

Sifaka Positional Behavior: Ontogenetic and Quantitative Genetic Approaches

Richard R. Lawler*

Department of Anthropology, Boston University, Boston, Massachusetts 02215

KEY WORDS lemur; locomotion; ontogeny; selection gradient; heritability

ABSTRACT In many primate species, hands and feet are large relative to neonatal body weight, and they subsequently exhibit negative allometric growth during ontogeny. Here, data are presented showing that this pattern holds for a wild population of lemur, Verreaux's sifaka (*Propithecus verreauxi verreauxi*). Using morphometric data collected on this population, it is shown that younger animals possess relatively large hands and feet. This ontogenetic pattern suggests a simple behavioral test: do juvenile animals with their larger, almost adult-sized hands and feet locomote on similarly sized substrates as adult animals? Using locomotor bout sampling, this question was tested by collecting positional behavior data on this population. Results from this test find no differences in locomotor behaviors or substrate use between yearlings and adult animals. To place these results in a broader evolutionary context, heritabilities and selection gradients of hands, feet, and other limb

elements for animals in this population were estimated. Among limb elements, heritabilities range from 0.16–0.44, with the foot having the lowest value. Positive directional selection acts most strongly on the foot (directional selection gradient = 0.119). The low heritability and positive selection coefficient indicate that selection has acted, and continues to act, on foot size in young animals. These results are interpreted within a functional context with respect to the development of locomotor coordination: larger feet enable young animals to use “adult-sized” substrates when they move through their habitat. It is suggested that the widespread pattern of negative allometry of the extremities in sifaka and other primates is maintained by selection, and does not simply reflect a primitive developmental pathway that has no adaptive basis. *Am J Phys Anthropol* 131:261–271, 2006.

© 2006 Wiley-Liss, Inc.

The study of primate positional behavior and anatomy is among the most investigated topics in evolutionary anthropology. Numerous researchers have explored the functional, behavioral, ecological, and/or ontogenetic bases of primate movement and postures (Jenkins, 1974; Morbeck et al., 1979; Martin, 1990; Strasser et al., 1998; Richmond et al., 2001). With few exceptions, all of these studies work within an adaptive framework. That is, many of the variables investigated by researchers—for example, leaping behaviors in *Saguinus* (Garber, 1991), bone-muscle configurations in *Presbytis* (Fleagle, 1977a,b), or growth trajectories in *Pan* (Doran, 1992)—are examined against the assumption that natural selection has acted, and continues to act, on these variables (Fleagle, 1979, 1984; Cant, 1992). A strong fit between anatomical form, biomechanical function, and a particular positional behavior is often interpreted as evidence that natural selection has shaped the overall locomotor pattern of the species under study (e.g., Fleagle, 1977a,b; Garber, 1980, 1991). This is not to say that researchers a priori assume the presence of adaptation in the things that they study; rather, they test a hypothesis of adaptation by evaluating the fit between form, function, and behavior (Bock and Von Walther, 1965; Fleagle, 1979; Cant, 1992). No doubt, nonadaptive factors also influence postcranial anatomy and positional behavior, but usually such arguments are made after assailing the adaptive basis of the system or species under investigation (Fleagle, 1985).

By framing studies within an adaptive framework, there is an implicit invocation of fundamental evolutionary parameters such as selection coefficients, fitness estimates, and trait heritabilities. And while it is well-established that adaptive evolution requires a connection

between fitness and heritable variation in phenotype, many of these fundamental evolutionary parameters are rarely estimated in wild primate populations. This is more a logistical problem than an epistemological one. Most primatologists would agree that estimating selection coefficients from wild primate populations would be enlightening, but most would also acknowledge that such information is difficult to collect. Studies of primate locomotion in the field or laboratory do not gather data from an entire population. Rather, one or a few social groups are followed through the forest, or several specimens of unknown kinship are measured in museums. Nevertheless, the unit of evolution is *the population*, and thus proper estimations of selection coefficients, heritabilities, and variation in fitness require phenotypic data from numerous animals with known fates and kinship. Such data are rarely available, and thus the degree to which selection acts on positional behavior and anat-

Grant sponsor: National Science Foundation; Grant numbers: DEB 9902146, DBI 0305074; Grant sponsor: Yale University; Grant sponsor: Peter and Marion Schwartz Foundation; Grant sponsor: Boston University; Grant sponsor: Liz Claiborne and Art Ortenberg Foundation.

*Correspondence to: Richard R. Lawler, Department of Anthropology, Boston University, 232 Bay State Road, Boston MA 02215.
E-mail: rlawler@bu.edu

Received 22 August 2005; accepted 18 January 2006.

DOI 10.1002/ajpa.20430

Published online 4 April 2006 in Wiley InterScience
(www.interscience.wiley.com).

omy, as well as how such traits respond to selection, is unknown.

In this study, data on selection coefficients and heritabilities among limb elements are presented. These data were all collected from a single wild population of Verreaux's sifaka (*Propithecus verreauxi verreauxi*; "sifaka," hereafter) and are used to investigate the interplay between ontogeny, positional behavior, and natural selection in sifakas. Adding an ontogenetic component to positional behavior studies provides additional insights into the adaptive nature of primate movement, because selection acts on the growing individual, not just on adult "endpoints" (e.g., Stearns, 1992; Carrier 1996; Pereira and Leigh, 2003). In this regard, ontogenetic approaches test functional relationships between growth-related changes in positional behavior (and anatomy) with respect to the demands imposed by structural or ecological factors (Jungers and Fleagle, 1980; Jungers and Hartman, 1988; Jungers and Cole, 1992; Doran, 1992; Turnquist and Wells, 1994; Carrier, 1996; Wells and Turnquist, 2001). One wide-ranging finding from ontogenetic studies of postcranial elements is the pattern of negative allometry of the distal limb elements (e.g., Jungers, 1985). In virtually all taxa examined, hands and feet (or some linear measurement thereof) exhibit negative allometric growth. That is, immature animals possess relatively large hands and feet, and subsequently, during ontogeny, hands and feet grow at a slower rate relative to body mass. This pattern manifests, for example, in *Macaca mulatta* (Grand, 1977; Turnquist and Wells, 1994), *Cebus albifrons*, *Cebus apella* (Jungers and Fleagle, 1980), *Ateles geoffroyi*, *Saimiri sciureus* (Ford and Corruccini, 1985), *Propithecus diadema*, *Propithecus tattersalli* (Ravosa et al., 1993), and *Macaca sinica* (Cheverud et al., 1992). In discussing the likely adaptive significance in this pattern, Jungers and Fleagle (1980, p. 476) note that, "Relatively large hands and feet probably reflect the selective importance of efficient gripping and grasping behaviors of young animals... All supports encountered by immature animals are of relatively large diameters, especially when they must negotiate the same arboreal pathways used by mature animals, and relatively large hands and feet are clearly advantageous in such situations."

In this study, two testable hypotheses are developed from Jungers and Fleagle's statement: A) that immature animals negotiate the same arboreal pathways as adult animals; and B) that natural selection is responsible for the pattern of negative allometric growth evidenced in the hands and feet. Using morphometric data, I show that sifakas (like other primates) also exhibit negative allometric growth of the hands and feet. This is demonstrated by examining growth allometries of the hands, feet, and other limb elements. Then, drawing from the results of the allometric analysis, I address three questions that operationalize the two hypotheses listed above: 1) Given that immature animals possess relatively large hands and feet, do younger animals exhibit similar locomotor behaviors and use the same-sized substrates as adults? 2) Is there evidence of past selection pressures acting on hands and feet in this population? 3) What is the strength of directional selection acting on hands, feet, and other postcranial elements? These three questions get at how the pattern of negative allometry exhibited in the hands and feet potentially influences positional behavior in juveniles (hypothesis A, from above), and whether the pattern of negative allometry can be linked to predictions from quantitative genetic

models of adaptive evolution (hypothesis B, from above). Specifically, I make the following predictions. I predict that juveniles and adults will exhibit similar patterns of locomotor behavior and substrate use. The functional basis for this prediction is that juveniles can use their relatively larger hands and feet to grasp and cling to larger, "adult-sized" substrates when moving through their habitat. Along these lines, if the pattern of negative allometric growth is a product of recent and/or persistent selection pressures, then heritability estimates for hands and feet should be lower than estimates for other postcranial elements. The quantitative genetic basis of this prediction is that when natural selection acts on a particular trait, it "chews up" the additive genetic variance in that trait (Fisher, 1930; Charlesworth, 1987). Because heritability is proportional to additive genetic variance, heritability values tend to be lower for traits under selection. If hands and feet are adaptively large, then I predict that selection continues to act on these elements to maintain their size relationship with body mass. In this case, directional selection coefficients should be positive and take on larger values for hands and feet relative to other limb elements. In particular, sifaka feet are adapted for grasping vertical branches (Gebo, 1985), and sifakas use the deep cleft between their big toe and lateral digits to push off and "catch" substrates when leaping between them (Demes et al., 1996). Therefore, I further predict that the quantitative genetic parameter values will be more pronounced in the foot relative to the hand.

METHODS

Parentage and morphometrics

The Beza Mahafaly sifaka population has been studied since 1984 (Ratsirarson, 2003). Each year, wild *P. v. verreauxi* are captured, measured, and marked, using color-coded collars and numbered tags (Richard et al., 1993, 2000, 2002). Twenty-three morphometric measurements, as well as dental casts, hair and tissue samples, and a range of qualitative data are gathered from each animal during the capture procedure. The population continues to be monitored, and census data yield information on population size, numbers of social groups, group composition (sex and age), transfers of individuals, disappearances, deaths, and births. The present study uses paternity data for all adult males in the population from 1989–1999. Details of the paternity analysis can be found in Lawler (2003) and Lawler et al. (2001, 2005a). The traits used in the present analysis consist of linear measurements taken on the following limb elements: upper arm length, lower arm length, hand length, upper leg length, lower leg length, and foot length. All measurements were taken on the left side of each animal. Descriptions of the measurements, sample size, and trait means and standard deviations are given in Table 1. Sample sizes for the various analyses used in this study are presented in Table 2.

To investigate differential patterns of growth among limb elements, allometry coefficients were calculated by regressing log-transformed trait values onto the cube root of log-transformed body-mass values. The y-intercept gives the value of the trait when body weight is zero; the slope is estimated by cross-sectional data (which include some animals captured more than once), and approximates the rate of growth of the trait relative

TABLE 1. Definitions and summary statistics for morphometric traits used in this study

Trait	Description: length (in cm) from	Mean	Standard deviation
Upper arm	Acromion process on scapula to lateral epicondyle on humerus	9.18	0.85
Lower arm	Lateral epicondyle on humerus radial styloid on radius	9.72	0.77
Hand	Base of thenar/hypothenar pad (i.e., palm) to tip of longest digit	9.08	0.60
Upper leg	Greater trochanter on femur to lateral epicondyle of tibia	16.30	1.16
Lower leg	Lateral epicondyle of tibia to lateral malleolus of fibula	14.53	1.17
Foot	Back of calcaneous to tip of longest digit	12.07	0.81

TABLE 2. Sample sizes for various analyses used in this study

Analysis	Sample size (no. of animals)
Morphometric	220–331
Positional behavior	11
Heritability	146
Selection gradient	160

to body size (Fleagle, 1999). Both ordinary least-squares (LS) regression and reduced major axis (RMA) regression are reported (Legendre and Legendre, 1998). When the allometry coefficient (i.e., the slope) is significantly below 0.33, this indicates the presence of negative allometric growth. Significance tests of LS slopes were determined by using a custom test with $P = 0.05$; the significance of RMA slopes was ascertained by looking at whether the 95% confidence interval for the slope overlapped with 0.33. Both tests were carried out in the statistical computer package JMP 5.1 (SAS Institute, Cary, NC).

Positional behavior data

Positional behavior data were collected in August of 2001 at Beza Mahafaly Special Reserve by R.R.L. and Jean Charles Razafimahazo. Prior to data collection, we tested for interobserver reliability, and obtained congruent results from our independent sampling efforts. Locomotor bout sampling was used (e.g., Fleagle, 1976), and 2,024 locomotor bouts were collected on nine adult and two juvenile animals in two different social groups. Adult animals were reproductively mature individuals older than 5 years (range, 6–25 years), and juvenile animals were all approximately 1 year old (i.e., yearlings). Thus, below, when I refer to “juvenile” or “immature” sifakas, I am talking about 1-year-old animals. Attempts were made to collect equal amounts of data on adults and yearlings: 1,027 locomotor bouts were collected for adult animals, and 997 locomotor bouts for yearlings. Sifakas achieve locomotor independence at about 5–6 months of age, but continue to gain mass over the next 5–6 years (Fig. 1). In this study, only locomotor behaviors, leaping distance, and substrate use data are presented. An ethogram and definition of substrate variables are presented in Table 3; the definitions of behaviors and substrate categories follow those of Dagosto (1994, 1995). Statistical significance in positional behaviors and substrate use between juveniles and adults was determined by nonoverlapping 95% confidence intervals. Confidence intervals were calculated using a bootstrap resampling procedure with 5,000 replicates. The resampling program to calculate confidence intervals was written in MATLAB programming language (Mathworks, Inc., Natick, MA), following the procedures in Kaplan (1999).

Quantitative genetics

Heritabilities (h^2) were estimated from father-offspring regressions. As sifaka males contribute negligible paternal care (Richard, 1976, 1978), father-offspring regressions eliminate any potential maternal effects (Cheverud and Moore, 1994; Lynch and Walsh, 1998). Unweighted regressions were used because family sizes were relatively small (Lynch and Walsh, 1998). To control for variation arising from differences in development and body size, trait values were quadratically regressed against body mass, and residuals from this regression were used to estimate heritability (Cheverud and Dittus, 1992). Heritability values are calculated as two times the value of the slope of the father-offspring regression (Falconer and MacKay, 1996).

Multivariate regression was used to determine patterns of viability selection on limb elements. Estimates of directional selection were achieved by regressing relative fitness (ω) on standardized trait values (z_i) (Lande and Arnold, 1983). To remove age effects, all linear measurements were regressed against age using a least-squares regression, and the resulting residuals were used to estimate the strength of selection. Ultimately, I want to know if the size of hands and feet is associated with viability over the period in which animals are still growing. To this end, the fitness measure examined the potential covariation between limb-element size and survivorship of animals up to age 8 years. Long bone and hand/foot growth trajectories “level off” at around age 5 years, and body mass “levels off” at about age 8 years (Fig. 1). Analyzing the covariation between limb elements and survivorship during the first 8 years of life maximizes the possibility that some of the variation in survivorship is due to variation in limb and hand/foot length. A discrete fitness measure was used: animals surviving for 8 or more years (scored as a “1”) vs. animals dying before age 8 (scored as a “0”). The sifaka population was not significantly growing or shrinking during this period (Lawler et al., 2005b), suggesting that the binary fitness measure is not affected by “background” mortality or reproduction (Manly, 1985). All traits were logarithmically transformed and standardized, so that they have a mean of 0 and a standard deviation of 1. The fitness measure was regressed against trait values using the following equation:

$$\omega = \text{intercept} + \sum \beta_1 z_i \quad (1)$$

In Equation 1, β_1 denotes the multivariate estimate of linear (i.e., directional) selection acting on individuals in the population. This coefficient measures the strength of directional selection acting directly on each trait, because the multivariate equation statistically removes the effects of indirect selection (Lande and Arnold,

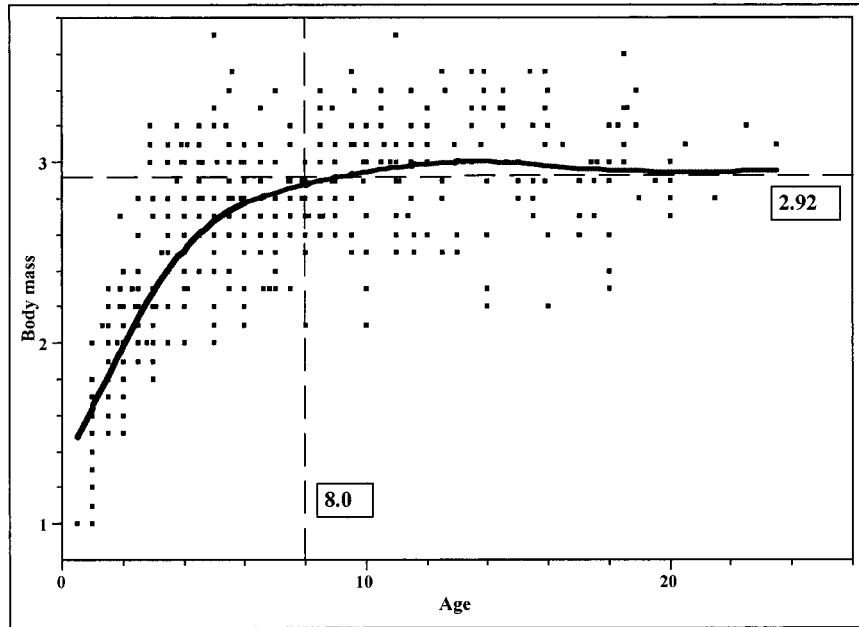


Fig. 1. Flexible spline fit of body mass by age. Dashed lines show point at which body mass mostly “levels off” during growth. This occurs around age 8 years, when body mass is just below 3 kg. Line was fit using smoothing spline function ($\lambda = 401.6$; $R^2 = 0.72$) in statistical program JMP-In (SAS Institute, Cary, NC).

TABLE 3. Ethogram and definition of substrate categories

Locomotor behaviors

Vertical leap: thigh-propelled, long-distance jumps between vertical substrates (usually >1 m). During take-off and landing, body is generally in orthograde position. Further discussion is given in text (see also Demes et al., 1996).

Leap: locomotor behavior that results in an “in-air” phase of movement from a nonvertical substrate. These leaps include short-distance leaps (usually <1 m).

Climb: movement on oblique substrates using all four limbs in irregular, nonstereotyped pattern.

Quadrupedal: movement using all four limbs equally; spine is pronograde.

Classification of substrates

Horizontal: branch angled 0–30° from horizontal.

Oblique: branch angled 30–60° from horizontal.

Vertical: branch angled 60–90° from horizontal.

Small: branch/trunk between 2.5 and 10 cm in diameter.

Medium: branch/trunk between 10 and 15 cm in diameter.

Large: branch/trunk greater than 15 cm in diameter.

1983). Positive coefficients indicate that larger trait values covary with survivorship, while negative coefficients indicate that smaller trait values covary with survivorship. There was no evidence of nonlinear selection acting on limb elements, so I do not present results for stabilizing, disruptive, or correlational selection coefficients. Statistical significance is set at $P = 0.05$, although it remains an open question as to what constitutes strong vs. weak selection (Conner, 2001). To help interpret selection coefficients that approach statistical significance (where the P -value is around 0.5), a neural network model was used. This model fits a multivariate surface to the data, and in the present context, allows one to visualize how fitness is dependent on trait values. The overfit penalty for the model was set at 0.075 and used three hidden nodes; these values captured the basic form of the fitness function specified by the selection coefficients. Further details of this technique are presented in Lawler et al. (2005a; see also Schluter and Nychka, 1994).

The neural network model was implemented using the statistical package JMP-In 5.1 (SAS Institute).

A few caveats should be noted about the methodology. First, the regression lines are calculated using data collected on animals that ranged in age from 1–25 years. No data are available from animals younger than 1 year old; thus it is possible that the inclusion of these latter animals could change the slope of the regression line. Second, the data set contains measurements for some animals that were captured up to three times. One would suppose that regression lines calculated from recaptured animals would approximate the regression lines calculated using the entire data set. This is not always the case, however, as slopes calculated only from recaptures generally underestimate the slopes calculated from the total data set. The discrepancy is likely due to statistical leverage problems (i.e., fitting a regression line to two or three data points) and the fact that adult body mass fluctuates seasonally, and some of the recaptures manifest this seasonal variation, resulting in negative slopes. Third, I argue that total hand/foot length is a proxy for the span between the divergent first digit and the lateral digits; this is, at best, a very rough stand-in for prehensile ability, and further data are required to substantiate my arguments. More data are needed on the scaling relationships among pedal elements in sifakas with respect to substrate use. In particular, the allometric relationship between first-digit length and total foot length requires quantitative substantiation.

RESULTS

Results pertaining to ontogenetic allometry are presented in Figure 2 and Table 4. Growth allometries of limb segments, as estimated by LS regressions, are all significantly different from 0.33 (Table 4). LS coefficients for the hand and the foot are the lowest among the postcranial elements. These coefficients are 0.21 and 0.18 for the hand and foot, respectively. Table 4 also provides coefficients estimated from RMA. For these coefficients, only the regression slopes for hand and foot are signifi-

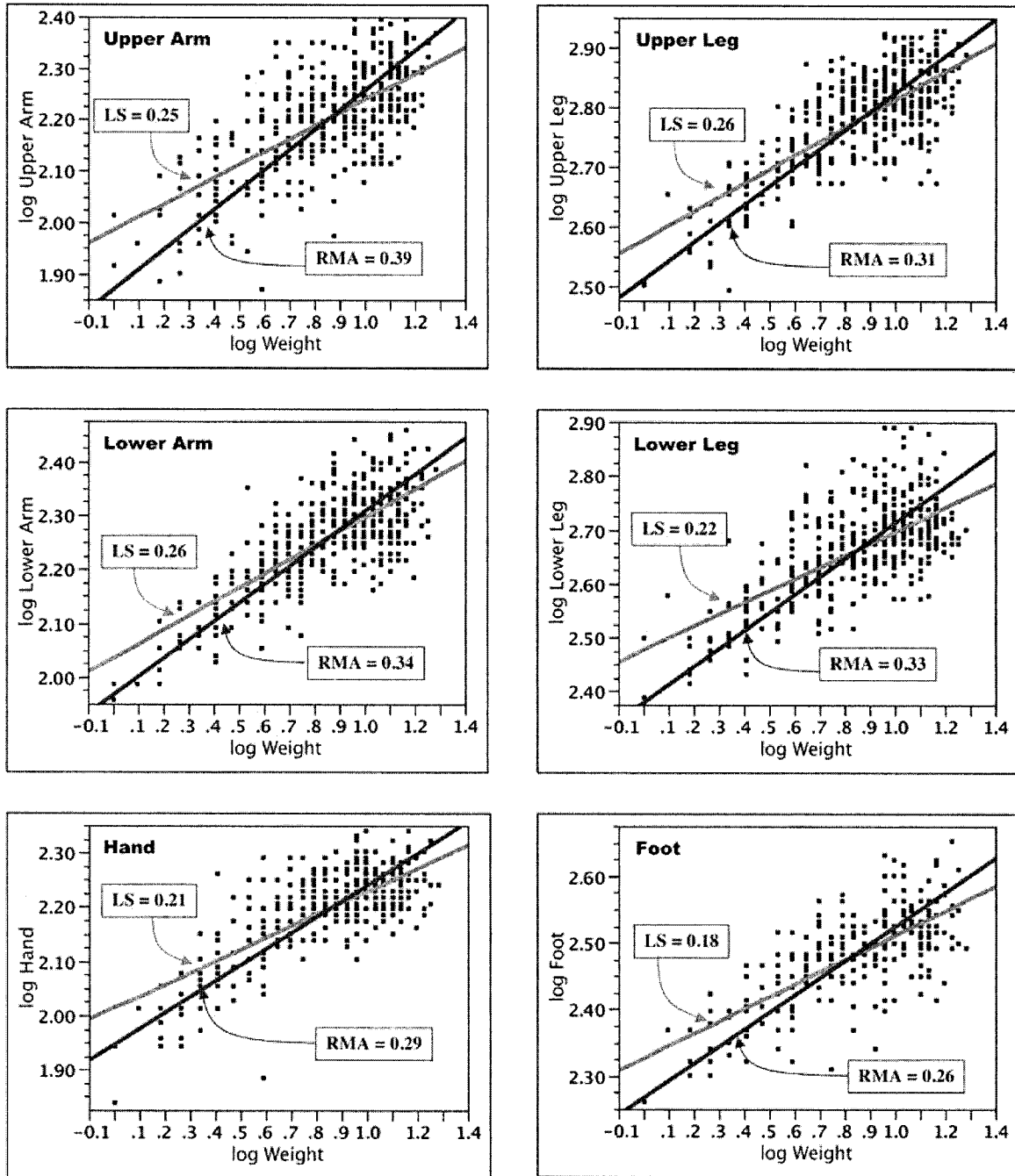


Fig. 2. Bivariate plots of limb elements and body mass. Each plot shows the least-squares (LS) and reduced major axis (RMA) estimate of the allometry coefficient.

TABLE 4. Regression statistics for allometric plots

Trait	R ²	LS intercept	Slope significantly lower than 0.33?	
			LS	RMA
Upper arm	0.43	1.99	Yes	No
Lower arm	0.57	2.04	Yes	No
Hand	0.54	2.02	Yes	Yes
Upper leg	0.57	2.58	Yes	No
Lower leg	0.44	2.48	Yes	No
Foot	0.52	2.33	Yes	Yes

cantly different from 0.33. These estimates are 0.29 for the hand, and 0.26 for the foot.

Results from the morphometric study indicate that hands and feet retain the lowest growth allometry coefficients among the postcranial elements. This deviation from geometric scaling demonstrates that juvenile animals have relatively larger hands and feet than adults. How do these patterns influence positional behavior and substrate use? Results pertaining to this question are presented in Table 5. Yearling and adult sifakas show no significant differences in the frequencies of any locomotor behaviors. Both adult and immature animals

TABLE 5. Frequencies of locomotor behaviors, substrate use, and leaping distance for yearling and adult sifakas

	Yearlings ¹	Adults ¹	Yearlings vs. adults significantly different?
Locomotion			
Climb	0.19 (0.16–0.22)	0.18 (0.15–0.21)	No
Leap	0.32 (0.28–0.35)	0.29 (0.24–0.32)	No
Vertical leap	0.48 (0.45–0.52)	0.53 (0.49–0.57)	No
Quadrupedalism	<0.01 (0.00–0.02)	<0.01 (0.00–0.02)	No
Branch size			
Small	0.62 (0.59–0.65)	0.67 (0.64–0.70)	No
Medium	0.29 (0.26–0.32)	0.24 (0.22–0.27)	No
Large	0.09 (0.07–0.11)	0.09 (0.07–0.11)	No
Branch angle			
Horizontal	0.12 (0.10–0.14)	0.19 (0.17–0.22)	Yes
Oblique	0.33 (0.30–0.36)	0.26 (0.24–0.29)	Yes
Vertical	0.55 (0.51–0.58)	0.55 (0.51–0.58)	No
Leaping distance (average distance in meters)	1.34 (1.29–1.40)	1.28 (1.22–1.33)	No

¹ Percent value (95% confidence interval).

TABLE 6. Heritability values and directional coefficients for limb traits

Trait	Heritability \pm SE	Directional coefficients (β)	
Upper arm	0.44 \pm 0.22	–0.007	($P = 0.90$)
Lower arm	0.28 \pm 0.22	–0.051	($P = 0.45$)
Hand	0.21 \pm 0.27	–0.034	($P = 0.58$)
Upper leg	0.43 \pm 0.21	–0.062	($P = 0.32$)
Lower leg	0.24 \pm 0.18	0.056	($P = 0.37$)
Foot	0.16 \pm 0.18	0.119	($P = 0.07$)

engaged primarily in vertical leaping (48% for yearlings, and 53% for adults) and leaping (32% for yearlings, and 29% for adults), followed by climbing (19% for yearlings, and 18% for adults) (Table 5). Yearlings and adults did not significantly differ with respect to use of different-sized substrates. Yearlings and adults primarily used small-sized substrates (62% vs. 67%, respectively), followed by medium-sized substrates (29% vs. 24%, respectively) and large-sized substrates (9% vs. 9%, respectively). There were no significant differences in use of vertical branches, but adults used significantly more horizontal branches than did immature animals (adults, 19%; yearlings, 12%), and yearlings used significantly more oblique branches than did adults (adults, 26%; yearlings, 33%). Leaping distance (which includes both types of leaping; see Table 3) was not significantly different between immature and adult animals.

Heritability values are presented in Table 6. The lowest heritability occurs in the foot ($h^2 = 0.16$). The hand has a heritability of 0.21. The upper arm and upper leg have similarly valued heritabilities of 0.44 and 0.43, respectively. The lower arm has a heritability of 0.28, and the lower leg has a value of 0.24. Coefficients of directional selection are also presented in Table 6. Elements of the upper limb experience very weak (i.e., negligible) directional selection. The upper arm experiences slight negative selection ($\beta_1 = -0.007$, $P = 0.90$), as does the lower arm ($\beta_1 = 0.051$, $P = 0.45$). The hand also experiences slight negative selection ($\beta_1 = -0.034$, $P = 0.58$). The upper leg is under weak negative directional selection ($\beta_1 = -0.062$, $P = 0.32$). The lower leg experiences very weak positive directional selection ($\beta_1 = 0.056$, $P = 0.37$), while the foot experiences stronger positive directional selection that approaches statistical significance ($\beta_1 = 0.119$, $P = 0.07$). Figure 3 shows

the fitness surface for hands and feet. This surface reveals the strong positive directional selection acting on foot length, as well as the very weak negative directional selection acting on hand length. Note that the surface is essentially planar, because fitness was coded as a binary variable.

DISCUSSION

Negative allometry of the foot: functional and ontogenetic considerations

The indriid foot is characterized by strong grasping capabilities that are associated with vertical clinging and leaping (Napier and Walker, 1967; Gebo, 1985). Sifakas have a greatly elongated, widely divergent big toe that opposes the other digits (and forefoot area) during halucial grasping (Jouffroy and Lessertisseur, 1979; Gebo and Dagosto, 1988). The deep cleft between the hallux and lateral digits allows the animal to grasp larger-diameter substrates than comparably sized lemurids (Jouffroy and Lessertisseur, 1979; Gebo and Dagosto, 1988). Gebo (1985) argued that the indriid foot is particularly adapted for grasping vertical substrates, with much of the gripping power coming from the first and second digits. The ankle-joint morphology reflects a configuration that allows for both stronger grips and greater eversion (Gebo and Dagosto, 1988). Several modifications of the three cuneiform bones serve to increase the angle between the hallux and other digits (Gebo, 1985). This joint configuration helps keep the hallux widely separated from the lateral digits, and this span serves an important role during leaping. In a detailed study of the kinematics of sifaka leaping, Demes et al. (1996) documented the movements involved in a vertical leap. In accordance with functional-morphological predictions, the sifaka foot is largely everted during take-off, and the majority of propulsive force comes from the thigh muscles (Demes et al., 1998). The deep cleft between the big toe and lateral digits forms an anchoring point during push-off. The animal rotates in midair, and lands feetfirst, using the same deep cleft to “catch” the incoming substrate. During leaping, the hands are used mostly for balance and stabilization, and provide very little propulsive force (Demes et al., 1996; R. Lawler, personal observations). The linear measurement of foot length used in this study captures the basic functional aspects

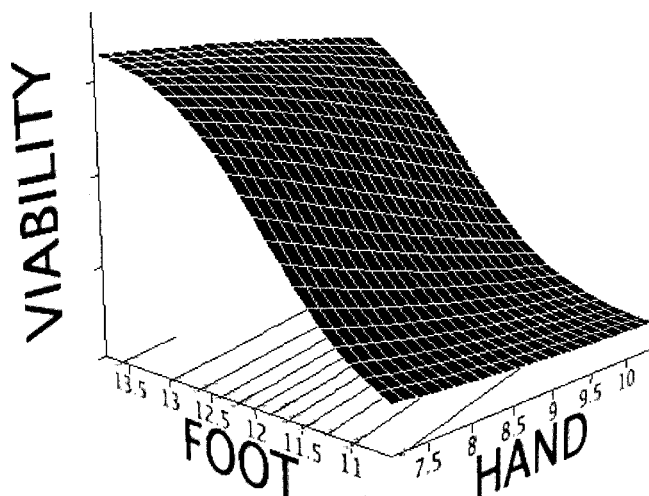


Fig. 3. Fitness surface showing the relationship between survivorship and hand and foot length. The surface is predominated by the dependency of fitness on larger values of foot length (indicating positive directional selection). Fitness increases along the vertical axis.

of the foot as it is used during leaping. Total foot length (i.e., from the calcaneus to the tip of digit IV) is positively correlated with the distance from the calcaneus to the tip of digit I (Jouffroy and Lessertisseur, 1979; R. Lawler, unpublished data); thus the single linear measurement down the length of the foot serves a proxy for the span between the first digit and the lateral digits. Longer feet have relatively more distance between the tip of the hallux and the tips of the lateral digits; thus, a longer foot length provides a larger area to receive approaching substrates during landing.

Sifaka yearlings utilize the same locomotor behaviors and same-sized substrates, and maintain similar leaping distances as adult sifakas. By all measures used in this study, sifaka yearlings do not engage in any behaviors that would suggest that they are under different ecological pressures to move around their habitat in a manner different from adults. I hypothesize that the strong negative allometry of the foot allows newly locomotor-independent sifakas to safely leap between substrates, using the relatively large span between the first and lateral digits as a push-off and “catch-point.” Leaping between substrates poses a substantial ecological challenge to young primates (Johnston, 1981), and it is clear that young sifakas, like other primates, “practice” leaping (Jolly, 1966; Richard, 1976; Wells and Turnquist, 2001). Leaping requires a combination of invariant movements (i.e., the animal’s overall trajectory from trunk to trunk) and movements that fine-tune or adjust joints and limb positions, based on immediate sensory feedback from the environment (Johnston, 1981). Studies of locomotor tuning show that animals must make immediate adjustments to their locomotor actions based on factors such as pliability and sway, as well as the physical properties of the substrate (Easton, 1972; Johnston, 1981). However, because motor coordination develops across the early juvenile period, locomotor tuning is an attribute that is partially acquired (discussed in Easton, 1972; Loeb, 1989; Sporns and Edelman, 1993; Carrier, 1996). In this regard, yearlings are less dexterous leapers than adult sifakas.

This hypothesis makes sense in the context of selection pressures acting on locomotor performance during ontogeny. Despite their smaller size and still-developing neuromuscular control, immature animals are subject to the same challenges of avoiding predators, finding food, and keeping up with group movements as adult animals (e.g., Janson and van Schaik, 1993; Carrier, 1996). However, juvenile primates have less locomotor stamina and agility than adults (reviewed in Hurov, 1991; Carrier, 1996). This lack of stamina comes from smaller energy reserves, coupled with a higher basal metabolic rate (due to growth) (Calder, 1988; Carrier, 1996). Their lack of agility is due to the interplay between the central nervous system and muscular coordination. Although the neurological infrastructure for coordinated movements is in place early in development (i.e., central pattern generators), young animals must develop a familiarity with neuromuscular control (Bekoff and Byers, 1981; Bekoff, 1988; Hurov, 1991; Carrier, 1996). Carrier (1996, p. 479) makes the point that in a growing animal, proprioceptive ability is compromised as different body parts (e.g., tips of the toes) shift positions relative to the rest of the body during development. In addition, changing body proportions result in different motor output from muscles during growth; these differences in motor output can result in “a conflict between the process of growth and the effective integration of sensory perception, neural muscular control, and motor output.” The lack of integration accounts for the widespread phenomenon of juvenile clumsiness, as witnessed in a variety of primates (Grand, 1981; Carrier, 1996; Workman and Covert, 2005). Additionally, juvenile animals must accommodate growth-related changes in bone mass (and composition) vs. muscle force (Keller et al., 1985; Hurov, 1991). As Hurov (1991) points out, the mass of the skeleton will increase as a cube of linear dimension, while muscle force will increase as a square of linear dimension; in this case, some sort of compensatory muscle growth must occur to maintain functional equivalence during ontogeny. All of these growth-related processes impinge on the proprioceptive abilities of young animals (Carrier, 1996). In this light, any morphological adaptation that enables young sifakas to securely move between substrates would be beneficial. I suggest that a larger span between the hallux and lateral digits qualifies as a beneficial feature that aids in safe landing. This suggestion is supported by the pattern of strong negative allometry in the foot, by similarities in substrate use and positional behavior between yearlings and adult sifakas, and by patterns of inheritance and selection acting on foot length.

Heritability and selection on hands and feet

A widely known equation from quantitative genetics states that the amount of change in the mean value of a phenotypic trait (z) is proportional to the additive genetic variance in that trait (V_A) multiplied by the strength of selection (dw/dz) (w is mean fitness) (Lande, 1976):

$$\Delta z = V_A/w \cdot dw/dz \quad (2)$$

In Equation 2, the dynamics of phenotypic evolution are governed by two terms: the additive genetic variance of the trait (i.e., the number of alleles segregating in the population that cause offspring to look like their parents), and the degree of covariation between fitness and phenotype. When V_A goes to zero, the average value

of the trait will not change independent of the amount of selection it experiences. An implication of Equation 2 is that traits experiencing selection will have lower amounts of additive genetic variance than traits not experiencing selection (Fisher, 1930; Robertson, 1966; Charlesworth, 1987). Because heritability is proportional to additive genetic variance, low heritability usually indicates the presence of past selection pressures (Roff, 1997).

The idea that traits closely associated with fitness should have low heritabilities was predicted by Fisher (1930), yet broad interspecific tests of this hypothesis did not appear until much later (e.g., Mousseau and Roff, 1987). In general, the prediction is borne out. Traits more closely associated with fitness (e.g., life-history traits) have lower heritabilities (Charlesworth, 1987; Roff, 1997; Kruuk et al., 2000). In sifakas, the foot has the lowest heritability of all limb elements. In principle, this low value could reflect the action of past selection pressures; however, there are complications with this viewpoint (e.g., Riska, 1989; Price and Schluter, 1991; Houle, 1992, 1998). Heritability is the ratio of additive genetic variance and phenotypic variance. Therefore, a low heritability value results from either decreasing the numerator or increasing the denominator. Because heritability can be defined as V_A/V_P , where $V_P = V_A + V_{ENVIRONMENT} + V_{DOMINANCE} + V_{MUTATION}$, traits with a lot of mutational input (which likely include limb elements; Wilkins, 2001) or environmental variation have lower heritabilities (Houle, 1998). Similarly, if one trait (trait x) is a function of another trait (trait y) (e.g., fertility is a function of body size), this will result in a lower heritability for trait x because environmental variation influences both trait x as well as the trait to which it is linked (Price and Schluter, 1991).

Nevertheless, both empirical and theoretical studies find a negative correlation between heritability and fitness (e.g., Charlesworth, 1987; Mousseau and Roff, 1987; Roff, 1997; Kruuk et al., 2000), and foot length in this study has a low heritability. Without detailed information on the genetic architecture of this trait, it is difficult to determine how much of a trait's heritability value can be ascribed to nonadditive effects such as maternal environment, and how much can be ascribed to selection. Limb allometries are set prenatally in *Propithecus* (Ravosa et al., 1993), suggesting that only maternal effects pertaining to gestation could contribute to nonadditive trait variation. In the absence of more detailed studies, I interpret low heritabilities as partially reflecting the action of past selection pressures. The heritability of the foot is the lowest among postcranial elements; therefore, this trait likely experienced the strongest selection pressures. This interpretation is also consonant with the findings of Ravosa et al. (1993). In a comparative study of growth in three sifaka species, they found that hindfoot length is relatively large and deviates from ontogenetic scaling among species. They suggest that this deviation is due to selection for compatibility between grasping ability and substrate size. Other studies of limb-element heritabilities show a similar pattern: lower values were generally found in the extremities (e.g., Cheverud and Dittus, 1992; Hallgrímsson et al., 2002), suggesting the action of past selection.

The standardized directional selection gradient acting on the foot is 0.119. If we assume that this trait is perfectly heritable and genetically uncorrelated with other traits, then the trait will change 11.9 standard deviation

units in 100 generations. Another way to think about a selection gradient of 0.119 is to note that relative fitness will increase by 11.9% for every one increase in the trait's standard deviation (Conner, 2001; Hersch and Phillips, 2004). It is important to keep in mind that I analyzed selection during the part of the life cycle in which I expected selection to act most strongly on hands and feet. Selection pressures on hands and feet are substantially weaker on adult animals past age 8 years (R. Lawler, unpublished data). A variety of factors will ensure that foot size will not continue to increase across generations. These include genetic correlations among traits, biomechanical constraints (e.g., large relative foot size could inhibit other aspects of locomotion), and the fact that selection may be partially acting on environmental, nonheritable variation (Rausher, 1992; Kruuk et al., 2001; Merila et al., 2001).

Why doesn't selection act as strongly on the hand vis-à-vis the foot in sifakas? It is possible that selection pressures acting on hands are strongest during the period of infant dependency when the sifaka infant's hands and feet play an equal role in securing it to its mother. A sifaka newborn is capable of clinging to its mother independently as she leaps between substrates (Jolly, 1966; Richard, 1978). Substantial acceleration forces are generated during leaping (Demes et al., 1995), and occasionally such movements jar the infant from the mother (Richard, 2003). Infant mortality is unusually high during the first year of life in sifakas (Richard et al., 2002; Richard, 2003), and the causes of mortality include lactational failure, hypothermia, and falls (Jolly, 1966; Richard, 1976, 1978, 2003). Such falls (if they occur because of poor grasping ability) could exert strong selection pressure on newborn grasping capabilities and strength. Upon reaching locomotor independence, however, selection pressures on hands should diminish, given the fact that hands are mostly used for stabilization and balance, and do not generate propulsive forces or serve as the primary element of contact during locomotion (Demes et al., 1996). Raichlen (2005; see also Grand, 1981; Ravosa et al., 1993) noted that selection pressures for secure grasping could account for the pattern of distally distributed limb mass seen in young baboons and macaques. In this interpretation, infants are born with larger distal limb masses and extremities, so that they can use the deep flexors surrounding their epipodials for secure grasping. If selection acts strongly on hands and feet prior to achieving locomotor independence, this hypothesis would help explain the near-universal pattern of negative allometry of hands and feet in primates, and would also explain why heritability values for these organs are low in primates (e.g., Hallgrímsson et al., 2002). This suggests a hypothesis about the relative roles of selection pressures acting on hands and feet in species using forelimb-suspensory vs. hindlimb-leaping behaviors: in both species, directional selection gradients acting on hands and feet should be of equal magnitude during the period of infant dependency (assuming that the infant uses both hands and feet to cling to its mother); however, upon reaching locomotor independence, selection pressures acting on the hands in forelimb-suspensory primates should remain strong, and those acting on the foot should diminish, while the opposite pattern should manifest in hindlimb-leaping species. One complication to this hypothesis is that hand morphology can also be shaped by selection for manipulative grasping during foraging, and not selected specifically for movement (e.g.,

Lemelin, 1996; Lemelin and Grafton, 1998; Bicca-Marques, 1999).

CONCLUSIONS AND IMPLICATIONS

I provide three pieces of evidence that, when taken together, suggest an adaptive basis for the negative allometry of the sifaka foot: 1) the positional behavior data offer a functional explanation for growth allometry, whereby yearling animals can use their relatively larger feet to traverse similar-sized substrates as adults; 2) heritability values calculated for limb elements indicate that foot length experiences strong selection; and 3) directional selection coefficients reveal that animals with relatively larger feet have a higher relative survivorship. However, an obvious problem with these arguments is that they can be applied to almost every primate. After all, negative allometric growth of the extremities is found across many primate species. Very often, such widespread interspecific allometric patterns are viewed as “primitive developmental pathways,” and thus implicitly serve no immediate functional or adaptive purpose (e.g., Gould, 1978; Lammers and German, 2002). I would argue that if one can show that such allometric patterns are under selective pressures, then such patterns can be viewed as adaptive, independent of their commonality (Reeve and Sherman, 1993). Thus, like others, I find that allometric relationships are not an explanation of animal morphology, but rather a description of phenotypic associations that require causal explanation (e.g., Jungers, 1984; Fleagle, 1985). This view requires that we define adaptation with respect to “phenotype existence” (Reeve and Sherman, 1993), and dispenses with the idea that widespread, clade-specific traits do not constitute adaptations in individual populations (e.g., Coddington, 1988; Harvey and Pagel, 1991).

Explanations for the evolution of diagnostic primate traits are largely sought within an adaptive context (e.g., Le Gros Clark, 1959; Cartmill, 1974; Martin, 1990; Sussman, 1991; Crompton, 1995). In particular, primates are characterized by prehensile hands and feet as well as a high degree of orbital convergence (Martin, 1990). In the context of the negative growth allometry of hands and feet, I speculate that early in primate evolution, there was strong selective pressure on hands and feet in infants and juveniles to increase and enhance their grasping ability. Theory suggests that such selection pressures will lead to canalization of clade-specific allometries. In this scenario, “... character complexes which serve a common function tend to evolve together” (Wagner, 1996, p. 42). This scenario explains the prevalence of negative allometric growth of the hands and feet in numerous primate taxa. However, the above results also indicate that selection is the force responsible for maintaining allometric patterns in wild populations. In fact, studies that specifically explore the evolution of allometry find that selection is the predominant force maintaining allometric relationships (e.g., Emlen, 1996; Frankino et al., 2004). Given the results above, I suggest that selection continues to play a role in preserving negative allometric growth of the hands and feet across numerous primate taxa. This suggestion (whether correct or not) specifies a testable framework for investigating the adaptive basis of allometric relationships in the primate order by merging ontogenetic and quantitative genetic data sets.

ACKNOWLEDGMENTS

For comments and discussions pertaining to the topics addressed here, I thank Susan Ford, Mathew O'Neill, Carol MacLeod, Jennifer Wernegreen, Alison Richard, Bob Dewar, James Rossie, Eric Sargis, David Watts, Laurie Godfrey, Joel Ratsisarson, Steve Leigh, and Pierre Lemelin. Two anonymous reviewers and *AJPA* editor Clark Spencer Larsen provided very helpful comments as well. All errors in interpretation are my own responsibility. I thank Jean-Charles Razafimahazo for helping me collect positional behavior data. I thank the Government of Madagascar for permission to conduct this research. I thank Joel Ratsisarson for making my many visits to Madagascar smooth, memorable, fun, and productive. The Beza Mahafaly Monitoring Team collected much of the primary data used in this study, and I am very grateful to the team's coordinator Joelisoa Ratsisarson and to team members Enafa, Elahavelo, Emady Rigobert, and Ellis Edidy. I thank Marion Schwartz for managing the sifaka database, determining age estimates from dental casts, providing me with copies of relevant data, and hosting a “sifaka summit.” I thank Laurie Godfrey for providing me with a “cleaned-up” version of the morphometric database.

LITERATURE CITED

- Bekoff M. 1988. Motor training and physical fitness: possible short- and long-term influences on the development of individual differences in behavior. *Dev Psychobiol* 21:601–612.
- Bekoff M, Byers AJ. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: an ethological hornet's nest. In: Immelmann K, Barlow G, Main M, Petrinovich L, editors. *Behavioral development: the Bielefeld Interdisciplinary Project*. Cambridge: Cambridge University Press. p 296–337.
- Bicca-Marques JC. 1999. Hand specialization, sympatry, and mixed-species associations in callitrichines. *J Hum Evol* 36:349–378.
- Bock WJ, Von Walther G. 1965. Adaptation and the form-function complex. *Evolution* 19:269–291.
- Calder WA. 1988. *Size, function, and life history*. London: Dover.
- Cant JGH. 1992. Positional behavior and body size of arboreal primates: a theoretical framework for field studies and an illustration of its application. *Am J Phys Anthropol* 88:273–283.
- Carrier DR. 1996. Ontogenetic limits on locomotor performance. *Physiol Zool* 69:467–488.
- Cartmill M. 1974. Rethinking primate origins. *Science* 184:436–443.
- Charlesworth B. 1987. The heritability of fitness. In: Bradbury JW, Andersson MB, editors. *Sexual selection: testing the alternatives*. Chichester: Wiley Press. p 21–40.
- Cheverud JM, Dittus WPJ. 1992. Primate population studies at Plonnuaruwa. II. Heritability of body measurements in a natural population of toque macaques (*Macaca sinica*). *Am J Primatol* 27:145–156.
- Cheverud JM, Moore AJ. 1994. Quantitative genetics and the role of the environment provided by relatives in behavioral evolution. In: Boake CRB, editor. *Quantitative genetic studies of behavioral evolution*. Chicago: University of Chicago Press. p 67–100.
- Cheverud JM, Dittus WPJ, Wilson P. 1992. Primate population studies at Plonnuaruwa. I. Somatometric growth in a natural population of toque macaques (*Macaca sinica*). In: Ravosa MJ, Gomez AM, editors. *Ontogenetic perspectives on primate evolutionary biology*. London: Academic Press. p 51–78.
- Coddington JA. 1988. Cladistic tests of adaptational hypotheses. *Cladistics* 4:3–22.

- Conner JK. 2001. How strong is natural selection? *Trends Ecol Evol* 16:215–217.
- Crompton RH. 1995. Visual predation, habitat structure, and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK, editors. *Creatures of the dark: the nocturnal prosimians*. New York: Plenum Press. p 11–30.
- Dagosto M. 1994. Testing positional behavior of Malagasy lemurs: a randomization approach. *Am J Phys Anthropol* 84:189–202.
- Dagosto M. 1995. Seasonal variation in positional behavior of Malagasy lemurs. *Int J Primatol* 16:807–834.
- Demes B, Jungers WL, Gross TS, Fleagle JG. 1995. Kinetics of leaping primates: influence of substrate orientation and compliance. *Am J Phys Anthropol* 96:419–429.
- Demes B, Jungers WL, Fleagle JG, Wunderlich RE, Richmond BG, Lemelin P. 1996. Body size and leaping kinematics in Malagasy vertical clingers and leapers. *J Hum Evol* 31:367–388.
- Demes B, Fleagle JG, Lemelin P. 1998. Myological correlates of prosimian leaping. *J Hum Evol* 34:385–399.
- Doran DM. 1992. A comparison of instantaneous and locomotor bout sampling methods: a case study of adult male chimpanzee locomotor and substrate use. *Am J Phys Anthropol* 89:85–99.
- Easton TA. 1972. On the normal use of reflexes. *Am Sci* 60:591–599.
- Emlen DJ. 1996. Artificial selection on horn length body-size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Evolution* 50:1219–1230.
- Falconer DS, MacKay TFC. 1996. *Introduction to quantitative genetics*. Harlow: Prentice Hall.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Fleagle JG. 1976. Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatol (Basel)* 26:245–269.
- Fleagle JG. 1977a. Locomotor behavior and muscular anatomy of sympatric leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Am J Phys Anthropol* 46:297–308.
- Fleagle JG. 1977b. Locomotor behavior and skeletal anatomy of sympatric leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yrbk Phys Anthropol* 20:440–453.
- Fleagle JG. 1979. Primate positional behavior and anatomy: naturalistic and experimental approaches. In: Morbeck ME, Preuschoft H, Gomberg N, editors. *Environment, behavior, and morphology: dynamic interactions in primates*. New York: Gustav Fischer. p 313–325.
- Fleagle JG. 1984. Primate locomotion and diet. In: Chivers DJ, Wood BJ, Bilsborough AL, editors. *Food acquisition and processing in primates*. New York: Plenum Press. p 105–117.
- Fleagle JG. 1985. Size and adaptation in primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 1–20.
- Fleagle JG. 1999. *Primate adaptation and evolution*. New York: Academic Press.
- Ford SM, Corruccini RS. 1985. Intraspecific, interspecific, metabolic, and phylogenetic scaling in platyrrhine primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 401–435.
- Frankino WA, Zwaan BJ, Stern DL, Brakefield PM. 2004. Natural selection and developmental constraints in the evolution of allometries. *Science* 307:718–720.
- Garber PA. 1980. Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates). *Int J Primatol* 1:185–201.
- Garber PA. 1991. A comparative study of positional behavior in three species of tamarin monkeys. *Primates* 32:219–230.
- Gebo DL. 1985. The nature of the primate grasping foot. *Am J Phys Anthropol* 67:269–277.
- Gebo DL, Dagosto M. 1988. Foot morphology, climbing, and the evolution of the Indriidae. *J Hum Evol* 17:135–154.
- Gould SJ. 1978. Generality and uniqueness in the history of life: an exploration with random models. *Bioscience* 28:277–281.
- Grand TI. 1977. Body weight: its relation to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. *Am J Phys Anthropol* 47:211–239.
- Grand TI. 1981. The anatomy of growth and its relation to locomotor capacity in *Macacca*. In: Chiarelli AB, Corruccini RS, editors. *Primate evolutionary biology*. Berlin: Springer-Verlag. p 35–43.
- Halgrímsson B, Willmore K, Hall BK. 2002. Canalization, developmental stability, and morphological integration in primate limbs. *Yrbk Phys Anthropol* 45:131–158.
- Harvey PH, Pagel M. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hersch EI, Phillips PC. 2004. Power and potential bias in field studies of natural selection. *Evolution* 58:479–485.
- Houle D. 1992. Comparing evolvability and variability in quantitative traits. *Genetics* 130:195–204.
- Houle D. 1998. How should we explain variation in the genetic variance of traits? *Genetica* 102/103:241–253.
- Hurov JR. 1991. Rethinking primate locomotion: what can we learn from development? *J Motor Behav* 23:211–218.
- Janson C, van Schaik C. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. *Juvenile primates: life history, development, and behavior*. New York: Oxford University Press. p 57–76.
- Jenkins FA, editor. 1974. *Primate locomotion*. New York: Academic Press.
- Johnston TD. 1981. Compensation for substrate elasticity in the kinematics of leaping by infant pigtailed macaques (*Macaca nemestrina*). *Brain Res* 184:467–480.
- Jolly AB. 1966. *Lemur behavior*. Chicago: University of Chicago Press.
- Jouffroy FK, Lessertisseur J. 1979. Relationships between limb morphology and locomotor adaptations among prosimians: an osteometric study. In: Morbeck ME, Preuschoft H, Gomberg N, editors. *Environment, behavior, and morphology: dynamic interactions in primates*. New York: Gustav Fischer. p 143–181.
- Jungers WL. 1984. Aspects of size and scaling in primate biology with special reference to the locomotor skeleton. *Yrbk Phys Anthropol* 27:73–97.
- Jungers WL. 1985. Body size and scaling of limb proportions in primates. In: Jungers WL, editor. *Size and scaling in primate biology*. New York: Plenum Press. p 345–382.
- Jungers WL, Cole MS. 1992. Relative growth and shape of the locomotor skeleton in lesser apes. *J Hum Evol* 23:93–106.
- Jungers WL, Fleagle JG. 1980. Postnatal growth allometry of the extremities in *Cebus albifrons* and *Cebus apella*: a longitudinal and comparative study. *Am J Phys Anthropol* 53:471–478.
- Jungers WL, Hartman SE. 1988. Relative growth of the locomotor skeleton in orangutans and other large-bodied hominoids. In: Schwartz JH, editor. *Orangutan biology*. Oxford: Oxford University Press. p 347–359.
- Kaplan DT. 1999. *Resampling Stats in Matlab*. Arlington: Resampling Stats.
- Keller TS, Lovin JD, Spengler DM, Carter DR. 1985. Fatigue of immature baboon cortical bone. *J Biomech* 18:297–304.
- Kruuk LEB, Clutton-Brock TH, Slate J, Pemberton JM, Brotherstone S, Guinness FE. 2000. Heritability of fitness in a wild mammal population. *Proc Natl Acad Sci USA* 97:698–703.
- Kruuk LEB, Merial J, Sheldon BC. 2001. Phenotypic selection on a heritable size trait revisited. *Am Nat* 158:557–571.
- Lammers AR, German RZ. 2002. Ontogenetic allometry in the locomotor skeleton of specialized half-bounding mammals. *J Zool Lond* 258:485–495.
- Lande R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–334.
- Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Lawler RR. 2003. Causes and consequences of differential reproductive success in male white sifaka (*Propithecus verreauxi verreauxi*). Ph.D. dissertation, Yale University, New Haven, CT.
- Lawler RR, Richard AF, Riley MA. 2001. Characterization and screening of microsatellite loci in a wild lemur population (*Propithecus verreauxi verreauxi*). *Am J Primatol* 55:253–259.

- Lawler RR, Richard AF, Riley MA. 2005a. Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *J Hum Evol* 48:259–277.
- Lawler RR, Richard AF, Dewar RE, Hunter CM, Caswell H. 2005b. Demographic analysis of a wild lemur population. *Am J Phys Anthropol [Suppl]*40:135–136.
- Legendre P, Legendre L. 1998. Numerical ecology. New York: Elsevier.
- Le Gros Clark WE. 1959. The antecedents of man. Edinburgh: Edinburgh University Press.
- Lemelin P. 1996. The evolution of manual prehensility in primates: a comparative study of prosimians and didelphid marsupials. Ph.D. dissertation, State University of New York at Stony Brook, Stony Brook, NY.
- Lemelin P, Grafton BW. 1998. Grasping performance in *Saguinus midas* and the evolution of hand prehensility in primates. In: Strasser E, Fleagle JG, Rosenberger AL, McHenry H, editors. Primate locomotion: recent advances. New York: Plenum Press. p 131–144.
- Loeb GE. 1989. Neural control of locomotion: how do the data fit together? *Bioscience* 39:800–804.
- Lynch M, Walsh B. 1998. Genetics and the analysis of quantitative traits. Sunderland, MA: Sinauer Press.
- Manly BFJ. 1985. The statistics of natural selection. London: Chapman and Hall.
- Martin RD. 1990. Primate origins and evolution: a phylogenetic reconstruction. Princeton: Princeton University Press.
- Merila J, Sheldon BC, Kruuk LEB. 2001. Explaining stasis: microevolutionary studies in natural populations. *Genetica* 112/113:199–222.
- Morbeck ME, Preuschoft H, Gomberg N, editors. 1979. Environment, behavior, and morphology: dynamic interactions in primates. New York: Gustav Fischer.
- Mousseau TA, Roff DA. 1987. Natural selection and the heritability of fitness components. *Heredity* 59:181–197.
- Napier JR, Walker AC. 1967. Vertical clinging and leaping, a newly recognized category of locomotory behavior among primates. *Folia Primatol (Basel)* 6:180–203.
- Pereira ME, Leigh SR. 2003. Modes of primate development. In: Kappeler PM, Pereira ME, editors. Primate life histories and socioecology. Chicago: University of Chicago Press. p 149–176.
- Price TD, Schluter D. 1991. On the low heritability of life history traits. *Evolution* 45:853–861.
- Ratsirarson J. 2003. Reserve Speciale de Beza Mahafaly. In: Goodman SM, Benstead JP, editors. The natural history of Madagascar. Chicago: University of Chicago Press. p 1520–1524.
- Raichlen DA. 2005. Ontogeny of limb mass distribution in infant baboons (*Papio cynocephalus*). *J Hum Evol* 49:452–467.
- Rausher MD. 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* 46:616–626.
- Ravosa MJ, Meyers DM, Glander KE. 1993. Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. *Am J Phys Anthropol* 92: 499–520.
- Reeve HK, Sherman PW. 1993. Adaptation and the goals of evolutionary research. *Q Rev Biol* 68:1–32.
- Richard AF. 1976. Preliminary observations on the birth and development of *Propithecus verreauxi* to the age of six months. *Primates* 17:357–366.
- Richard AF. 1978. Behavioral variation: case study of a Malagasy lemur. Lewisburg: Bucknell University Press.
- Richard AF. 2003. *Propithecus*, sifakas. In: Goodman SM, Benstead JP, editors. The natural history of Madagascar. Chicago: University of Chicago Press. p 1345–1348.
- Richard AF, Rakotomanga P, Schwartz M. 1993. Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar. *Am J Primatol* 30:1–20.
- Richard AF, Dewar RE, Schwartz M, Ratsirarson J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *J Hum Evol* 39:381–391.
- Richard AF, Dewar RE, Schwartz M, Ratsirarson J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka *Propithecus verreauxi verreauxi*. *J Zool Lond* 256:421–436.
- Richmond BG, Begun DR, Strait DS. 2001. Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Yrbk Phys Anthropol* 33:70–105.
- Riska B. 1989. Composite traits, selection response, and evolution. *Evolution* 43:1172–1191.
- Robertson A. 1966. A mathematical model for the culling process in dairy cattle. *Anim Prod* 8:95–108.
- Roff DA. 1997. Evolutionary quantitative genetics. London: Chapman and Hall.
- Schluter D, Nychka D. 1994. Exploring fitness surfaces. *Am Nat* 143:597–616.
- Sporns O, Edelman GM. 1993. Solving Bernstein's problem: a proposal for the development of coordinated movement by selection. *Child Dev* 64:960–981.
- Stearns SC. 1992. The evolution of life histories. Oxford: Oxford University Press.
- Strasser E, Fleagle JG, Rosenberger AL, McHenry H, editors. 1998. Primate locomotion: recent advances. New York: Plenum Press.
- Sussman RW. 1991. Primate origins and the evolution of angiosperms. *Am J Primatol* 23:209–223.
- Turnquist JE, Wells JP. 1994. Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. *J Hum Evol* 26:487–499.
- Wagner GP. 1996. Homologues, natural kinds, and the evolution of modularity. *Am Zool* 36:36–43.
- Wells JP, Turnquist JE. 2001. Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): II. Postural and locomotor behavior and habitat use in a free-ranging colony. *Am J Phys Anthropol* 115:80–94.
- Wilkins AE. 2001. The evolution of developmental pathways. Sunderland, MA: Sinauer Press.
- Workman C, Covert HH. 2005. Learning the ropes: the ontogeny of locomotion in red-shanked douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacourii*), and hatinh langurs (*Trachypithecus hatinhensis*): I. Positional behavior. *Am J Phys Anthropol* 128:371–380.