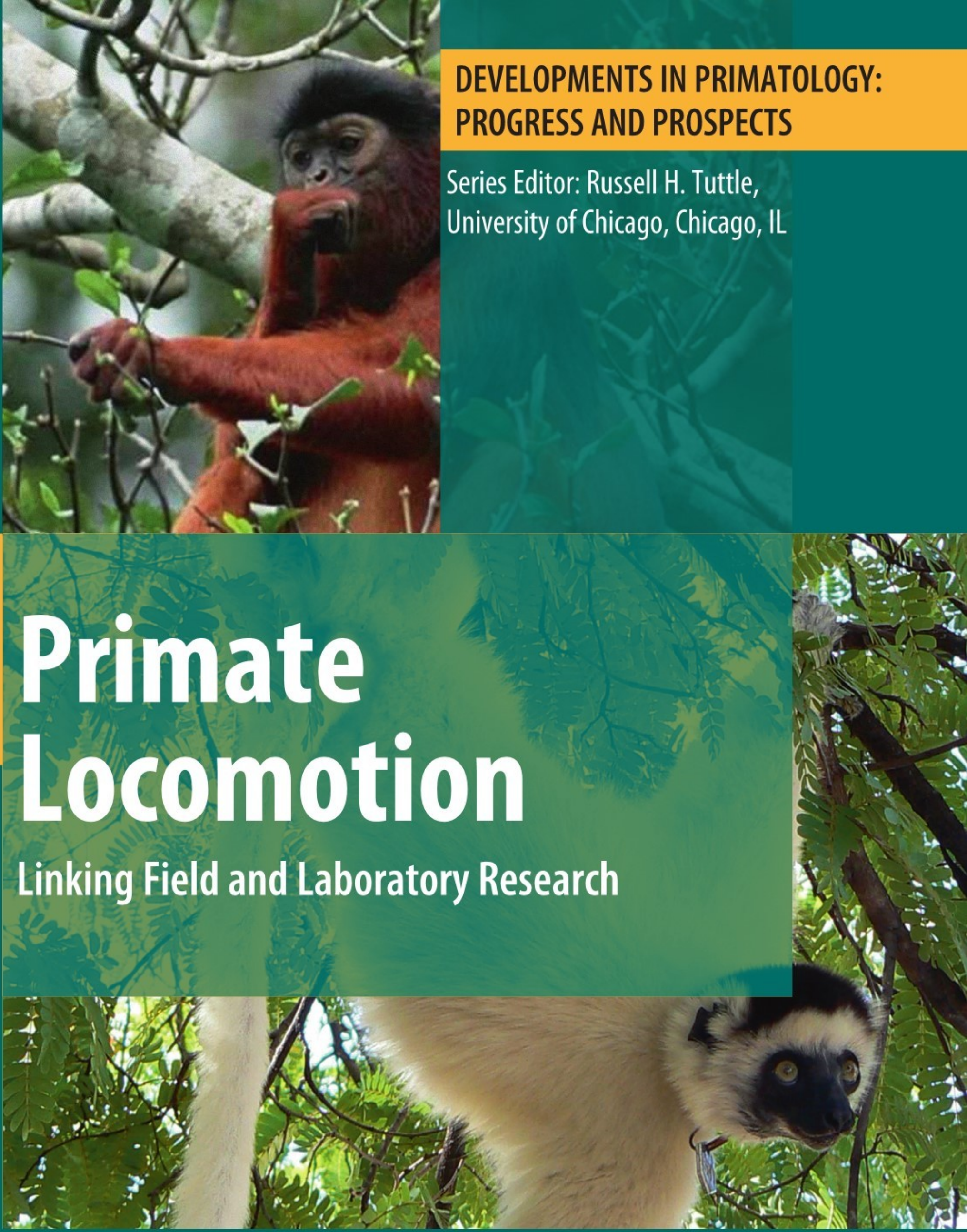

DEVELOPMENTS IN PRIMATOLOGY:
PROGRESS AND PROSPECTS

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Primate Locomotion

Linking Field and Laboratory Research

Kristiaan D'Août
Evie E. Vereecke
Editors

Springer

Developments in Primatology: Progress and Prospects

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Foreword

Studies of primate locomotion in the field and in captivity spanned the entire 20th century and first decade of the current century, and, as highlighted in *Primate Locomotion: Linking Field and Laboratory Research*, they promise to continue for many more decades as newer generations of scientists devise and employ ever more refined tools and approaches. Major events in the evolutionary history of vertebrates such as the tetrapod shift from water to land, and befeathered reptiles taking to the air, have held special interest for scientists and laypersons alike. Standing prominently among these evolutionary puzzles, human bipedalism also generated great interest in how other primates are built and move and are motivated to do so, thereby stimulating research to test models of precedent positional behaviors and changes that might have occurred in the transition from quadruped to hominid biped. Although the anthropological bias has been strong, many scientists have also pursued topics on nonhuman primate species and a wide variety of other tetrapods simply for their own sake or to illuminate broad biomechanical principles that apply to them (Howell 1944; Young 1957; Hildebrand 1967; Alexander 1968, 2003; Biewener 2003).

Sir Arthur Keith must be counted among the earliest scientists to employ behavioral observations and laboratory experiments, in addition to comparative morphological studies on nonhuman primates to illuminate our peculiar mode of posture and locomotion. While a medical officer in Thailand (1889–1892), Keith set up a primitive dissection laboratory in the dense forest where he resided. His initial goal was to dissect gibbons (*Hylobates lar*) and sympatric colobine monkeys (*Trachypithecus germaini*: Groves 2001; Roos et al. 2008) to see whether they, like his patients, suffered from malaria (Keith 1940, 1950). Following earlier anatomists, he noted marked differences between their internal and external structures, with gibbons more closely resembling humans. He further observed distinct differences between how brachiating gibbons and quadrupedal monkeys negotiated the forest canopy.

When he returned to the United Kingdom he continued to dissect a greater variety of apes and monkeys and conducted experiments to understand possible selective effects of gravity on the human body in relation to obligate orthograde posture and locomotion. For instance, he inserted a mercury manometer into his stomach and rectum (one expects in that sequence) to measure pressures on the pelvic floor, abdominal wall, diaphragm, and viscera as he assumed a variety of postures (Keith 1923).

Basic research slowed during World Wars I and II, but during the latter, Elftman and Manter (1935a,b; Elftman 1944) published much-cited informative comparisons of human and chimpanzee footprints and feet as the subjects walked bipedally. Later researchers have supported many of their observations on the functional morphology of human and chimpanzee feet, but some of their generalizations from a single 5-year-old chimpanzee can be challenged. For instance, chimpanzees more commonly walk with extended lateral toes and an abducted hallux than with curled lateral toes and an adducted hallux (Tuttle 1970, 1987, 1990, 2008; Tuttle et al. 1990, 1991, 1992, 1998). I suspect the extent to which subjects are comfortable during experiments is a factor.

Studies, research papers, symposia, and books on primate locomotion and postcranial morphology in extant and fossil primates burgeoned from the 1960s onwards (Kinzey 1967; Kondo et al. 1975; Jenkins 1974; Morbeck et al 1979; Kondo 1985; Strasser et al. 1998; Ishida et al 2006; Stevens and Carlson 2008), and virtually all meetings of the American Association of Physical Anthropologists, International Primatological Society, and American Society of Primatologists have hosted symposia and podium and poster presentations on these topics.

Clearly, although we have learned a good deal in comparison with the level of pre-20th century knowledge, there are many more puzzles remaining to be solved and envisioned. As a pioneer in the adaptation and application of fine-wire electrode electromyography to apes (Tuttle et al. 1972, 1979, 1983, 1992; Tuttle and Basmajian 1973, 1974a,bc, 1977, 1978a,b; Tuttle 1974, 1994; Tuttle, Basmajian, and Ishida 1975, 1978, 1979; Ishida, Tuttle et al. 1978; Tuttle and Watts 1985; Tuttle, Hallgrímsson, and Basmajian 1994, 1999), I must warn that the return of useful information about the adaptive complexes of subject species, and especially the application of it to interpret fossil primates, is very limited. The same holds for new and refined technologies employed by researchers who report and reflect on their projects in *Primate Locomotion: Linking Field and Laboratory Research*.

As some of the authors remind us, the environments in which one must work are increasingly restricted by rules governing studies on primates, particularly great apes. The good news is that some researchers meet the challenge by creatively crafting protocols that limit or eliminate invasive techniques and physical restriction of their subjects. A further encouraging sign for future advances is that there are many more researchers, laboratories, field sites, and focal species than when I began collaborative research with John V. Basmajian in the United States and Hidemi Ishida, Tasuku Kimura, and Morihiko Okada in Japan. For instance, the 45 authors in *Primate Locomotion: Linking Field and Laboratory Research* are from 8 nations (Belgium, France, Germany, Greece, Japan, Madagascar, the United Kingdom, and the United States).

Finally, I urge all laboratory workers, especially ones who have spent their lives in urban settings, to venture into the field and spend notable spans watching primates and other animals moving on natural substrates. Films are fine, but they really are not the same as one's own direct observations to inform creative laboratory experiments and to bound evolutionary models based on them.

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Chapter 1
Introduction. Primate Locomotion: Toward a Synergy of Laboratory and Field Research

Evie Estelle Vereecke and Kristiaan D'Août

Researchers have studied primate locomotion over a considerable period of time, e.g., baboon locomotion by Muybridge (1899), and it continues to receive a great deal of attention from primatologists, anthropologists, and biomechanists worldwide. There are several good reasons for this, many boiling down to the primates possessing several "unique" features, which are thought to relate to their ancestral arboreal niche, and that presumably opened options for the evolution of hominins (as bipeds). In the past, primate locomotion had been tackled from a variety of perspectives. Field primatologists have collected quantitative data on locomotion and posture since the 1960s (e.g., Napier and Napier 1967; Richard 1970; Grand 1972; Rose 1973, 1976; Chivers 1974; Mittermeier and Fleagle 1976; Mittermeier 1978); in-depth biomechanics research on primate locomotion has been conducted since as early as 1935, with Elftman and Manter's study on chimpanzee bipedalism, and Fleagle and colleagues could be considered pioneers in combining both approaches (e.g., Fleagle 1974, 1976, 1992, 1999; Fleagle and Mittermeier 1980).

Whatever the specific research aims, ultimately any primatologist needs to understand the integrative story behind the species' locomotor behavior: how the individual is able (and has been able) to perform adequately in its natural habitat. The seminal paper by Arnold (1983) provides a good framework (see also Wunderlich et al.,Chapter 8). This framework can be expanded (e.g., Aerts et al. 2000), but in its basic form it links morphology, performance, and fitness. Usually, the performance gradient (linking morphology to performance) has been tackled by lab-based researchers in projects *ex situ*, whereas the fitness gradient (linking performance to fitness) has been dealt with mostly *in situ*, by field primatologists. Functional morphology, for instance, studying the relationship between skeletal structure and locomotion, is a good example of the performance gradient (see also

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International Journal of Primatology, special volume, 2010). Insights enable the interpretation of fossils and, by doing so, the locomotor mode of extinct species.

Arnold's scheme is a full circle per generation, and does not allow for missing links if we are to understand fully the adaptive process. Therefore, it is essential that field and laboratory-based primatologists communicate or collaborate. The IPS symposium "Primate Locomotion: Linking *Ex Situ* and *In Situ* Research" in Edinburgh (August 2008) had exactly this purpose, and this book builds upon this initiative. It includes chapters by all symposium participants as well as chapters by invited authors who have contributed significantly to our understanding of primate locomotion and adaptation. As the aim of this volume is to bring together field and laboratory-based primatologists and stimulate future collaboration, we have attracted primatologists from a diversity of research backgrounds, each presenting their recent work and proposing opportunities and/or improvements that could be made by integrating both approaches.

This first chapter sets a general framework, illustrating how the various chapters support the idea of the book, and present issues that were raised during the general discussion at the conference.

There are various ways in which the lab and the field can approach each other, which can largely be attributed to four categories (all of which are illustrated in this volume).

In the first approach, field and lab stay basically separated, but both disciplines communicate by means of publications, meetings, and personal contacts. This approach is best established, as it is the option requiring the least effort. Often, the approach taken is dictated by the research question, leaving little room for a choice between laboratory or field research.

Schmitt (Chapter 2) provides a very good overview of the problems encountered in both field and laboratory studies. Not only does it map those problems in a transparent manner, but more importantly, it also proposes practical suggestions for solving these problems, for instance, by providing examples of how high-tech laboratory data can yield simplified proxies for ecologically crucial variables, e.g., energetic efficiency, and thus enable field workers to address easily the typical "laboratory" link.

This volume contains some clear examples of research that could not have been conducted in the wild, but is possible only in the laboratory, in zoos, or in other captive populations. Ogihara et al. (Chapter 4) use a combination of CT-scanning and high-resolution kinematic data to construct a dynamic model of Japanese monkey walking. Such advanced techniques are strictly limited to the laboratory, and are in fact a step beyond experimental laboratory studies (although field data can provide some input for modeling studies). Berillon et al. (Chapter 5) describe an integrated research project in which 3D-kinematics, dynamic measurements, and morphometrics of a large and well-documented baboon group, and for all ontogenetic stages, are combined. Again, studies from the wild would not provide the same level of detail in any of these topics. Interestingly, this study shows that typical quadrupeds may be adept bipedal walkers, and so the latter behavior, which has been observed in the wild, often considered atypical, may be an integral part of the baboon locomotor repertoire. Schmidt and Krause (Chapter 6) present data on the kinematics of the shoulder, which become fully visible only by using X-ray videography, limited to experimental setups in the laboratory. However, it is demonstrated how the resulting data can be brought to the field. Specifically, the laboratory data suggest that the invisible (for conventional, portable videography) aspects of shoulder function are quite similar within mammals. In this way, field data miss some information that can—with caution—be supplemented by knowledge from the laboratory, albeit of different individuals or different species). On the other hand, observational data from unconstrained wild individuals can indicate how large the proportion of locomotor behavior is in the total positional repertoire, often overlooked in experimental setups designed only for studying locomotion. Examples of neglected behaviors are sitting and sleeping, illustrated by McGraw and Sciulli (Chapter 12). In this study, detailed behavioral observations (such as posture and substrate use) in seven species of cercopithecids are linked to the morphometrics of ischial tuberosities of museum samples. These data were respectively collected in the field and in the laboratory, but combining them yields new insights into the ecological function of an anatomical feature, i.e., sitting pads.

Finally, as pointed out by Cheyne (Chapter 11), laboratory studies can provide baseline data for field studies and allow calibration; field studies can feed the laboratory, by indicating what the natural locomotor repertoire of the animals is, in what context particular locomotion patterns occur, what locomotor aspects require further investigation in the laboratory, etc.

The second approach is to “bring the lab to the field” (Williams et al. 2008). In this approach, the same type of questions are asked that are traditionally addressed in laboratory research, but the data are collected in the wild, most often in an effort to increase the relevance of the observed locomotor behavior and guarantee that individuals are performing naturally. Often, this (still) requires invasive laboratory techniques that are brought to the field and it can (and should) be questioned how invasive one can be without impeding the benefits of field-based research. This is a fine balance that will vary for different species and research questions.

The chapters by Blanchard et al. (Chapter 10) and Cheyne (Chapter 11), both based on field research, deal with such questions: what kind of quantitative locomotor data can be reliably collected in the wild, and what kind of data remain bound to the laboratory floor? At the same time, Blanchard et al. point out how rapid technological advances, such as the availability of inexpensive, portable high-speed video recorders, are rapidly blurring the boundaries between fieldwork and laboratory studies. Cheyne (Chapter 11), using field work with gibbons as a case study, brings forward suggestions of how (former) laboratory techniques can be brought effectively into long-term field studies. Importantly, she points out how, with a minimal additional effort, such an approach can foster new insights into a variety of aspects related to an integrated understanding of primate locomotion, including biomechanics and ecology, e.g., knowing the energetic cost of moving on compliant supports.

The third way in which field-based and laboratory-based workers can more closely integrate is to “bring the field to the lab.”

This approach aims to include more complexity in experimental setups of laboratory locomotor studies, to accurately reproduce the conditions in the wild (e.g., Stevens et al., Chapter 16, and several other contributors to this volume). It is, of course, impossible to truly bring the complexity of the natural habitat into the laboratory, yet selected aspects of the field *can* be brought to the laboratory and studied, while guaranteeing the full relevance of their origin *in situ*. The contribution by Carlson et al. (Chapter 9) is a good example; in the chapter, the authors performed morphometric analyses on skeletal material collected in the field. This as such is not groundbreaking, but the merit of the study is that the osteological material came with detailed background information of life history of the population (unlike most osteological material available in, e.g., museum collections). In this way, a detailed analysis of long bone structure in different populations of chimpanzees, confined to the laboratory, can be linked to behavioral data collected in the field. Such an approach should be encouraged, for instance, by providing anatomists and biomechanists with well-documented cadaver material from the field (with known life history) and not just from captive populations or museum collections.

Finally, the fourth approach is to truly combine disciplines that were traditionally limited to either the laboratory or the field and use existing, or develop new, techniques for the assessment of the performance and fitness gradient as noninvasively as possible. Several chapters in this volume address how such true integration of primate field and laboratory research can be accomplished.

Watson et al. (Chapter 7) have studied load carrying in humans and apes, with data collected in the field, in zoos, and in the laboratory. Taking the example of human load carrying, they have gathered field observations of carrying behavior in all apes. These observations not only yielded insight in potential carrying modes of our hominin ancestors, but also dictated the protocol for the laboratory-based section of their study. Wunderlich et al. (Chapter 8) explicitly address the link among morphology, performance, and fitness, pointing out that Arnold already argued for an integration of laboratory and field work in his seminal paper of 1983. Wunderlich et al. closely integrate morphological, behavioral, and fitness data collected in the field, and functional analyses collected in the laboratory, of *Propithecus*, exploiting the unique strengths of both approaches. By doing so, they have gained insights that could not have been obtained by either approach in isolation. A good example is how leg shape is biomechanically shown to affect performance and, as a consequence, reproductive success in males, hence their suggestion to expand an understudied topic in primate locomotion: the impact of sexual selection. Guillot (Chapter 13) has further suggestions for tackling the full adaptive process, crucial aspects, e.g., performance measures, heritability studies, that remain understudied in primates when compared to other species.

Youlatos and Gasc (Chapter 14) show that is possible to perform quantitative analysis of kinematics in the field, specifically of red howlers (*Alouatta seniculus*) in primary rain forest, despite technical limitations. The latter are likely to become smaller due to technical advances in sensitivity, autonomy, and cost of video equipment. In Youlatos and Gasc's study, field data support (preliminary) laboratory observations; Stevens et al. (Chapter 16) directly compared field and laboratory data, and also found them to correspond well. Even though the good accordance between laboratory and field data in both studies is reassuring, many contributors state that the obvious decrease of complexity of laboratory setups compared to natural habitat remains a challenge. Shapiro et al. (Chapter 17) demonstrate this point in their contribution, which contains the first quantitative analysis of quadrupedal kinematics of *Saimiri* in the wild. Their study of locomotion on idealized supports, e.g., poles in the laboratory, and natural supports (branches) shows that gait flexibility on less complex supports is reduced, even though basic gait parameters, such as interlimb coordination and duty factors, are similar. Guillot's study of suspensory gait in two cebid species (Chapter 13) is in line with this idea. She has shown that locomotor data collected in the wild may reveal features of gait, such as asymmetries and ways of dealing with pliant and unreliable supports that may be concealed in simplified ("impoverished") laboratory setups. Both of these studies prove the point made by Stevens et al. (Chapter 16), i.e., that we have relatively little information regarding kinematic solutions or locomotor strategies primates employ to navigate their habitats. Laboratory studies should incorporate setups of a higher complexity than is often the case to date, even though an exact replication of natural complexity may remain impossible, or even undesirable in some cases (Stevens et al., Chapter 16). In any case, field workers should try to quantify substrate characteristics such as compliance.

Pontzer et al. (Chapter 15) address the energetic cost of locomotion in chimpanzees. Traditionally, there has been a trade-off between accuracy of energetic cost estimate per distance traveled (best in the laboratory) and an insight in locomotor activities, including time budget and distance traveled (limited to the field). Pontzer et al. review the literature and present concrete ways of combining both, allowing for a more accurate estimate of ranging cost than would be obtained by using biomechanical data or observational data in isolation, while still refraining from invasive experiments in the field, e.g., by using doubly labeled water.

Together, the chapters of this book prove that many primatologists are open to stepping beyond their field (or laboratory) of expertise, by combining work that used to be limited to either field or laboratory settings, or, when theoretical or practical issues prevent doing so, by collaborating intensively. May such interdisciplinary approaches be even strengthened in the future and contribute to an ever increasing understanding of our common interest: an integrated view on primate locomotion.

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Chapter 2
Translating Primate Locomotor Biomechanical Variables from the Laboratory to the Field

Daniel Schmitt

Abstract One of the critical goals of primate evolutionary morphology is to understand the functional anatomy of muscular and osteological features to infer behavior in the fossil record. One of the most productive approaches for testing functional hypotheses is the comparative experimental approach first advocated by Washburn in the early 1950s. Since that time, laboratory-based approaches have provided profound insights into the biomechanics of primate locomotion and helped anthropologists understand important aspects of limb design. However, a lack of connection to naturalistic data collected from the field has limited the full value of these data. This chapter proposes that there are a number of simple variables that can be collected both in the laboratory and the field that reflect important underlying aspects of locomotor biomechanics. These include gait choice, limb phase, and joint yield all of which appear to be associated with joint loading and center of mass movements. Using these measures, this chapter provides a model for the way in which laboratory-based and field-based data may be analyzed to provide a complete perspective on primate locomotion.

Keywords Forces • Gait • Locomotion • Primate

Abbreviations

COM	center of mass
DS	diagonal sequence
KE	kinetic energy
PE	potential energy
TE	total energy

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Introduction

For as long as I have been doing research, beginning with my dissertation, whenever I give a talk there is always someone who comes up to me after my presentation to discuss all the limitations of data collected in a captive environment. The person always ends by saying: “Wouldn’t it be cool to take your force plate and put it in a tree in the wild?” I always agree that it would be cool, but it would also be prohibitively difficult and expensive. Nonetheless, despite the significant pragmatic limitations, understanding the biomechanics of primates in their normal environment is an important goal and over the past fifteen years many anthropologists have been trying to do the next best thing. We have been gathering the kind of information that would allow us to make reasonable connections between the kind of detailed data you can collect in the laboratory and the kind of data that can be collected in the field. That is why the symposium that Evie Vereecke and Kristiaan D’Août organized in 2008 in Edinburgh, Scotland at the meeting of the International Primatological Society and the resulting volume is so exciting. In the chapter that follows I use the occasion of this project to try and see how close we have gotten to moving the force plate, at least metaphorically, into the field. The goal therefore is to make use of more than 15 years worth of laboratory-based studies of primate locomotor biomechanics to identify simple variables that seem to reflect clearly deeper underlying biomechanical patterns.

The intersection between field-based and laboratory-based studies has a long been a sore point in our field, and has been frequently discussed but rarely acted upon. It was discussed in numerous chapters of an important volume in 1979 (Morbeck et al. 1979), a revisiting of that volume (Plavcan et al. 2002), and a recent symposium (Grossman 2006) and has been touched on repeatedly over the years. By way of example, over the past forty years we can look to several important papers that have tried to make quantitative observations of locomotor behavior in the wild and relate those back to biomechanical aspects of primate locomotion. Grand’s two seminal papers in 1968 on howler locomotion are strong examples of this approach (Grand 1968a, b). John Fleagle’s (1974) paper on gibbon locomotion is another excellent example of how combining field and lab approaches provide new insights. In 1979, Mike Rose and Maryellen Morbeck published profound chapters on locomotor behavior in the field of vervets and black and white colobus monkeys. More recently, Dunbar and Badam’s (2000) work on bonnet macaques and Byron and Covert’s (2004) work on langurs also serve as models of what can be done and what should be done. Yet, connecting laboratory-based and field-based data remains something we just have not been doing enough. Moreover, as good as these papers are, they lack explicit connection to laboratory-based data that include movement and force or muscle patterns.

There are some clear reasons for this lack of connection between field and laboratory data. First, there has always been an odd resistance among biological anthropologists to data collected in the laboratory (see Fleagle 1979; Lemelin and Schmitt 2007, Schmitt et al. 2008 for a more detailed discussion). The history of laboratory-based research in physical anthropology begins in earnest with the work of Elftman and Manter (1935) which is followed by Sherwood Washburn's (1951a, b) call for a "modern experimental comparative anatomy". Washburn's argument for an objective mechanism of providing quantitative biomechanical data was compelling and timely. The biological sciences were already developing a vibrant field of laboratory-based research. But this experiment-oriented approach was not immediately embraced by our field. Washburn's approach using laboratory-based data to resolve conflicts in scenarios of human evolution was not always well received by his peers at the time. Many of his peers saw the experimental method as a major threat because "they thought it was destroying the evidence" (DeVore 1992: 417).

In spite of the obvious theoretical strengths and 50 years of observed success of an experimental comparative approach, few physical anthropologists today test their functional models with experimental data. There are several reasons for the lack of rigorous testing using laboratory data. Many anthropologists misunderstand how the experimental approach can be used to test functional hypotheses. Too often criticisms are made about small sample sizes, unnatural laboratory conditions, and the highly technical aspect of methods used in the laboratory. These concerns inhibit the willingness of physical anthropologists to collect experimental data and the acceptance of such data when they are presented. In the absence of experimental data, confirmation of a functional model can be achieved only via traditional comparative anatomy, e.g., the prediction that long legs are mechanically critical for leaping primates is confirmed by the observation that other leaping animals have long legs. This mode of checking functional models may lead to correct conclusions, but as Bock (1977), Homberger (1988), and others have noted, this is not always the case. Lauder (1996:56) noted that such conclusions are based on untested assumptions and that:

> …in our desire to draw conclusions about biological design and to support theoretical views of how organism are built, we have been too willing to make assumptions about the relationship between structure and mechanical function…[and]… we have not often conducted the mechanical and performance tests needed to assess the average quality of organismal design.

Second, and more relevant to this volume, the practice of "field biomechanics" is difficult, and data collected in the field cannot be as accurate or precise as data collected in controlled conditions. Even if we overcome the practical issues of equipment and animal behavior. there are other serious constraints for collecting any acceptable kinematic data, let alone data on substrate reaction forces, oxygen consumption, bone strain, or muscle activity. Most of these constraints concern how the animals move and how well that movement can be defined. Moreover, the equipment and software programs are very expensive.

This last concern has recently been relieved. Very recent innovations have made high-speed high-quality video analysis inexpensive and easy. There are now several commercially available hand-held cameras that can record at least 250 images per second and some can go as high as 1000 frames per second and do so even in low light. This type of camera was unthinkable until recently.

In addition, durable, inexpensive, lightweight computers make storage and manipulation of video output possible in the field. Video data can be edited, split, and filtered with freeware programs like VirtualDubMod (http://virtualdubmod.sourceforge.net/). With this software alone footfall data and velocity can be collected with ease. Further analysis including joint angles segment velocities and accelerations are made possible with DLTDataivewer (http://www.unc.edu/~thedrick/software1.html), a freeware add-on module for Matlab (The Mathworks, Natick, MA). This simple, yet sophisticated, tool written by Ty Hedrick (Hedrick 2008) will allow any researcher to collect coordinate data from multiple cameras. With just these tools we can now collect and analyze video data right in the field.

Variables That Can Be Collected Under Field and Laboratory Conditions

There are, of course, serious limitations regarding which variables we can collect in the field. Although the new technology allows a quite ambitious approach, this chapter begins with a limited and simple set of variables that can connect field and laboratory work. Using video recordings that one can easily collect under field and laboratory conditions, it is possible to examine the following.

Gait Choice

Using simple video analysis techniques (or even in some cases by eye), researchers can record the type (walk, gallop, canter, bound, amble; see Fig. 2.1a–c), context (substrate used and whether the animal uses this gait during normal travel or rapid escape), and the frequency of each gait in the wild. If reliable data exist as to the mechanical or physiological criteria that govern gait choice, it will be possible to infer the underlying mechanical processes. More importantly, field data will provide the relevant context for gait choice. If it can be determined, for example, that a specific gait is particularly efficient or moderates load, then understanding the context in which the individual chooses that gait can reveal some of the priorities associated with gait choice.

Footfall Sequence and Limb Timing

This includes both the binary distinction between diagonal and lateral sequence walking gaits (Fig. 2.2a) as well as quantification of diagonality (Cartmill et al. 2002).

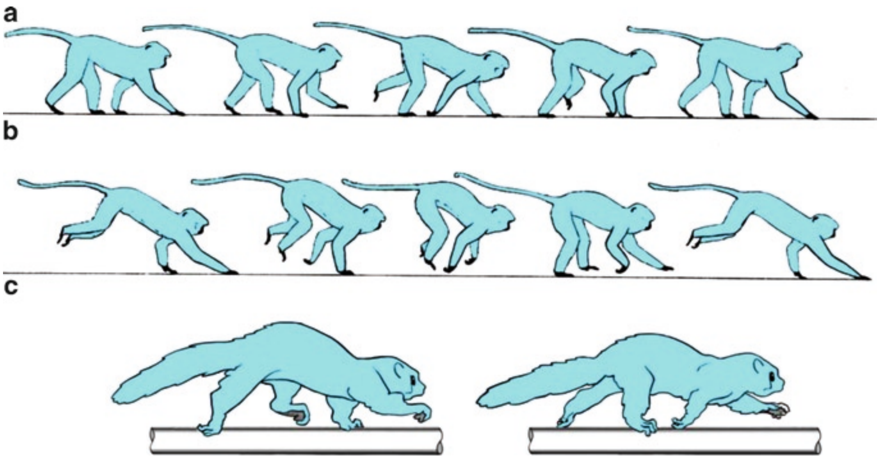

Fig. 2.1 Three gait types commonly used by primates. (**a**) A walking gait in which the hind foot contact is followed by a contralateral forefoot contact. There is no aerial phase and as a result the duty factor (contact time/stride time) for any foot is greater than 0.5. (**b**) A gallop in which forefoot contact is followed by the second forefoot, followed by an aerial phase, and then the contact of the two hindfeet in sequence. The duty factor of any foot is less than 0.5. Many primates adopt a canter (Howell 1944; O'Neill 2008) that is a slow gallop (based on foot contact sequence) but does not have an aerial phase. The images for (**a**) and (**b**) are derived from Schmitt et al. (1994). (**c**) An ambling gait in which hind limb contact is followed by forelimb contact but there is an aerial phase for the two hind limbs and/or two forelimbs. The definition and image are from Schmitt et al. (2006)

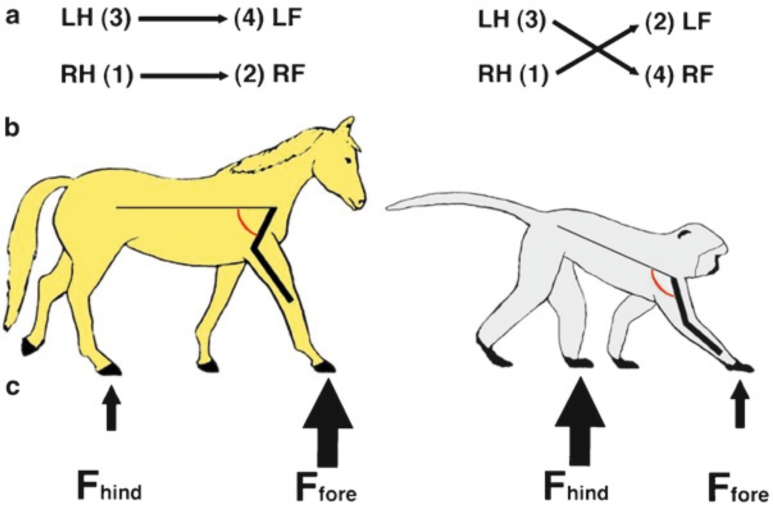

Fig. 2.2 Summary of the commonly accepted differences that are believed to distinguish the walking gaits of most primates from those of most nonprimate mammals. Nonprimates generally use (**a**) lateral sequence walking gaits, (**b**) have a humerus that—at ground contact—is retracted relative to a horizontal axis passing through the shoulder, and (**c**) have greater peak vertical forces on their forelimbs than they do on their hind limbs. Primates show the opposite pattern. (From Schmitt and Lemelin 2002)

Simple video recordings can be easily collected and analyzed for timing. A discrete approach to gait analysis, e.g., walk, trot, amble, canter, gallop, has value but does not necessarily reveal underlying mechanics nor the continuity across categories. But assessing the degree of diagonality does reveal the change across gaits and also allows for inferences concerning the movements of the center of mass (COM) and energy exchange (Griffin et al. 2004; Bishop et al. 2008).

Limb Protraction and Retraction

Limb protraction and retraction is the angle of the humerus or total forelimb and femur or total hind limb relative to the body at the beginning and end of stance, respectively (Larson et al. 1999, 2001) (Fig. 2.2b). Depending on the stiffness of the limb, increased protraction can result in increased vertical oscillations of the COM, which (as discussed later) can influence the energetic costs of movement.

Contact Time

Defined as support phase duration in seconds, this simple variable probably deserves to be part of the section Footfall Sequence and Limb Timing, preceding. It is discussed separately because of its effect on peak loads. For a given force impulse (area under a force curve) applied by the individual at a given speed, increased contact time (Fig. 2.3a) will lower peaks along the curve as the base of the curve is extended while the area remains the same (Schmitt 1998) (Fig. 2.3b). Similarly, a short contact time will result in high peak forces.

Elbow Yield

Elbow yield can be defined by the decrease in elbow angle from touchdown to mid-support (Schmitt 1999; Larney and Larson 2004). This has been seen largely as a measure of limb stiffness that may influence both load (Fig. 2.3c) and possibly oscillations of the COM (Schmitt 1998, 1999, 2003c). Changes in limb yield have been implicated as part of the explanation for the unusual distribution of forces in primates in which peak forces are generally higher on the hind limbs than they are on the forelimbs (Schmitt 1998, 1999, 2003c).

These five variables are chosen because they are easy to quantify with simple video techniques and also appear to reflect important underlying mechanical processes during quadrupedal walking in primates. The point of this chapter is

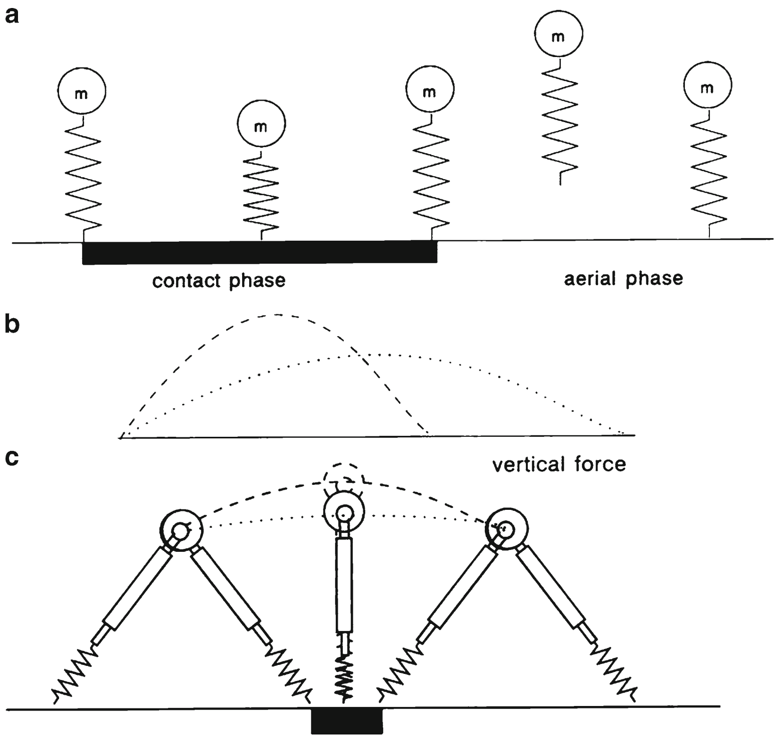

Fig. 2.3 Representation of the mechanical effects of limb compliance. (**a**) Influence of spring stiffness on contact time (shaded in black). If the spring stiffness were reduced, the model bouncing would spend longer in contact with the ground and have a much lower bounce height. (**b**) The model spring applies force to the ground during contact time. If the spring stiffness is reduced and the same force is applied over a longer contact time, the force values at every point in the curve will be reduced. (**c**) If the leg-spring is modeled more realistically, changes in spring stiffness (joint yield) lead to reduced vertical pathways of the center of mass

to illustrate the connection between simple measures of gait mechanics and deeper underlying processes. These data can then be put into the broader service of understanding the potential selective value of locomotor choices in primates. Even small changes in contact or oscillations of the COM on a stiff versus yielding leg can have profound effects on potentially critical aspects of animal fitness.

In the laboratory, it is possible to examine an entire biomechanical system, break it down into its constituent parts, collect complex variables using force plates and high-speed video, and then calculate important performance measures like load and cost. Once a clear relationship between simple variables like gait choice, contact time, joint yield, and more complex variables and performance measure is established, it is then possible to take that information into the field and use the simple measures as a surrogate for the performance measures.