

Chapter 8

Field and Experimental Approaches to the Study of Locomotor Ontogeny in *Propithecus verreauxi*

Roshna E. Wunderlich, Richard R. Lawler, and Abigail E. Williams

Abstract In this chapter, we use field-behavioral, morphometric, and laboratory-based data to demonstrate complex links among morphology, performance, and fitness. Although *Propithecus verreauxi* become “ecological adults” at a very young age, skeletal growth of *Propithecus* is slow. This incongruity creates a challenge for a small, developing animal to move efficiently when traveling along the same pathways with larger adults. To explore the effects of this disparity, we quantified the relationships among postcranial morphology, behavior, and fitness in an ontogenetic sample of wild *Propithecus* and subsequently tested functional relationships in the laboratory. Juvenile *Propithecus* exhibit growth allometries and functional changes in locomotion related to decreasing emphasis on pedal grasping and increasing emphasis on thigh-powered leaping. Whereas adult *Propithecus* use their long, muscular thigh and leg segments to increase leaping distance and reduce collisional costs during galloping on the ground, juvenile *Propithecus* increase angular excursions and acceleration and use a hopping gait on the ground that reduces the number of collisions. We show how this juvenile locomotor strategy and other aspects of the “locomotor phenotype” are associated with fitness. Understanding how variation in morphology influences variation in performance throughout ontogeny and the consequences of these associations on fitness should be a major focus of both field and laboratory studies.

Keywords Biomechanics • Fitness • Locomotion • Ontogeny • *Propithecus*

Abbreviations

COM center of mass
RMA regression reduced major axis regression

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Introduction

The quest to understand the patterns and processes of biological adaptation has formed the basis of much of modern evolutionary biology. Bock and von Wahlert (1965; Bock 1965) defined an evolutionary adaptation as a form-function complex whose “biological role” interacts with some selective forces. They recognized that energy conservation is one important aspect of performance (their effective fulfillment of biological role) and survivability. Nevertheless, studies of adaptation, especially in primates, tend to focus on design (form-function complex), performance, *or* selection rather than the integration of all three aspects of adaptation. Arnold (1983) formalized the ideas of Bock and von Wahlert (1965) and others and provided a framework to connect morphological design and fitness. He argued that because variation in morphology could be associated with variation in fitness through the critical intermediate variable, *performance*, one could measure the effect of a trait on some aspect of performance (the “performance gradient”) and one could measure the effect of performance on fitness (the “fitness gradient”). Similar to the theme of this current volume, Arnold (1983) argued for the integration of laboratory and field studies; specifically, aspects of performance can best be measured in the laboratory, while aspects of fitness can best be measured in the field. Here, we apply the morphology-performance-fitness framework to locomotion in *Propithecus verreauxi*, the sifaka, but we do so from an ontogenetic perspective to provide a more comprehensive understanding and test of these relationships throughout an animal’s life.

From an evolutionary perspective, organisms are life cycles (Rice 2002). Life cycles encapsulate the biologically important stages of a particular species. Selection is expected to construct organisms that maximize fitness at every stage in the life cycle, recognizing that both constraints and trade-offs will operate within and among stages (Stearns 1992). Individual animals flow through the life cycle with different propensities for survival, growth, and reproduction. As such, fitness is measured as one turn in the life cycle (Fig. 8.1) and it measures the average reproductive success

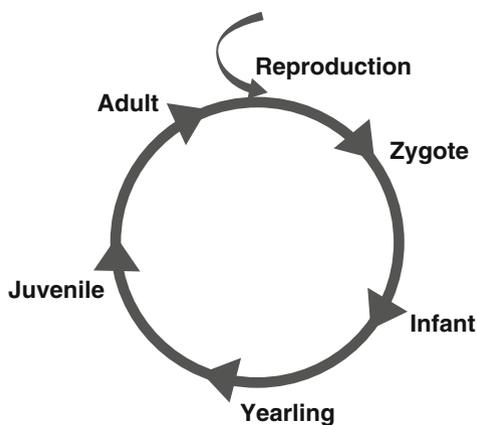


Fig. 8.1 Life cycle of a typical primate. Because fitness is measured as one complete turn in the life cycle, it is important to document patterns of selection acting on developmental stages throughout ontogeny

and/or population growth rate of the species in question. Given that fitness is measured across the life cycle, focusing only on one stage in the life cycle, such as adults, misses much of the evolutionary picture because each stage in the life cycle might have its own set of unique ecological demands and selection pressures.

When compared to other mammals, the primate life cycle is characterized by a substantially longer juvenile stage (Harvey and Clutton-Brock 1985; Pereira and Fairbanks 1993). Numerous theories have been proposed concerning the role of the extended juvenile period in primates as well as the risks associated with it (Poirier and Smith 1974; Clutton-Brock and Harvey 1979; Martin 1981, 1985; Janson and Van Schaik 1993; Joffe 1997; Deaner and Platt 2003; Leigh 2004; Walker et al. 2006). Although considerable work has addressed the evolutionary causes and consequences of the extended juvenile period on diet and foraging in primates, comparatively little work has considered the evolutionary causes and consequences for locomotor performance (Vilensky and Gankiewicz 1989; Dunbar and Badam 2000; Raichlen 2005a, b, 2006; Workman and Covert 2005; Herrel and Gibb 2006; Lawler 2006; Shapiro and Raichlen 2006). Compared to studies of adult animals, only a handful of locomotor field studies have explicitly sought to examine the ontogenetic bases of primate movement (Doran 1992, 1997; Wells and Turnquist 2001; Workman and Covert 2005; Lawler 2006).

Juvenile primates have to navigate the same ecological and social environment as adults, including keeping up with the social group, accessing food resources, and escaping predators. Yet, juveniles are less experienced with the environment in which they are moving, and they are also likely constrained by development of neuromuscular control of balance and locomotion, ongoing differentiation of tissues, and smaller overall body size (Hurov 1991; Carrier 1996; Wells and Turnquist 2001; Main and Biewener 2006, 2007). The juvenile period, therefore, is a time of great locomotor demand and great skeletal risk; due to these factors, selection on juvenile locomotor performance is probably very strong (Carrier 1996; Le Galliard et al. 2004). This effect is likely to be particularly enhanced in primates with a relatively long juvenile period that inhabit a three-dimensional arboreal environment.

In this chapter, we focus on locomotor ontogeny in *Propithecus verreauxi*, an indrid primate found exclusively in Madagascar. *Propithecus verreauxi* are group-living arboreal folivores that live in a highly seasonal environment in the dry and spiny forests of western Madagascar. The timing of dental development and weaning in *Propithecus* are closely tied so that juveniles can take advantage of transient food resources (Eaglen 1985; Godfrey et al. 2004). Juvenile *Propithecus* cope with seasonal food availability by having extremely fast dental growth, allowing them to become “ecological adults” at a very young age (Schwartz et al. 2002; Godfrey et al. 2004). *Propithecus* are born with their deciduous teeth fully erupted and are completely weaned by 6 months of age (Godfrey et al. 2004). Although it is typical for folivorous primates to exhibit more advanced dental development at the time of weaning (Janson and Van Schaik 1993; Leigh 1994), *Propithecus* is particularly precocious in this aspect compared to all other primates.

Propithecus are not precocious in other aspects of their development, and the evolutionary explanations for this pattern are explored in Godfrey et al. (2004) and Ravosa et al. (1993). At the time of weaning (ca. 6 months), juvenile *Propithecus* are still quite small (Fig. 8.2), and somatic growth proceeds slowly. By the time



Fig. 8.2 Adult female *Propithecus verreauxi coquereli* and a juvenile, six-months old. *Propithecus* manifest precocious dental development but their somatic and postcranial development is comparatively slow

juvenile *Propithecus verreauxi* are 8–9 months old, they are only about one-third of adult body mass. In fact, skeletal evidence suggests it takes 2–3 years for *Propithecus verreauxi* to approximate adult skeletal size and longer for the epiphyses to fuse completely (Godfrey et al. 2004). Upon sampling a large number of living individuals at Beza Mahafaly, Lawler (2006) found changes in body mass did not level off until age 8 in *Propithecus verreauxi verreauxi*. Individuals, in general, grow considerably more slowly than lemurids of similar body mass, yet individuals have considerably faster dental development. Juvenile *Propithecus*, therefore, must fulfill “adult-like” behaviors regarding group movements and foraging, but they do so with juvenile skeletal proportions and small body mass.

Given their slow somatic development, *Propithecus* are ideal for studying the consequences of small body size on juvenile locomotion. Not only are they under pressure to perform in a manner similar to adults relatively early in their life cycle, but their growth to adult size is postponed to relatively late in their life cycle. Moreover, their primary forms of locomotion (leaping, bipedal galloping) are associated with high potential joint loads, high energetic expense, and high risks of suboptimal performance. Juvenile *Propithecus* follow adults during travel, often leaping on the same sequence of substrates (Wunderlich and Lawler, unpublished data), and juveniles risk injury or death if they do not land on the substrate or keep up with the group. Both juveniles and adults use bipedalism on the ground. Bipedalism comprises 7–12% of the locomotor repertoire of wild *Propithecus verreauxi verreauxi* (Wunderlich and Lawler, unpublished data) and 13–26% of locomotor bouts in captive *Propithecus verreauxi coquereli* (Williams 2007). Bipedalism, although not intended to be a model for leaping, is kinematically similar to leaping in that it involves high hip and knee angular excursions, and stride length is facilitated by long hind limbs that allow long accelerations times. Whereas leaping distance is determined by the distance between trees, bipedal stride length can be more variable because of the substrate continuity and may therefore offer more opportunities for gait variations. Here we examine postcranial growth and locomotor dynamics in juvenile and adult *Propithecus* to ask how these ecologically precocious, yet postcranially small, individuals function such that they can keep up with adults. We then examine how postcranial traits associated with their habitual forms of locomotion affect fitness.

We measure performance variables using 1) ontogenetic data on limb growth in wild and captive *Propithecus*, 2) experimental data on kinematics and kinetics of locomotion in juvenile and adult *Propithecus*, and 3) field and captive behavioral data on juvenile and adult *Propithecus*. We measure fitness by merging genetic and demographic data with phenotypic measurements. In this way, selection can be measured in two stages: the relationship between the phenotype and performance and the effect of performance on fitness.

Methods

We draw from the morphology-performance-fitness framework to examine the locomotor behavior of *Propithecus verreauxi*. First, we examine aspects of postcranial morphology in wild and captive *Propithecus*. Ontogenetic series of limb measurements were taken on *Propithecus verreauxi verreauxi* at Beza Mahafaly reserve in southwest Madagascar and *Propithecus verreauxi coquereli* at the Duke University Lemur Center (Fig. 8.3a). Methods for measuring *Propithecus* are described in detail in Lawler (2006) and summarized in Table 8.1. Field measurements were taken at 1 year of age because of the limitations of capturing young animals. We measured a cross-sectional sample of 443 (103 resampled) *Propithecus verreauxi verreauxi* between the ages of 1 year and 30 years in the field. The use of captive individuals allows us to extend our growth series into the range between

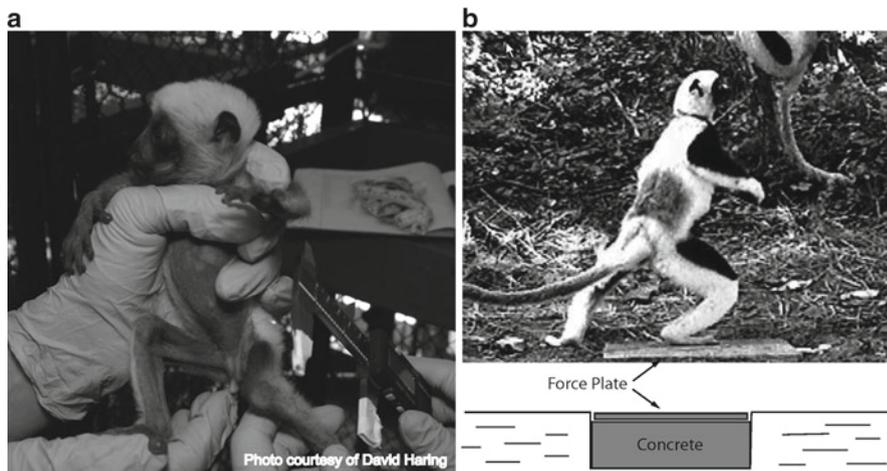


Fig. 8.3 Examples of some of the measurements used in this study. In (a), a newborn *Propithecus verreauxi coquereli* is measured using calipers. In (b), an adult sifaka bipedally traverses a Kistler force-plate buried flush with the ground on a concrete slab. Both individuals reside at the Duke Lemur Center

Table 8.1 Definition of morphometric traits used in this study

Trait	Description
Arm	Acromion process to lateral epicondyle of humerus
Forearm	Lateral epicondyle of humerus to radial styloid
Hand length	Base of thenar/hypothenar pad to tip of longest manual digit
Thigh	Greater trochanter to lateral epicondyle of tibia
Leg	Lateral epicondyle of tibia to lateral malleolus
Foot length	Back of calcaneus to tip of longest pedal digit
Circumferences	Circumference of arm, forearm, thigh, and leg were taken at the midpoint of each segment
Leg shape	First principal component of thigh length, tibia length and thigh circumference. Each linear measurement was first divided by the cube root of body mass for this trait
Body mass	Measured in kilograms

birth and 1 year of age. We measured six captive *Propithecus verreauxi coquereli* every 2 weeks for the first 6 months, every month for the second 6–9 months, and every 3 months in the second year. Because these two data sets are on two different subspecies of *Propithecus verreauxi* and because captive individuals tend to have higher *absolute* growth rates, we present each set of data separately. We performed reduced major axis (RMA) regressions on log-transformed data in JMP 7.0 (SAS Institute, Cary, NC). We used RMA because there is error associated with the data on both axes in these regressions (e.g., Martin et al. 2005). We used these analyses to examine patterns of allometric growth of the limbs.

We examined juvenile postcranial morphology in a functional context by examining one aspect of their locomotion, bipedalism, experimentally. Bipedalism is not

intended to be a model for leaping. Bipedalism comprises about 10% of the locomotor repertoire of wild *Propithecus verreauxi* and more for captive individuals. It is therefore an important part of their locomotor repertoire. Further, studying bipedalism affords an opportunity to quantify kinematics and kinetics of locomotion in *Propithecus verreauxi* on a continuous substrate on which animals have more opportunities for gait variation. Methods for kinematic and kinetic analysis are described in detail elsewhere (Schmitt and Lemelin 2002; Kilkenny 2004; Wunderlich and Schaum 2007) and summarized here. We filmed subjects with lateral, frontal, and 30° cameras (60 Hz) while galloping bipedally along a path within their seminatural forested enclosure. In this setting, they are not limited by space and are moving along a natural dirt substrate. For some of these trials, as well as a number of trials conducted within the subjects' large indoor enclosure, a Kistler portable 9286A or a Kistler 9281B force plate was mounted on a cement block and buried along the runway such that it was flush with the runway (Fig. 8.3b). We encouraged subjects to move bipedally along the pathway by removing nearby vertical supports and using food rewards. We digitized anatomical landmarks (head, shoulder, elbow, wrist, hip, knee, ankle, foot) and filtered them using Peak Performance motion analysis software (Peak Performance Technologies, Centennial, CO), and calculated duty factor, maximum/minimum joint angles, joint angular excursion, and center of mass (COM) movement. All three components of raw force data were imported into MS Excel for analysis. Forces were sequentially integrated to obtain velocity and position (Cavagna 1975; Blickhan and Full 1993; Willems et al. 1995; Griffin et al. 2004; Bishop et al. 2008), and collisional mechanics were analyzed.

Performance measures of leaping and bipedalism used for this study include two primary factors: 1) distance traveled per stride (this is fixed when leaping between trees but not on the ground) and 2) energetic costs. The latter includes internal costs of each stride and collisional costs of the transition between strides. Collisional costs have recently been suggested to be a significant cost of locomotion (Ruina et al. 2005). A collision occurs when the limbs apply work to redirect the COM from generally downward to generally upward. We analyzed collisional mechanics by assessing the number of collisions per stride, the number of footfalls per collision, and the pseudo-elasticity of the collisions. We calculated the latter as the angle of the COM velocity to the substrate reaction resultant before and after the redirection of the COM (Ruina et al. 2005; Baumgartner et al., 2009).

We also assessed leaping and bipedal performance in both wild and captive *Propithecus* via behavioral measurements. We used locomotor bout sampling (Fleagle 1976) to collect data on juvenile (only 1-year-old individuals) and adult (6–25 years) individuals in the wild and in captivity. Definitions of locomotor behaviors are presented in Table 8.2. We calculated locomotor frequencies as well as distances per leap for juveniles and adults.

To estimate the effect of phenotypic differences on fitness, we estimated fitness surfaces via a combination of genetic, demographic, and morphometric data. Any time that one plots variation in some fitness measurement against variation in some trait, the function that unites these two variables is called a fitness function; when two traits are plotted against a fitness measurement, the function becomes a surface. Any number of regression techniques can be used to

Table 8.2 Descriptions of locomotor behaviors used in this study

Leap: a Thigh-propelled, long-distance jump between vertical or oblique substrates. During take-off and landing the body is generally in an orthograde position (also see Demes et al., 1996)
Bipedal: Movement using hind limbs only along a continuous substrate (usually the ground)

calculate the fitness function, including linear regression, polynomial regression, or any number of nonlinear techniques. We generated fitness surfaces by fitting a nonlinear neural network model to pairs of traits as well as a fitness measurement. Neural networks, like splines (Schluter 1988), provide a means to visualize the “basic shape” of the relationship between fitness and phenotypes. The shape of the fitness surface, in turn, can reveal what types of selection are acting on the traits in the analysis, e.g., a sloped surface often indicates directional selection, a hump-shaped surface indicates stabilizing selection, etc. These types of visualization techniques do not make any *a priori* assumptions about the form of the fitness surface but are a powerful method for providing an overall “picture” of which combinations of trait values confer the highest fitness (Schluter 1988; Schluter and Nychka 1994). We present two fitness surfaces. One surface reveals the relationship among hand length, foot length, and survival from age 1 to age 8. Survival data come from extensive field censusing collected on the Beza Mahafaly sifaka population (Richard et al. 2002). Both hand and foot length were corrected for age, using a least-squares regression, with the resulting residuals used in the analysis. The other surface shows the relationship between body mass, leg shape, and male fertility. We assessed male fertility using census data in conjunction with paternity analysis; fertility is measured as the number of offspring sired by a male divided by his reproductive lifespan. All males were adults, ages 5 and older. The fitness surfaces shown here are based on the statistically significant multivariate selection coefficients (Lande and Arnold 1983) that capture the relationship between some measure of fitness, i.e. survival or male fertility, and trait values. We analyzed several traits for their association with fitness; we present only fitness surfaces for traits found to be under strong selection (strong selection means the traits have significant *p*-values as measured via multivariate regression, and the fitness surface for these traits has a distinct, nonlinear shape). Further details of this methodology can be found in Lawler et al. (2005) and Lawler (2006).

Results and Discussion

Phenotype

In general, femur length exhibits strong positive allometry during the first year of life and grows isometrically in later years. Figure 8.4a illustrates the results of longitudinal growth measurements of six *Propithecus verreauxi coquereli*

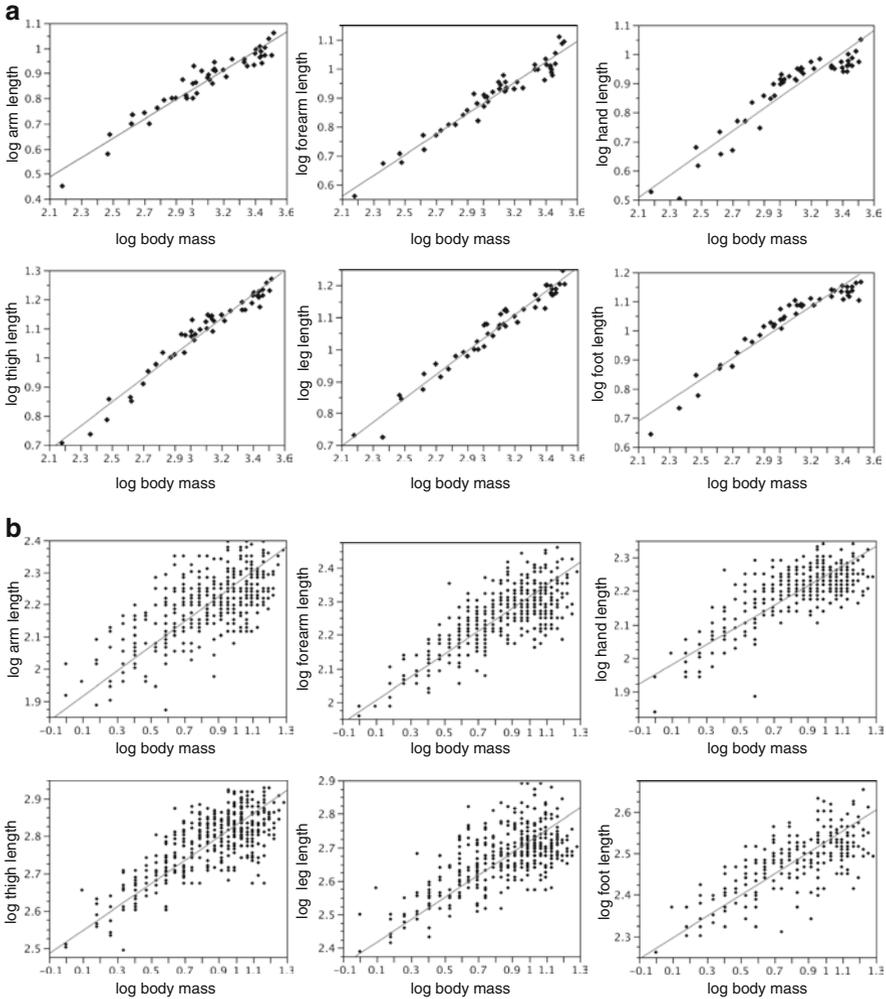


Fig. 8.4 Bivariate plots of limb segment lengths against body mass. In (a), the data come from captive *Propithecus verreauxi coquereli* ranging in age from 2 weeks to 18 months. During this time period, femur length exhibits strong positive allometry. In (b), the data come from wild *P. v. verreauxi* ranging in age from 1 year to 30 years old. During this time period, hand and foot length exhibit strong negative allometry

from the Duke University Lemur Center. These data are from a longitudinal sample of individuals 2 weeks to just over 1 year of age. The data from wild *Propithecus verreauxi verreauxi* represent a cross-sectional sample of individuals ages 1 year to 30 years (Fig. 8.4b). Tibia length, hand length, and foot length exhibit slight positive allometry during the first year of life, but hand and

foot length exhibit negative allometry after year 1. Arm length exhibits slight positive allometry throughout ontogeny, while forearm length consistently grows isometrically.

The morphological characteristics of juveniles in comparison with adults can be summarized as relatively shorter thigh segments and relatively longer hand and foot segments in younger individuals. The thigh segment grows rapidly during the first year of life as young individuals begin independent locomotion, resulting in the strong positive allometry observed in thigh length. The hands and especially feet grow fast during the first year of life, such that they are relatively longer in yearlings compared to adults, resulting in negative allometry after year 1.

Function

These morphological data have behavioral and kinematic correlates. Foot length influences locomotor performance because foot length correlates positively with the span between the first and second digits. The space between these digits is used to grasp a branch during leaping and as a “catch-point” when landing from a leap (Fig. 8.5; Gebo 1985; Demes et al. 1996). During bipedal galloping, *Propithecus* use the span of their foot to produce a foot roll-over from lateral to medial on the trail foot and medial to lateral on the lead foot. This may reduce the work of step-to-step transitions in much the same way as the rollover process in humans (Adamczyk 2006). The larger hand and foot spans can also enhance the grasping capabilities of young *Propithecus* (Lawler 2006) and may contribute to propulsive power during bipedal hopping. Longer feet also require higher foot clearance during terrestrial locomotion, and we demonstrate that kinematic differences in juveniles may accommodate these differences.

Although we present only kinematic and kinetic data on bipedalism here, sifaka bipedalism is kinematically similar to leaping in that it involves high hip angular excursions. Adult *Propithecus* use a unique form of bipedal galloping locomotion in which trail and lead limbs are sequenced, and the trunk is positioned 30° to the direction of travel (Fig. 8.6a). Juvenile *Propithecus*, however, use a bipedal hop on the ground (Fig. 8.6b). If we compare juvenile hopping to adult bipedal galloping, hopping strides tend to be longer and reach greater heights, ensuring foot clearance during the aerial phase as well as fewer contacts per distance traveled. Hopping strides involve much greater hip and knee angular excursions and much higher hip angular acceleration (Table 8.3, Fig. 8.7). Hopping may allow the use of two limbs to produce power in the absence of the increased time for acceleration afforded by the longer thighs of adults (see below); however, they have to produce higher peak vertical forces and greater impulse to accomplish the long and high bipedal hop.



Fig. 8.5 Photo showing how the span between the first and second digit on the foot plays a key role in grasping substrates as well as landing on vertical substrates. The span between the digits is relatively large in yearling sifaka

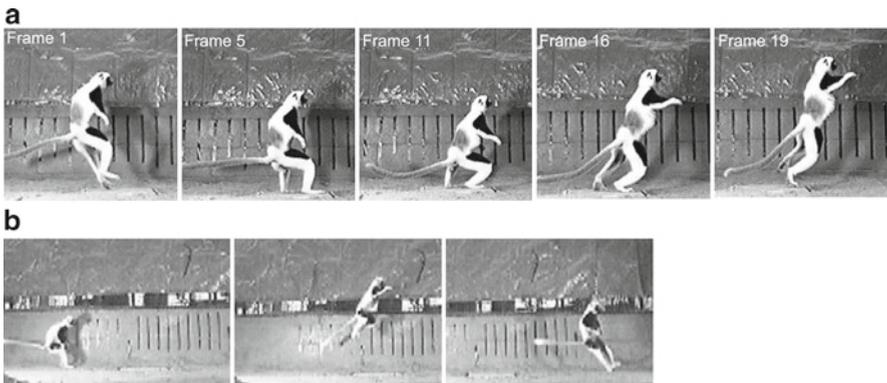


Fig. 8.6 Frame captures from video data. In (a), an adult *Propithecus verreauxi coquereli* is engaging in bipedal galloping. In (b), a juvenile *P. v. coquereli* is engaging in bipedal hopping

Performance

We evaluated locomotor performance based on stride length (leaping and bipedalism) and collisional energy loss (bipedalism). Wild and captive behavior studies indicate that leaping distance is similar in juveniles and adults (Table 8.3), but bipedal stride length is greater in juveniles than in adults. *Propithecus* tend to travel by following one another on the same substrates, so juveniles have to accomplish a similar level of leaping performance or choose another (“untested” and hence potentially riskier) route. Small-bodied adult prosimians use kinematically different leaping styles than larger-bodied prosimians (Demes et al. 1996) and sacrifice energetic efficiency by taking off at less-than-optimal angles to attain higher horizontal speeds (Crompton et al. 1993; Warren and Crompton 1998). Juveniles too have less time to accelerate because of their relatively shorter limbs, yet they have greater muscular cross-sectional area relative to body mass with which to produce greater force. We still do not know whether juvenile prosimians exhibit a leaping style that is kinematically different from adults or if juveniles simply leap with greater energetic cost. On the ground, however, hopping juveniles tend to take fewer, longer strides than galloping adults (Table 8.3). While this may increase the internal costs of the stride, it results in fewer collisions.

Baumgartner et al. (2009) demonstrate that galloping reduces costs of re-directing the COM. While galloping, *Propithecus* use pseudoelastic collisions, that is, the angle of the incoming (pre-collision) and outgoing (post-collision) velocity vectors are close to orthogonal (Fig. 8.8). Pseudo-elastic collisions, even without elastic recovery, reduce energetic costs by one-quarter relative to a purely absorbing collision (Ruina et al. 2005). Galloping also allows *Propithecus* to distribute each collision over two limb contacts and over the horizontal distance between them, again reducing the energetic expense of the collision (Fig. 8.8). Juvenile hopping does not distribute the collision over two limb contacts, resulting in greater costs for redirecting their COM (Ruina et al. 2005). It is unknown whether their larger joint excursions are indicative of storage and recovery of elastic energy.

Table 8.3 Kinematic and performance data for juvenile and adult *P.v.coquereli*

Variable	Juveniles	Adults
Hip Angular Excursion (degrees)	109	76
Knee Angular Excursion (degrees)	94	52
Stride Duration – Bipedalism (seconds)	0.67	0.74
Duty Factor – Bipedalism	0.31	0.44
Average distance per leap (meters)	1.34	1.28
Average number of strides or hops per bipedal series	1.8	3.5
Average distance traveled per bipedal series (meters)	1.6	2.4
Average length of bipedal stride or hop (meters)	0.9	0.7

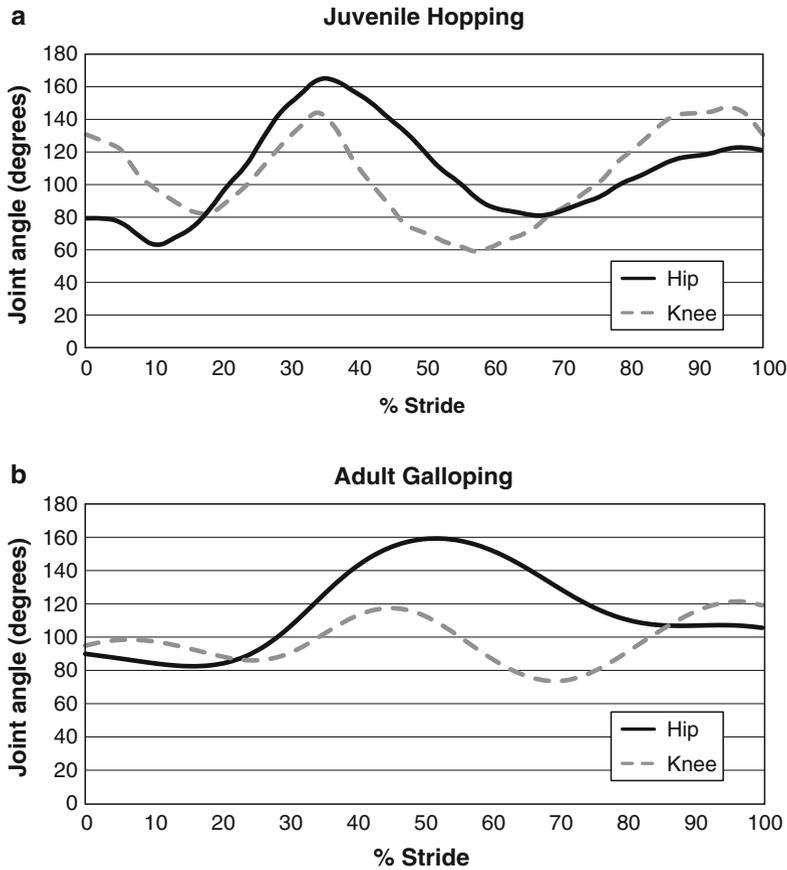


Fig. 8.7 Joint angles of hip and knee during a representative bipedal stride for (a) juveniles and (b) adults. Juveniles manifest larger joint angles during bipedal hopping relative to adult galloping

Fitness

Though some performance variables are best measured in the lab, estimating fitness and selection is probably best done using field data from a single population. This is because the unit of evolution is the population, and estimating the evolutionary consequences of variation in fitness requires large-sample data on individuals with known fates, phenotype, and kinship. Selection is a key component of the adaptive process, and it can be defined as the covariance between some aspect of fitness and some aspect of phenotype (Rice 2004). When selection acts on heritable traits, the distribution of the trait will change across generations and the population will adaptively evolve.

Using data from a long-term field study of wild *Propithecus*, we were able to estimate selection by collecting phenotypic measurements from individuals captured and released in the wild. In addition, we were able to estimate aspects of fitness using

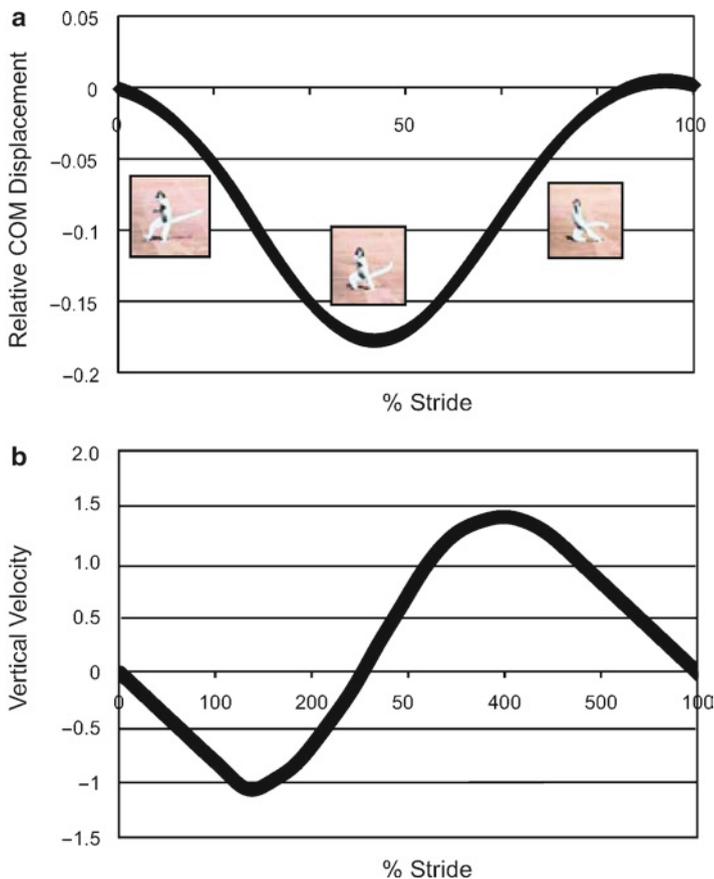


Fig. 8.8 (a) Center of mass (COM) and (b) vertical velocity plotted over time for a representative bipedal stride in *Propithecus verreauxi coquereli*. These individuals exhibit only one collision per stride, i.e., one change in direction of COM path, and one point per stride where vertical velocity shifts from negative to positive

information on the survival and reproduction of individual subjects. As mentioned previously, the fitness surfaces are generated by examining patterns of selection acting on postcranial traits. Three-dimensional fitness surfaces reveal the relationship between postcranial traits and their relationship with either survival or reproduction (Figs. 8.9, 8.10). One of the fitness surfaces we present (Fig. 8.10) does not concern ontogeny, per se, but we discuss it in the general framework of measuring selection in wild primate populations.

The fitness surface in Fig. 8.9 reveals the relationship between foot length and survivorship. This surface was generated by looking at all individuals that either survived past the age of 8 or died before this age. Foot length, but not hand length, shows a positive relationship with survivorship, indicating the action of positive directional selection. Individuals continue to gain body mass up until the age of 8, thus this surface reveals how foot length contributes to survival during

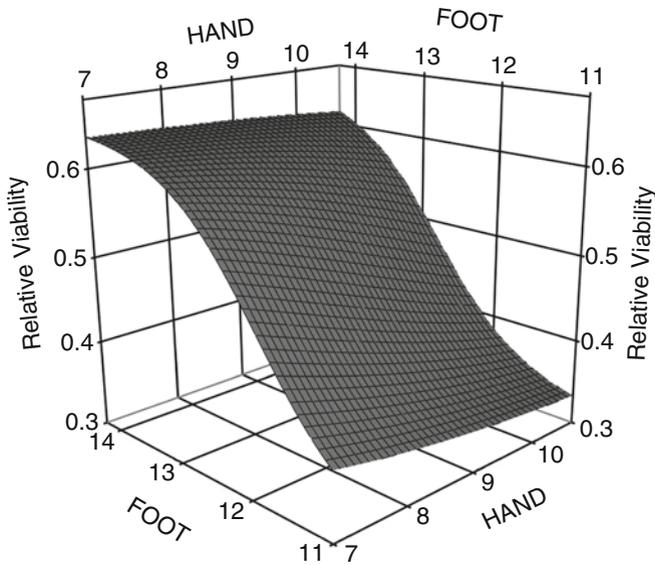


Fig. 8.9 Fitness surface for hand and foot length against relative survival in terms of living beyond age of 8 or dying before age of 8. The surface shows the positive relationship between foot length and survival, indicating positive directional selection on foot length. There is no selection on hand length

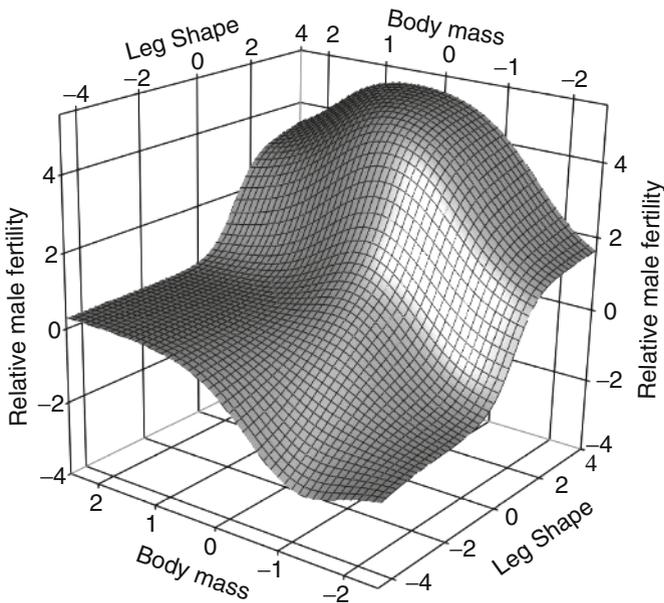


Fig. 8.10 Fitness surface for body mass and leg shape against relative male fertility (offspring sired per year/per male). The surface shows a concave relationship between body mass and fertility, indicating stabilizing selection. The surface also shows a positive relationship between leg shape and male fertility, indicating positive directional selection. Both male fertility and the two traits are standardized

a time when young individuals are still gaining body mass. The functional basis for this relationship was described earlier. Foot length increases grasping span and therefore provides a large “catch-point” when landing from leaps (Gebo 1985; Demes et al. 1996) and presumably during bipedalism. *Propithecus* achieve locomotor independence around 6 months but they must develop locomotor coordination throughout early ontogeny when their limbs and neuromuscular systems are still developing. Larger feet enable young *Propithecus* to grasp safely as well as leap between vertical substrates during the period of locomotor coordination (Lawler 2006). Large feet may also contribute to propulsion during bipedal hopping, although our data cannot speak to relative power generation across joints at this point. Our data reveal that young *Propithecus* have relatively large hands and feet, and we argue that this pattern is actively maintained by selection to allow *Propithecus*, particularly young *Propithecus*, to navigate safely between vertical substrates. However, relatively larger foot size may necessitate higher clearance during terrestrial locomotion, and the kinematically different bipedalism of young *Propithecus* affords this clearance. These data show how variation in morphology, specifically foot length, is associated with variation in fitness, in this case survivorship.

A fitness surface examining the relationship between male fertility, body mass, and leg shape illuminates the pattern of selection on male body mass and leg shape (Fig. 8.10). Selection favors a particular combination of traits with respect to successful reproduction. During the mating season, male *Propithecus* compete with each other for access to females. Mating competition takes on two primary forms: contact aggression and arboreal chases. The total pattern of selection acting on males suggests that traits related to locomotor contests, not aggression, are key determinants of fitness. Directional selection was not found to be operating on body mass or canine size (Lawler et al. 2005). Instead, traits pertaining to arboreal movement are under selection. Stabilizing selection acts on adult male body mass, favoring males that are not too large or too small, while directional selection acts on leg shape, favoring adult males with long legs and muscular thighs. Leg shape encapsulates limb length and thigh circumference and therefore muscle volume. Longer limbs can be used to accelerate for longer periods, thereby generating longer leaps. Thigh circumference represents cross-sectional area of the quadriceps femoris and hamstring muscle groups, major muscle groups used by *Propithecus* for leaping (Demes et al. 1998). Larger “thighed” males can generate more muscle force, and potentially more power, than smaller males. Thus successful males can use their strong, long legs and “streamlined” body mass to out-manuever and/or out-last their sexual rivals during the mating season, ultimately leading to increased reproductive success. In this regard, intermediate body mass and leg shape are sexually selected traits (Lawler et al. 2005). This last set of results calls attention to an understudied area within locomotor studies: sexual selection. Within the context of sexual selection, locomotor traits pertaining to agility, maneuverability, and speed should be examined with respect to their influence on mate acquisition and mating competition.

Conclusions

Juvenile *Propithecus* exhibit growth allometries and functional changes in locomotion related to decreasing emphasis on manual and pedal grasping and increasing emphasis on thigh-powered leaping. Young *Propithecus* need to keep up with adults despite their small size, and locomotion such as vertical leaping comes with specific performance demands; changes in kinematics of locomotion associated with differences in postcranial shape are associated with performance. Whereas adult *Propithecus* use their long, muscular thigh and leg segments to increase leaping distance and reduce collisional costs on the ground, juvenile *Propithecus* increase angular excursions and acceleration, presumably to produce greater force at take-off. Using a hopping rather than galloping bipedal gait, they reduce the number of collisions on the ground rather than using multiple limb contacts to reduce energy loss as in adults.

As we have shown, morphological features can be related to fitness in wild *Propithecus*. In juvenile *Propithecus*, foot length experiences directional selection and ensures that the span between the first and second digit is large; this span facilitates grasping, leaping, and landing in growing *Propithecus* and may influence energy savings and propulsive power during bipedal hopping. In addition, directional selection targets leg shape in adult male *Propithecus*. These males also experience stabilizing selection on body mass. These traits are likely related to arboreal mating competition and indicate that locomotor contests rather than fighting are key determinants to male reproductive success. Although our field and lab analyses have, at times, focused on different behaviors, we have linked particular traits in growing *Propithecus* to performance and functional parameters and we have also ascertained their influence on fitness.

Future analyses need to examine more thoroughly the relationships among morphology, function and performance. These include the forces produced during locomotion, ontogenetic differences in leaping kinematics and kinetics, and the energetic consequences of juvenile design. The results of this study emphasize that both field and laboratory studies should design experiments that measure aspects of *performance* in order to link morphological variation to variation in fitness. Field primatologists often take a “standardized” set of morphometric measurements on wild animals (e.g., Richard et al. 2002; Kappeler and Schaffler 2008) in order to provide a “snapshot” of information on growth, size, health, and mass of each animal. However, these measurements were not initially defined with respect to functional or locomotor questions. To the extent that field studies include research on locomotion, we suggest that field primatologists move beyond collecting the standard set of measurements and consider taking measurements that are relevant to specific functional/biomechanical concepts or hypotheses. Similarly, laboratory studies should continue, when possible, to include realistic aspects of the species ecology and environment when studying performance variables in the lab. Not only should these studies incorporate aspects of the structural environment, e.g., branch compliance, but they should also pay attention to field studies

that report locomotor differences between males and females as well as between age classes. Unlike field studies, laboratory studies have the power to isolate and analyze functional and biomechanical differences in locomotion among the biologically relevant stages that characterize primate ontogeny. We argue that an ontogenetic perspective is needed when studying locomotion. Given that selection likely operates differently on different developmental stages, it is important to document if developmental stages are associated with changes in locomotion. Understanding how variation in morphology influences variation in performance *throughout ontogeny* should be a major focus of both field and laboratory studies. Once we understand the ontogenetic associations between performance and morphology, we should strive to assess the fitness consequences of these linkages. Van Valen aptly observed the following: “Evolution is the control of development by ecology (1973: 488).” In this regard, the morphological configurations and locomotor behaviors we see in adult animals are ultimately the products of selection acting throughout the life cycle.

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