tractable to study in laboratory settings. However, animals naturally perform locomotion in a broader world of space and time, through which they move over diverse terrain (Birn-Jeffrey and Higham 2014; Wunderlich et al. 2014; Collins et al. in press) and develop, grow, and evolve (Blob et al. 2014; Gillis et al. 2014). New tools for the measurement of untethered locomotor mechanics in natural habitats have allowed the collection of previously intractable data, e.g., field measurement of speed and acceleration in hunting cheetahs (Wilson et al. 2013). As further integrative data from diverse systems are collected in natural settings, the future holds great promise for a new understanding of how locomotion contributes to the survival and fitness of terrestrial animals.

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