

Preface

Locomotion is one of the three key functional capacities of mammals, along with feeding and reproduction. An understanding of locomotion is imperative to understanding how adaptive evolution has allowed an organism and its ancestors to exploit the environmental opportunities and deal with the constraints and obstacles encountered in daily activity. Comparative analysis of terrestrial locomotion is an area of widespread interest, but the diversity of forms, as well as physiological and behavioral differences, make a comprehensive analysis of all animal forms a challenge to either produce or assimilate.

In this volume, the main focus is on a single group of specific interest – in this case, my colleagues and I have (largely) chosen the terrestrial mammals (I say largely, because some of the concepts are mentioned in the context of other clades, where these species serve as particularly good examples of the ideas being discussed, or where a discussion of the generality of the concept(s) is of value). The book presents a collection of chapters that will give the reader insight into some important factors that influence how mammals move using legs to travel in the terrestrial environment, and how we can use this understanding to interpret form and performance. Although each chapter should stand on its own, the collected pieces are intended to sum to a

good introduction to the field of terrestrial locomotion and the concepts that are useful (imperative?) when delving into these issues.

As the title indicates, there are two main objectives of this volume. One is to identify some important concepts that should be understood by those with an interest in investigating terrestrial locomotion. These are meant to serve as a starting-point for discussions of the issues involved in investigating the “how and why” of terrestrial locomotion. Even though detailed analysis is important in order to verify precisely how a system works, it is conceptual understanding that allows the perception of patterns and the interpretation of meaning that will not be evident based on observation alone, regardless of how detailed or precise that observation (measurement) is. Concepts allow the interpretation of the patterns that exist in nature, and provide the insight into why the patterns exist as they do. As Aristotle stated; “*We have to examine the reasons for all these facts, and others cognate to them; that the facts are such is clear from our Natural History, we have now to ask the reasons for the facts.*” (Aristotle, *On the gaits of Animals*, ASL Farquharson, trans.).

Sometimes, the most important concepts are evident only in highly obscured behaviors, hidden as apparently smaller features of more impressive aspects of mammalian movement. These “little things” are sometimes very difficult to observe, indeed, but can actually be the determining features of an important functional behavior, such as locomotion. I learned this early in my career, when I was investigating arboreal locomotion in gibbons. Following many others, I was able to describe how gibbons moved across a series of handholds but, no matter how closely I observed and analyzed these motions, discovering the reasons why these animals chose the movement paths they did was elusive. As often happens when delving into the natural world, some aspects of the motions were trivial to interpret, while other features did not fit into any obvious category.

However, once I had established a collaboration with a colleague who knew very little about gibbons, but knew a great deal about the dynamics of objects physically interacting with each other, it was possible to realize that our current perspective on gibbon locomotion lacked a critical feature – the recognition that energetic loss occurs when the path of the mass of the organism changes abruptly (see Chapters 5 and 6 for a specific discussion of this). Ironically, avoiding this energetic loss is so important to successful brachiation that it is, for all intents and purposes, eliminated from the locomotion of gibbons (at least when brachiating). The implication of this, of course, is that the most important dynamic feature of this animal’s locomotion is not directly observable!

It is only through an analysis of alternative movement strategies (that are not used by the organism, because they are so disadvantageous) that the key determinant can be identified. Sometimes, the most obvious aspects of movement are not the most important, and some factors that appear diminishingly small can be far more influential than expected. Hopefully, this volume will provide a number of such “insights” that will build toward a sophisticated perspective on mammalian locomotion.

The second objective of this volume is to introduce and discuss how these concepts can be applied. Thus, many of the chapters provide specific examples of how fundamental concepts are applied to locomotion research to interpret the meaning of the form and function of locomotion. However, it is fully acknowledged that the interpretation of observations through the formulation and application of concepts continues to generate controversy now, just as it has done in the past. When dealing with systems as complex

as those occurring in the natural world, working to a final and unambiguous conclusion on a system is a hard-forged and iterative process. As with our personal progress in learning, however, the objective of our exploration of the natural world is not so much to rid ourselves of all questions, but to replace simple questions with ones that are more and more sophisticated.

George Bernard Shaw proposed that "*All great truths begin as blasphemies*". Following from that, I might contend that all lesser truths begin as controversies. And, as much as we might eventually be interested in great truths, most of us spend our day-to-day research lives working on lesser truths (where the practical potential to document progress is much more achievable). The scientific method has many complexities, but one view of scientific progress is the systematic identification and resolution of controversies. With regard to the locomotion of terrestrial mammals, this book is intended to assist with that process.

There is no intention here to produce an authoritative compendium of answers but, instead, the volume should be viewed as a guide to some important questions currently present in locomotion studies – an attempt to lead the reader to the edge of the "envelope", as it were. The exploration of concepts and their application, with the inevitable revelation (and not necessarily immediate resolution) of controversies is the scientific process – a much broader and intellectually rich endeavor than is the simple application of the scientific method.

Rather than try to provide proof to resolve controversies, an important objective of this volume is to expose these controversies within the context of the concepts on which they are based. Identifying and discussing these controversies serves the purpose of stimulating the next generation of researchers to embrace the discussion and to work to expand our understanding of this important aspect of mammalian biology, to solve those particular controversies and to replace them with the next set, as thought radiates into currently unoccupied "logical space". It is really for the next generation of researchers in locomotion biomechanics that this volume was assembled.

This is a particularly interesting time to be studying locomotion. We are the beneficiaries of a suite of new technical tools that allow the measurement and analysis of a wide range of animal movements and novel concepts. These promise to provide new insights into both the "how" and "why" of the movements we observe, and the morphological specializations they are dependent on.

Of even greater importance, however, is my contention that the field of locomotion mechanics is currently undergoing a revolution of perspective of such substance that it borders on a complete paradigm shift. Mammalian terrestrial locomotion has been of academic interest since academic interest originated (see the Aristotle reference above, for instance, or Chapter 1), yet substantial questions remain, in spite of sophisticated investigative tools currently at our disposal. For instance, the fastest quadrupedal gait – the gallop – demonstrates a number of apparently ambiguous mechanical features that have defied the understanding of the mechanical function of this gait (although it remains extremely well-described). That such a roadblock to understanding the meaning of the gait exists, in the face of highly technical advances in analysis techniques, indicates that it is not a technical limitation that prevents our full understanding of this important locomotion strategy, but a conceptual one.

The general approach of the volume is to explore the dynamics of locomotion in terrestrial legged mammals, with some consideration of the mechanics behind these motions. In the process, we are particularly searching for some general principles that can be used to understand and explain how morphology (form) and behavior (action) influence locomotory performance, broadly defined.

Often, locomotion is considered in terms of the neural control responsible for the active motions that can be observed. It will be noticed that there is not much mention of neural control in this volume. This is not because neural control is not acknowledged to be of critical importance in locomotion, but because the focus of the discussions move toward understanding how the biological entity, the organism, interacts and is influenced by its physical environment. The brain is, indeed, the driver of the locomotory system and, just like the driver of an automobile, it is ultimately in charge and directs the motion of the vehicle. However, like any good driver, an individual operating a vehicle must find his/her way between the boundaries of the specific roadway and obey the traffic regulations.

In one sense, this book can be considered an exploration of the "road map" that locomotion navigates, and the "highway regulations" governing how the brain must operate the system in order to be a successful "driver" of locomotion. No matter how much the brain would like it otherwise, in locomotion " F " (force) always equals " ma " (the product of mass and acceleration), and the influence of gravity cannot be avoided (no matter how fast an animal runs, it still weighs the same). Often, control of locomotion is approached from the perspective that "anything is possible", and the specific control patterns selected are analyzed with respect to the internal patterns and relationships between signals. Activity of the neural system, of course, results in activity of the limbs, trunk and other components of the organism. It is those patterns of motion that interact with the external world, and that interaction has consequences, both positive and negative, that we need to be aware of if we are to interpret locomotion effectively (even the central nervous system's role in that process).

One crucial aspect of observing and deciphering the interaction of the organism with its physical environment during the dynamic movements of locomotion is distinguishing the "phenomenon" of locomotion from the "mechanisms" of locomotion. Not much consideration is usually given to this, because the focus is more often on meticulously measuring (often under adverse circumstances, working with uncooperative animals) the dizzying array of movements that occur at all levels of system organization. It is the contention here, however, that the "dizzying array" of motions can only really be interpreted if what they accomplish for the organism can be identified. What is accomplished for the organism is the phenomenon of locomotion, while most of the readily observable motions constitute the mechanism(s) through which the phenomenon is achieved. The chapters in this work try to identify features of the phenomenon of locomotion, and the structural form of mammals organized to achieve locomotion, and to describe its relationship to the mechanisms responsible for making it happen. In so doing, the discussions direct attention to a new and, hopefully, insightful perspective on mammal locomotion.

A range of authors appear in this volume. They were selected on two criteria: that they had something interesting to contribute, and had demonstrated expertise. It will be noted that many of these individuals are not at the end of their careers, unlike we see in many summary texts designed to exploit the perspectives of those with extensive

experience in the field. Rather, in keeping with my prediction that the field is moving through an important change of perspective, I have invited individuals to participate with me in this volume who are contributing to those changes.

Some of the chapters were invited because they provide a description of the important concepts, but most were invited because they described the application of those concepts, so they could relay some of the important controversies. All chapters were evaluated by one, or more, independent reviewers. Some of these reviewers came from within the ranks of the contributors to this volume, while others were solicited externally, because of their particular expertise. For their contributions in this regard, I would like to particularly thank R. McNeill Alexander, University of Leeds, J. Max Donelan, Simon Fraser University, Brock Fenton, University of Western Ontario, and Colin Pennycuik, University of Bristol. As always, however, the views portrayed in the chapters of this book are those of the authors, with whom the responsibility for producing and approving each contribution lies.

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1.1 INTRODUCTION

This chapter is meant only as a subjective description of some important landmarks along the route that has brought the field of terrestrial (primarily) mammalian locomotion to its current position. I have not been particularly interested in documenting the sequence of specific events, but have instead tried to follow the often circuitous path of ideas as they originate, are modified and are passed along to influence others.

In evaluating the current status of the field of terrestrial locomotion, I find that those of us working in this area are part of a long, and often very illustrious, community of individuals who seek out novel and creative methods of divining the constraints and opportunities exploited by animals in attaining movement within the physical world. The motivation for the development of this volume is to focus attention on the role of mechanics in understanding animal locomotion and, particularly, that of terrestrial mammals. The field is currently undergoing a substantive change in perspective, as new

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