Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*)

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Abstract

Studies of sexual selection show that both female choice and male-male competition can influence the evolution and expression of male phenotypes. In this regard, it is important to determine the functional basis through which male traits influence variation in male reproductive success. In this study, we estimate the strength and type of sexual selection acting on adult males in a population of wild lemur, Verreaux's sifaka (*Propithecus verreauxi verreauxi*). The data used in this study were collected at Beza Mahafaly Special Reserve, southwest Madagascar. We conducted paternity analyses on 70 males in order to estimate the distribution of reproductive success in this population. Paternity data were combined with morphometric data in order to determine which morphological traits covary with male fitness. Five morphological traits were defined in this analysis: body size, canine size, torso shape, arm shape, and leg shape. We utilized phenotypic selection models in order to determine the strength and type of selection acting directly on each trait. Our results show that directional selection acts on leg shape (a trait that is functionally related to locomotor performance), stabilizing selection acts on body mass and torso shape, and negative correlational selection acts on body mass and leg shape. We draw from biomechanical and kinematic studies of sifaka locomotion to provide a functional context for how these traits influence male mating competition within an arboreal environment. Verreaux's sifaka and many other gregarious lemurs are sexually monomorphic in body mass and canine size, despite a high frequency and intensity of male-male aggressive competition. Our results provide some insight into this paradox: in our population, there is no directional selection acting on body mass or canine size in males. The total pattern of selection implicates that behaviors relating to locomotor performance are more important than behaviors relating to fighting ability during intrasexual contests.
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Keywords: Sexual selection; *Propithecus*; Lemur; Sexual dimorphism; Locomotion; Phenotypic selection

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Introduction

Primate males and females often differ in physiological investment of reproductive resources, life history schedules, and potential reproductive rates. Because of this, the manner in which they acquire mates and fertilizations often differs (Dunbar, 1983; Smuts, 1987; Clutton-Brock, 1991; Clutton-Brock and Parker, 1992; Andersson, 1994; Plavcan, 2001). Reproductive output is a major component of fitness, and much attention has been directed toward understanding the phenotypic factors that affect mating and successful reproduction in males and females. If variation in male fitness is determined by conspecifics within the context of mate acquisition, then evolutionary change will proceed via sexual selection (Arnold, 1983b; Andersson, 1994; Schuster and Wade, 2003). Theoretical studies of sexual selection have demonstrated that both female mating preferences and male-male competition influence the evolution and expression of male phenotypes (e.g., Lande, 1981; Kirkpatrick, 1982; Maynard Smith and Brown, 1986; Iwasa et al., 1991; Wiley and Poston, 1996; Kokko et al., 2002). In this regard, establishing associations between male phenotypes and variation in male reproductive success is important for determining the behavioral and ecological mechanisms underlying sexual selection (Heisler et al., 1987; Andersson, 1994; Plavcan, 2001).

Empirically establishing such associations in wild primate populations can be difficult because information on individual trait values and/or parentage is often unavailable. Because of these complications, the most common approach to studying sexual selection in primates is to infer the operation of selection using the comparative method (e.g., Kay et al., 1988; Kappeler, 1990, 1996; Plavcan and van Schaik, 1992, 1997; Ford, 1994; Mitani et al., 1996; Plavcan, 1999). Although this approach is a very powerful means to test or generate hypotheses of adaptation, it cannot directly measure the strength or type of selection pressures acting on male traits (Reeve and Sherman, 1993; Leroi et al., 1994; Hansen, 1997). Directly measuring the operation of sexual selection requires, at minimum, information on how male reproductive output depends on male phenotypes within a population (Arnold, 1983b, 1994; Arnold and Duvall, 1994). This, in turn, requires data on male fertility and information on how particular traits are used to acquire mates. When paternity data and phenotypic measurements from individually marked animals become available, it is possible to estimate the current selective pressures using phenotypic selection models (Lande and Arnold, 1983; Arnold and Wade, 1984a, 1984b; Arnold and Duvall, 1994). Combining estimates of selection with field observations provides the behavioral context through which sexually selected traits are used to achieve a mating advantage (Wilkinson et al., 1987). That is, estimating selection pressures can point to *which* traits are experiencing selection (e.g., canine size) and relevant morphobehavioral data can reveal *how* these traits are leveraged to produce a fitness consequence (e.g., by agonistically signaling a sexual rival).

Intrasexual selection theory predicts a host of morphological traits that are likely targets of selection during male-male competition (Andersson, 1994; Plavcan, 2001) (see Table 1 for examples). One cue to the operation of intrasexual selection is sexual dimorphism (Andersson, 1994). Although the etiology of sexual dimorphism is complex and not exclusively due to intrasexual selection pressures (Cheverud et al., 1985; Plavcan, 2001), many studies focus on the potential advantages that relatively large male trait values confer during male mating competition. Comparative studies find a strong correlation between the intensity of male-male competition and degree of sexual dimorphism in body mass and canine size (e.g., Kay et al., 1988; Ford, 1994; Plavcan and van Schaik, 1992, 1997; Plavcan, 2001). Almost invariably, this pattern is interpreted as the consequence of directional selection acting to enlarge male trait values (relative to female trait values) due to male-male competition (cf. Plavcan, 2001). A prominent exception to this pattern is found among the gregarious lemurs. These lemurs maintain high intensities of male-male aggressive competition for mates despite very low levels of sexual dimorphism in body mass and canine size (Kappeler, 1990, 1991, 1996; Richard, 1992). Additionally, some of these same species appear to experience very little sperm competition (Kappeler, 1996). Many

Table 1
Examples of intrasexually selected male morphological traits

Trait	Pre- or post-copulatory[a]	This trait or complex assists in…	Example[b]
Overall body mass	Pre-copulatory	overpowering/outlasting sexual rivals	Patas monkeys
Testes volume/size	Post-copulatory	sperm deposition/plugs and/or rival sperm displacement	Ring-tailed lemurs
Canine size	Pre-copulatory	wounding/threatening sexual rivals	Hamadryas baboons
Locomotor elements	Pre-copulatory	out-maneuvering sexual rivals	Many arboreal anthropoids
Body fat distribution	Pre-copulatory	out-lasting sexual rivals during mate competition	Rhesus macaques
Pelage/skin coloration	Pre-copulatory	threatening displays	Vervet monkeys

[a] Pre/post-copulatory refers to the phase of male-male competition in which the trait is used to gain a reproductive advantage.
[b] References: Chism and Rogers, 1997; Sauther, 1991; Kummer, 1971; Leutenegger and Kelly, 1977; Bercovitch and Nurnberg, 1996; Fedigan and Fedigan, 1988.

hypotheses have been put forth to explain this paradoxical pattern in gregarious lemurs (see Discussion), but none have directly measured the strength of intrasexual selection pressures in these species. Fundamentally, sexual monomorphism in body mass and canine size coupled with aggressive male mating competition suggests that winning fights does not always have a positive fitness consequence (Richard, 1992), and/or that other types of behaviors, for example agility, may be favored by selection during male-male competition (Richard, 1974; Leutenegger and Kelly, 1977; Kappeler, 1991, 1996; Lindenfors, 2002). This raises several possibilities concerning the action of intrasexual selection on males: 1) despite aggressive mating competition, directional selection does not target body mass and canine size; 2) different types of selection, for example stabilizing selection, act on these traits; or 3) body mass and canine size experience no selection pressures at all, but other non-obvious traits—for example, torso length—do experience selection. [It also should be kept in mind that selection on female traits can contribute to sexual monomorphism (Plavcan, 2004)]. Comparative studies cannot address these possibilities because they only infer the presence of *directional* selection based on interspecific correlations (Leroi et al., 1994; but see Hansen, 1997). Determining which male traits experience intrasexual selection requires direct measurements of selection.

The objectives of this paper are twofold: 1) to estimate the strength and type of intrasexual selection acting on male traits in a wild population of gregarious lemur; and 2) to illustrate how the sexually selected traits influence the performance of particular behaviors during intrasexual contests (Arnold, 1983a, 2003; Kingsolver and Huey, 2003). The data for these analyses come from an on-going study of a wild population of Verreaux's sifaka (*Propithecus verreauxi verreauxi*) located at Beza Mahafaly Special Reserve, southwest Madagascar. Morphological and behavioral data have been collected on individually marked animals in this population over the last 19 years (see Richard et al., 2002) and an analysis of paternity has recently been completed (Lawler, 2003). In this study, we limit our analysis to pre-copulatory morphological traits that (potentially) experience *intra*sexual selection. Factors such as testes size, social group composition, the role of female-choice, and life history traits will be considered elsewhere. We employ the "selection gradient" approach of Lande and Arnold (1983; see also, Arnold and Duvall, 1994) to measure selection acting on male traits. This approach has been used successfully to measure sexual selection in numerous taxa (e.g., water striders: Fairbairn and Preziosi, 1996, water snakes: Weatherhead et al., 2002; newts: Jones et al., 2002; dung flies: Blanckenhorn et al., 2003), but to our knowledge has not been applied to primate populations. Briefly, this method uses a partial regression of fitness on traits of interest, where the regression coefficients indicate the strength (i.e., magnitude) and type of selection (e.g., directional, stabilizing, disruptive) acting on the traits included in the

regression model (Lande and Arnold, 1983; Arnold, 1994). In this study, we regress male fertility on traits relating to male-male competition. By regressing male fertility (and not, for example, male survivorship) on male phenotypic traits, we explicitly capture how variation in reproductive output is dependent on variation in trait values (see Fairbairn and Preziosi, 1996; Weatherhead et al., 2002). Furthermore, the function connecting fitness to phenotype—the selection gradient—has an explicit grounding in formal selection theory (Arnold and Duvall, 1994). Other measures of sexual selection, for example, operational sex ratios (Emlen and Oring, 1977), time spent searching for mates (Sutherland, 1985), and potential reproductive rates (Clutton-Brock and Parker, 1992), often lack the theoretical framework to link variation in male reproduction to selection on particular traits (Arnold and Duvall, 1994; Andersson, 1994: 89-95; Jones et al., 2002).

Verreaux's sifaka are interesting animals for studying the effects of intrasexual selection. Sifaka at Beza Mahafaly are sexually monomorphic in canine size and body mass (Richard, 1992). Group size ranges from 2-13 animals and the mean adult socionomic sex ratio within social groups is about 1.0 (Richard et al., 1993; unpublished data). Sifaka have a mating season that lasts 6-8 weeks beginning in mid-January. During this time, males seek mates both within and outside of their resident social group (Brockman, 1999), and a paternity analysis confirmed that some males sire offspring outside their resident social group (Lawler et al., 2003). Behaviorally, male-male competition for females during the mating season encompasses fierce fighting as well as non-contact chasing and lunging (Richard, 1992; Brockman, 1999). An ideal study of intrasexual selection would treat these behavioral outcomes of male-male competition (e.g., number of fights won) as the "traits" in phenotypic selection models (Plavcan, 2001). However, regressing male fitness on behavioral traits is complicated. Males do not follow a fixed behavioral pattern over a given mating season, or even a given day. Male-male contests vary across groups and time, resulting in a complex pattern of male mating behaviors. Female choice and the mating season breakdown

of male dominance relationships further complicate this pattern (Richard, 1992; Brockman et al., 1998; Brockman, 1999). Because of this, there is no fixed set of male behaviors to use as the independent variables in selection models. Measuring phenotypic selection requires normally distributed data from an entire *population* (Lande and Arnold, 1983; Heisler, 1994; Fairbairn and Reeve, 2001). Few behavioral studies—including those conducted on this population (Richard, 1992; Brockman et al., 1998; Brockman, 1999)— can provide the necessary sample sizes to meet this requirement.

To get around these complications, we focus on how selection acts on morphological traits. Unlike behavioral traits, morphological traits are often normally distributed and show minimal change over a particular mating season. Additionally, we have morphological data for the majority of males in the Beza Mahafaly population. The basis for choosing which morphological traits to include in our analysis comes from a consideration of intrasexual selection studies of wild primates (see Table 1), as well as observations of male-male competition in the sifaka population. Operationally, we separate male-male competition into two behavioral categories: fighting and chasing. The justification for distinguishing these two categories of male mate competition is based on detailed studies of sifaka reproductive behavior (Richard, 1978, 1992; Brockman, 1994, 1999). The behavioral categories are described below:

1) *Fighting episodes*. These episodes involve physical combat. Sifaka primarily bite, cuff, or grab their opponents during combat and this is accompanied by lunging, threat displays, and a variety of dominant and submissive gestures between interactants. Fighting takes place on tree branches of all orientations, as well as the ground. Fighting can be fierce, with animals suffering open wounds and gashes. The most serious wounds are inflicted by biting with the incisors and canines. Agonistic episodes often arise when non-resident and resident males compete for mates, although there can be considerable agonistic contests within a single group.

2) *Chasings episodes*. These episodes include sustained periods of rapid back and forth arboreal movement, often accompanied by aggressive and submissive displays. Typically, competitors will move towards each other and veer away at the last moment. During chases, sifaka mostly utilize vertical clinging and leaping, although they may also rely on other forms of locomotion. Chasing and lunging episodes can last several hours until the competitors are visibly exhausted.

These two categories of mating competition do not represent fixed, alternative mating strategies (see Andersson, 1994); all males in the population can engage in both types of behaviors. Nevertheless, the two categories are behaviorally distinct and implicate different suites of morphological traits that may be important determinants of male reproductive success. Drawing from these categories, we define and analyze traits that show some biomechanical or functional relationship with one or both of these two types of competition. Specifically, we assess the strength and type of selection acting on the following traits: body mass, canine size, torso shape, arm shape, and leg shape. The definitions of these traits are given in the methods section and in Table 2.

Some of the traits we analyze, for example body size, are likely to show a functional relationship with *both* chasing and fighting. However, we expect different patterns of selection to act on these traits depending on whether male reproductive success is predominantly determined through physical combat, or whether male reproductive success is predominantly determined through chases. If mate acquisition and reproductive success depends on physical combat, we expect that directional selection will target traits associated with fighting. For sifaka males, such traits include body mass, canine size, and arm strength (Richard, 1992). We do not expect stabilizing or disruptive selection to act on these traits in any detectable manner. The functional basis for this prediction is that larger animals will have a strength advantage in maintaining mate exclusivity by aggressively overpowering, cuffing, or biting their sexual rivals (Andersson, 1994; Plavcan, 2001). If mate acquisition and reproductive success depends on bouts of chasing and lunging, we expect that intermediate values of body mass and torso size will be favored (i.e., stabilizing selection), whereas leg shape will be under directional selection. The functional basis for this prediction is that stronger, larger legs coupled with a more "stream-lined" body mass will be advantageous during non-contact arboreal chases. In this case, traits related to locomotor performance should be favored (Leutenegger and Kelly, 1977; Kappeler, 1990, 1991, 1996; Lindenfors, 2002). Table 2 summarizes these predictions.

Table 2

Description of traits used in this study and predicted action of selection acting on traits under different types of male mating competition

Trait name	Description	If mates are predominantly acquired through:	
		Fighting	**Chasing**
		Then selection should…	
Body mass	Body mass of adult males during mating season	INCREASE (directional selection)	OPTIMIZE (stabilizing selection)
Canine size	Upper canine height measured from gumline to tip	INCREASE (directional selection)	NOT TARGET
Torso shape	Principal component of circumference of chest and length of spine length and length across hips	INCREASE (directional selection)	OPTIMIZE (stabilizing selection)
Arm shape	Principal component of length of upper and lower arm and circumference of upper arm	INCREASE (directional selection)	WEAKLY INCREASE (weak directional selection)
Leg shape	Principal component of length of upper and lower leg and circumference of thigh	WEAKLY INCREASE (weak directional selection)	INCREASE (directional selection)

Materials and methods

The study population, paternity analysis, and morphometrics

The Verreaux's sifaka population at Beza Mahafaly has been the focus of numerous studies, including analyses of sifaka life history (Richard et al., 2000, 2002), demography (Richard et al., 1991, 1993), reproductive endocrinology (Brockman et al., 1998; Brockman and Whitten, 1996), population genetics (Lawler et al., 2001, 2003), and social behavior (Richard, 1992; Kubzdela, 1997; Brockman, 1999). Beginning in 1984, wild *P. v. verreauxi* were captured, measured, and marked using color-coded collars and numbered tags (Richard et al., 1991). During the capture procedure, 23 morphometric measurements, dental casts, hair and tissue samples, and a range of qualitative data were gathered from each animal. Bilaterally symmetric measurements were taken on the left side of each animal. 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.

Seven polymorphic microsatellite loci were isolated and screened on this population in order to determine parentage and kinship (Lawler et al., 2001; Lawler, 2003). The number of alleles at these seven loci ranged from 6-11, and heterozygosity ranged from 0.62 to 0.75, with a mean heterozygosity of 0.70 across all loci. The probability of these seven loci to exclude a random individual from parentage when one parent is known is 99% (Lawler et al., 2001). Paternity was determined by maximum likelihood estimation, as implemented in the program CERVUS 2.0 (Marshall et al., 1998). We assumed a genotyping error rate of 0.01, and that the proportion males sampled was 0.9. For a given offspring, CERVUS assigns a likelihood-based "LOD score" to each candidate sire, with the highest LOD score indicating the most likely sire. CERVUS determines confidence levels by taking the difference in LOD scores (called a Δ-value) for the most likely candidate sires of a particular offspring and comparing this Δ-value to a distribution of simulated Δ-values. Following

convention (e.g., Coltman et al., 1999; Storz et al., 2001), we set confidence levels for paternity assignment at the 80% and 95% levels. We ran paternity assignments with and without a known mother. Maternity was determined through extensive census data (Richard et al., 2000, 2002) and checked against genetic data. All paternity assignments made by CERVUS were subsequently checked against independent information; such information included age, location, number of genetic mismatches, and survivorship for the assigned father. On the occasion when the most likely father could not possibly have sired the offspring (e.g., the assigned sire was an age-mate—i.e., brother or half brother—of the offspring) then the next most likely sire was assigned. All paternity assignments used in this analysis made biological "sense," i.e, assigned sires were of the proper age, alive at time of likely conception, and residing in or adjacent to the group where their offspring were born (see Lawler et al., 2003, for details on relatedness, dispersal, and paternity). To test for deviations in random mating and reproduction, we compared the distribution of paternity in our sample to a Poisson expectation of paternity; the Poisson distribution assumes each male has an equal probability of siring an offspring (Wright, 1938). The Poisson distribution was parameterized using the mean of the total reproductive output of males in our sample.

Body mass fluctuates seasonally in adult sifaka and can potentially influence morphometric measurements. To eliminate any biases brought in by seasonal effects, we only included animals captured in November through May. These months correspond to a time when body weights are seasonally elevated (Richard et al., 2000, 2002). Animals captured during November through May had a significantly higher average body mass than animals captured in the remaining months, indicating that this time period was appropriate for eliminating seasonal effects ($F = 77.36$, $df = 1$, 553, $p = 0.0001$). Our sample size consisted of 70 adult males captured and measured between 1989 and 1999. For those males captured and measured more than once in this time period, we took the average of each set of measurements. There were no differences in morphometric trait values for

males who sired offspring within their resident group and those who sired offspring outside their resident group (see Lawler et al., 2003). Thus we pooled all males together; pooling also helped to keep our sample size large.

Three traits—arm shape, leg shape, and torso shape—are composite traits based on combinations of linear measurements that correspond to a particular anatomical region of the animal. The other two traits—body mass and canine size—are based on single measurements. Body mass was measured in kilograms. Canine size was measured from gum line to the tip of the upper canine (using dental casts; see Richard et al., 1991). Because canines wear down with age, we tested several different measurements of canine size that are independent of crown height. Measures of both mesiodistal length and buccolingual width did not yield significant results concerning the action of selection (canine length: directional selection coefficient, $p = 0.21$, stabilizing selection coefficient, $p = 0.88$; canine width: directional selection coefficient, $p = 0.63$, stabilizing selection coefficient, $p = 0.25$) and visualization of fitness surfaces (see below) revealed no pattern of selection acting on these traits. For shape-based traits, all linear measurements (in mm) were first divided by the cube root of body mass (Darroch and Mossimann, 1985; Jungers et al., 1995). Each shaped-based trait is the first principal component extracted on a set of ratios defining the trait. Principal components analysis is a standard ordination technique for defining traits in multivariate selection models (Lande and Arnold, 1983). Arm shape is defined as the first principal component extracted from the following set of linear measurements: length of humerus, length of radius, and circumference at the midpoint of the upper arm. Leg shape is defined as the first principal component extracted on length of femur, length of tibia, and circumference at the midpoint of the thigh. Torso shape is defined as the first principal component extracted on length of spine, length across hips, and circumference of chest at nipples. The shape-based traits allowed us to see if selection targets a particular anatomical region independent of its covariation with overall body mass (recalling that each linear measurement was first divided by the cube root of body mass). For all three shape-based traits,

the first principal component captured more than 50% of the total variation and all components had positive eigenvectors. The positive eigenvectors for each trait indicate that principal component scores (below referred to as trait values) can be interpreted as a measure of overall trait size. For example, when we refer to "larger values of leg shape," we are referring to principal component scores that reflect larger values of the linear measurements that define leg shape; in this case, larger "values of leg shape" means that an individual is characterized by a relatively longer femur and tibia and larger thigh circumference.

The linear measurements used to define each shape trait were measured as follows: upper arm length was measured from the acromion process on the scapula to the lateral epicondyle on the humerus; lower arm length was measured from the lateral epicondyle of the humerus to the radial styloid on the radius; upper leg length was measured from the greater trochanter on the femur to the lateral epicondyle of the tibia; lower leg length was measured from the lateral epicondyle of the tibia to the lateral malleolus of the fibula. Chest circumference was taken at the level of the nipple; torso length was measured along the spine from the base of the head to the base of the tail; and length across hips was measured across the iliac processes (Richard et al., 1991). For these analyses, we assumed that the measurements taken from each adult male give some indication of genetic and physiological quality, and that male phenotypes remain relatively constant throughout their breeding career. The latter assumption is supported indirectly by the fact that both somatic and long bone growth (on which the linear measurements are based) cease around age 5 in male sifaka and all the males in our sample were ages 5 and older (Richard et al., 2002).

Sample period, fitness, and selection coefficients

The present study used paternity data for all offspring born into the population during the years 1989 to 1999. All reproductively active adult males who were in the population during 1989 to 1999 and captured between November and May were considered to be potential sires. Because the sample

period included males who were reproductively active prior to 1989 but died prior to 1999, we ran the risk of underestimating the fertility for these males. To examine this possibility, we eliminated these males from our analysis and compared the results to analyses in which these males were included. There were no differences in the statistical significance of results, i.e., traits that showed significant selection gradients with these males included remained statistically significant with the males excluded (at p = 0.05). To further control for age and sampling-time effects, we used a measure of male fertility that accounted for the time each male spent in the sample period. This fitness measure is defined as the number of offspring sired by a male during the sample period divided by the number of years a male was reproductively active during the sample period. This measure of fitness gives the per-year reproductive rate of males during the period 1989-1999. It does not rule out the possibility that age, itself, influences male reproductive success; however, including age-controlled effects into our measure of fitness allowed us to focus on parameter estimates pertaining to morphological trait values.

The five traits in our analysis (denoted as z) were standardized so that they had a mean of 0 and a standard deviation of 1. We divided our measure of fitness (ω) by mean fitness to provide a measure of relative fitness. Thus, the selection coefficients reveal the relationship between relative fitness and the variation in the trait measured in standard deviation units (Lande and Arnold 1983). We use β to denote multivariate estimates of selection. We will refer to β_1 as the "directional" coefficients, β_2 as the "nonlinear" coefficients (i.e., these coefficients capture the curvature of the fitness function), and β_3 as the "correlational" coefficients. The beta coefficients ($\beta_{1,2,3}$) measure the strength of selection acting directly on traits (or pairs of traits as in the case of β_3) because the multivariate equation statistically removes the effects of indirect selection due to phenotypic correlations among traits (Lande and Arnold, 1983). We used the following equation to estimate intrasexual selection:

$$\left[\omega = \text{intercept} + \sum \beta_1 z_i\right] + 0.5 \sum \beta_2 z_i^2 + \sum \beta_3 z_i z_j$$

$$(1)$$

We estimated the directional coefficients (β_1) using the bracketed portion of Equation (1) and we estimated the nonlinear and correlational coefficients (β_2 and β_3) using all of Equation (1) (Lande and Arnold, 1983). When the directional coefficients take positive values, this indicates the operation of positive directional selection (and negative values indicate the operation of negative directional selection). When the nonlinear coefficients take negative values, this implies the operation of stabilizing selection (and positive values indicate disruptive selection). Correlational selection (β_3) measures the joint effects of direct selection on particular pairs of traits and these coefficients can take positive or negative values (Endler, 1986; Brodie et al., 1995; Fairbairn and Reeve, 2001). Depending on the amount of traits in the dataset, the number of coefficients to be estimated for directional (β_1) and nonlinear selection (β_2) in a multivariate framework can quickly outstrip the number of individuals (N) in the dataset. To maintain statistical power it is desirable to have $N \gg \beta_1 + \beta_2(\beta_2 + 1)/2$.

To help interpret selection coefficients we used visualization techniques derived from neural network models (implemented in the statistical program JMP-In, version 5.1, SAS Institute, Inc.). These models fit a surface to pairs of traits and male fitness using a nonlinear optimization procedure. Neural networks are one of many techniques that can approximate a smooth function to an arbitrary degree of accuracy (Nelles, 2001). Very accurate approximations are highly particular because the function (i.e., surface) "visits" every data point; this makes the model highly accurate but reduces its ability to make generalizations about the data. Reducing the number of parameters (called "hidden nodes" in neural network parlance) and/or imposing a more strict penalty for overfitting the model produces a smoother surface (i.e., a surface that is less accurate but more predictive). Our rationale for parameterizing the neural network model was straightforward: we adjusted the number of hidden nodes (i.e., parameters) and overfit penalty in order to produce a smooth fitness surface that visually captured the major types of selection acting on traits, as specified by the selection

coefficients. Three hidden nodes and an overfit penalty of 0.1 produced a surface that was not jagged or prone to the effects of outliers. Schluter (1988; Schluter and Nychka, 1994) introduced the use of nonlinear and nonparametric methods to visualize fitness surfaces. These techniques are useful for interpreting the action of selection because they do not make any a priori assumptions about the form of the fitness surface (e.g., imposing a quadratic approximation) (Schluter, 1988; Phillips and Arnold, 1989).

In general, we de-emphasized the role of p-values in this analysis (here, conventionally set at $p = 0.05$); we did this because it is an open question as to what constitutes strong versus weak selection (Conner, 2001; Kingsolver et al., 2001; Hersch and Phillips, 2004). Our approach for determining "strong selection" relied on a combination of small p-values and visualization techniques. For all traits that we deemed "significant" (traits that have p-values near or below 0.05), we used visualization techniques to independently confirm the strength of selection. In this context, we have not corrected for multiple comparisons. Multiple comparisons tests are overly conservative

and penalize any investigation that conducts multiple tests versus a single test (see Gotelli and Ellison, 2004; Nakagawa, 2004). Multivariate selection models require multiple traits (and multiple tests) in order to remove the indirect effects of selection; we feel the strength of this technique should not be penalized by a post hoc (and arbitrary) significance test.

Results

Fig. 1 shows the distribution of reproductive success for males in this analysis. Overall, of the 70 males in our study, 36 males sired no offspring and 34 males sired a total of 90 offspring. Average offspring production is 1.3 per male and the variance is 3.3. We note here that male variation in reproductive success during the sample period exceeds that of females (R. Lawler, unpublished data). Reproductive success is highly skewed and deviates from a Poisson expectation of male reproductive success. Among the sires, many of the males fathered only one or two offspring (n = 21), and three males were highly successful
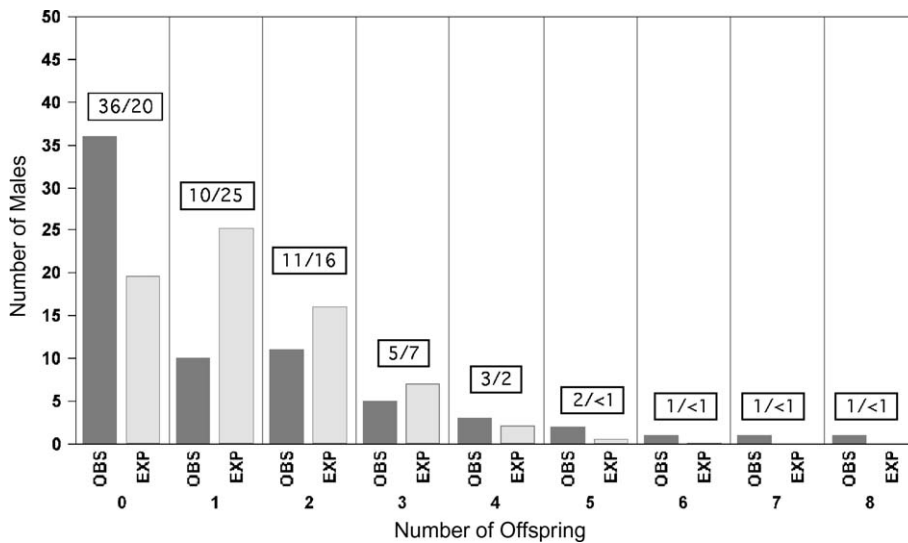

Fig. 1. The distribution of reproductive success among males in the study during the period spanning 1989-1999. Shown are the observed (OBS) and Poisson-expected (EXP) number of males who sired zero offspring, one offspring, two offspring, three offspring…up to eight offspring. The numbers above the bars give the values for observed versus expected number of males (Obs/Exp). For example, 10 males in our sample each sired one offspring whereas the Poisson-expected number is 25.
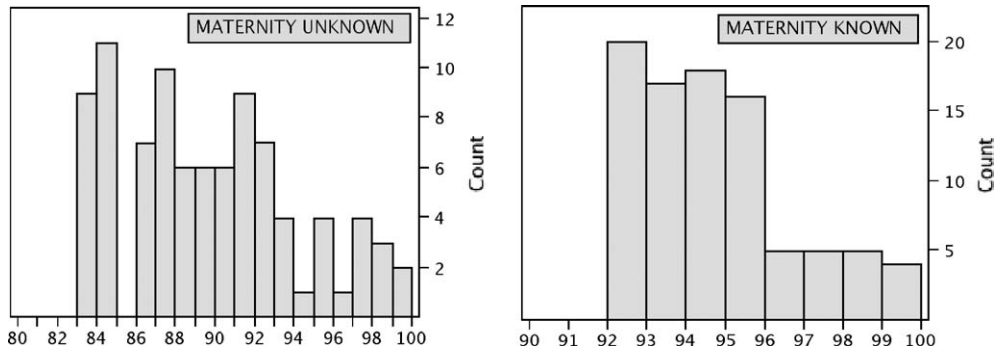
Fig. 2. The distribution of maximum likelihood confidence values for paternity assignments assuming maternity is unknown (left) and with maternity known (right). The x-axis gives the confidence level. The y-axis gives the number of paternity assignments made at the particular confidence level.

(relative to the Poisson expectation), siring six, seven, and eight offspring, respectively (see Fig. 1). Fig. 2 presents information on confidence values for paternity assignments. Assuming no known mothers, the average confidence value for paternity assignments is 90%. This value is significantly higher than 80%—the lowest conventionally accepted confidence value used in paternity studies (one-tailed Wilcox signed rank = 2047.5, p = 0.0001). Using a known mother, as determined by behavioral and genetic data, the average confidence in paternity assignments was 95%.

Table 3 gives the estimates of the selection coefficients (β). Only one trait—leg shape—stands out as a target of strong directional selection (leg shape $\beta_1 = 0.479$, p = 0.061). No other traits experience any significant directional selection. The β_2 coefficients reveal nonlinear selection. As shown in Table 3, stabilizing selection acts on body mass, as indicated by the positive and nonsignificant directional coefficient and the significant and negative stabilizing component (body mass $\beta_2 = -0.509$, p = 0.050). Torso shape also experiences stabilizing selection (torso shape $\beta_2 = -0.527$, p = 0.052), whereas canine size, arm shape, and leg shape do not experience strong nonlinear selection.

Fig. 3 shows bivariate fitness surfaces for leg shape and body mass. These surfaces were produced using the neural network models. Fig. 3A shows the fitness surface produced by relating male fertility to leg shape. The steep

Table 3

Estimates and statistical significance of multivariate directional (β_1), nonlinear (β_2), and correlational (β_3) selection coefficients for traits listed in Table 2 [a]

	Body Mass	Canine Size	Torso Shape	Arm Shape	Leg Shape
Directional coefficients	0.193 (p = 0.372)	−0.025 (p = 0.915)	−0.265 (p = 0.199)	0.179 (p = 0.410)	0.479 (p = 0.061)
Nonlinear coefficients	−0.509 (p = 0.050)	−0.129 (p = 0.526)	−0.527 (p = 0.052)	−0.009 (p = 0.947)	0.122 (p = 0.745)
Correlational coefficients					
Body Mass	—	−0.254 (p = 0.745)	−0.619 (p = 0.305)	−0.670 (p = 0.259)	−1.756 (p = 0.038)
Canine Size		—	0.218 (p = 0.764)	0.969 (p = 0.162)	1.471 (p = 0.150)
Torso Shape			—	−0.597 (p = 0.408)	1.373 (p = 0.153)
Arm Shape				—	−0.834 (p = 0.296)

[a] Correlational coefficients and p-values are given for pairs of traits in an above-diagonal matrix in the bottom portion of this table.
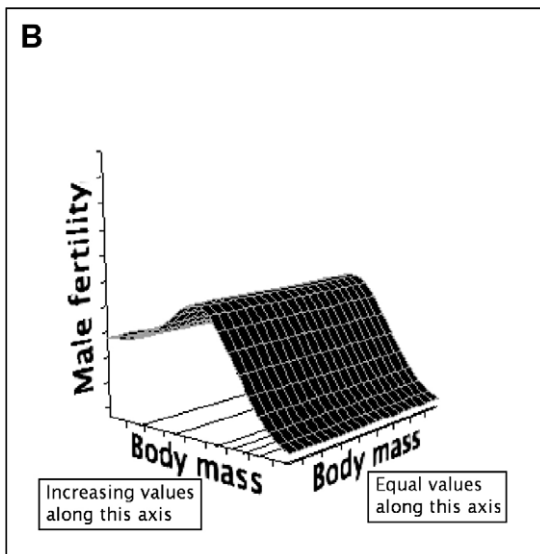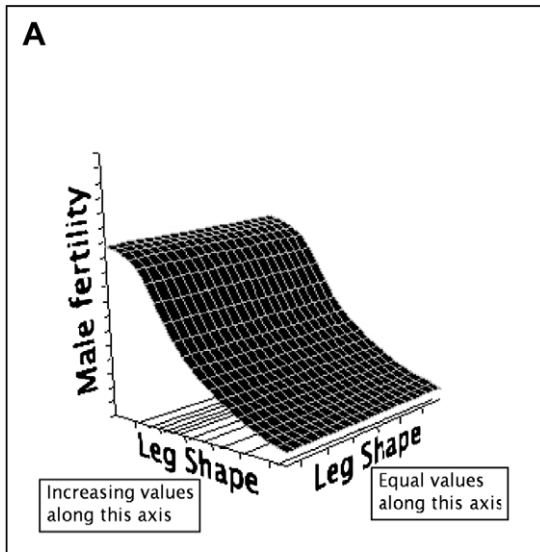
Fig. 3. Bivariate fitness surfaces of male fertility against leg shape (A) and body mass (B). In both figures male fertility increases along the vertical axis. Trait values only increase along one axis (from right to left) and take equal values along the other axis. Directional selection acts on leg shape as evidenced by the positive surface relating fitness to leg shape. Stabilizing selection acts on body mass as evidenced by the concave surface relating fitness to body mass. Compare with Fig. 4.

shows the fitness surface produced by relating male fertility to body mass. Intermediate values of body mass are associated with the highest values of male fertility, indicating the operation of stabilizing selection. This surface visually reveals the negative (i.e., concave) coefficient, as specified by the multivariate selection model. Torso shape shows a similar fitness surface to body mass. Leg shape and body mass also experience significant negative correlational selection ($\beta_3 = -1.756$, p = 0.038). Fig. 4 shows the fitness surface for these two traits. Examination of this fitness surface reveals how the two traits interact to determine fitness; fitness is highest for those males who have a combination of intermediate body mass and large values of leg shape. Fitness surfaces for traits other than leg shape, body mass, and torso shape did not reveal any significant action of selection.

The above results highlight the importance of presenting non-significant results along with significant results. By testing a hypothesis about the
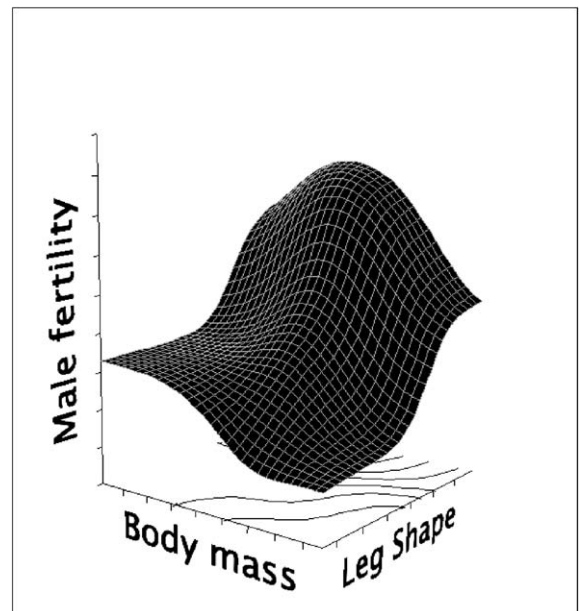

Fig. 4. Fitness surface for leg shape and body mass. Trait values increase as they move along their respective axes away from the bottom anterior corner. Male fertility increases along the vertical axis. High fitness corresponds to the region in which body mass values are intermediate while leg shape values are near maximum. Compare with Fig. 3.

positive slope reveals that fitness increases with increasing leg shape. This slope is congruent with the positive directional selection coefficient specified by the multivariate selection model. Fig. 3B

action of selection acting on traits, a failure to detect selection becomes just as important as a success. We bring this up because it is suspected that only studies finding a significant selection gradient make it into the scientific literature (Kingsolver et al., 2001). This publication bias can be ameliorated if such studies sought to outline the predicted action of selected acting on particular traits using pertinent contextual information, such as potential trait function, behavioral and ecological information, and/or deducing predictions from relevant comparative studies (as in Table 2).

Discussion

Intrasexually selected traits and their biomechanical basis

Drawing from observations of male sifaka sexual contests, we hypothesized that selection would target different sets of morphological traits depending on whether male reproductive success was more dependent on fighting versus chasing. By directly estimating the strength of selection acting on each trait, we were able to identify which traits actually contribute to male fertility. Positive directional selection does not operate on body mass, canine size, and arm shape. However, positive directional selection acts on leg shape, and stabilizing selection acts on body mass and torso shape. In addition, significant correlational selection acts on leg shape and body mass, favoring males with intermediate body mass and large values of leg shape. We propose that the total pattern of selection implicates behaviors relating to locomotion are stronger determinants of male reproductive success than behaviors relating to physical combat. The proposal that reproductive success is contingent on locomotor behaviors, such as agility, endurance, maneuverability, leaping strength, etc., is not new (Clutton-Brock and Harvey, 1977; Leutenegger and Kelly, 1977; Kappeler, 1990, 1996; Richard, 1992; Lindenfors, 2002); however, no studies have actually demonstrated a connection between reproductive success and traits related to locomotion in primates. Below, we draw from kinematic and

biomechanical data to show how variation in leg shape, body mass, and torso shape relate to biologically meaningful performance factors that influence sifaka positional behavior (Arnold, 1983a; Kingsolver and Huey, 2003).

Leg shape likely plays the following role in male mating competition. Sifaka utilize a specialized form of arboreal locomotion called *vertical clinging and leaping* (VCL), which connotes a reliance on sequentially leaping from one vertical tree trunk to another (Napier and Walker, 1967). A typical locomotor sequence starts with the animal clinging in a vertical position on a tree trunk with the thighs abducted and hands and feet holding the animal in place. Facing the trunk, sifaka use the deep cleft between their big toe and other digits to push off the vertical trunk and then rotate in mid-air to face the oncoming vertical trunk. The major propulsive force during a leap comes from the well-developed musculature of the thigh and indirect force is provided by a push-off from the arms (Demes et al., 1996, 1998). The sifaka postcranium shows numerous osteological and myological adaptations that reflect the demands of this type of positional behavior (Walker, 1974; Gebo and Dagosto, 1988; Anemone, 1993; Demes et al., 1998). At Beza Mahafaly, vertical clinging and leaping accounts for 50% of all locomotor behaviors in this population (Lawler 2004; R. Lawler, unpublished data).

By measuring limb lengths and circumferences, our definition of leg shape captures the biomechanically important aspects of this type of locomotion because it approximates muscle forces and lever-arm mechanics. Circumferences at the midpoint of the thigh encapsulate muscles used for leaping and movement. These include some of the extensor (i.e., propulsive) muscles of the knee and thigh (Gebo and Dagosto, 1988; Demes et al., 1998). Demes et al. (1998) documented that the quadriceps femoris group—and not the hip extensors, such as the gluteal group—constitutes the largest muscle group in prosimian leapers. They argued that, during leaping, muscle power from the knee extensors gets transferred to the substrate via a joint reaction force. For purposes of our trait definition, this indicates that measurements taken at the midpoint of the thigh encom-

pass the major propulsive muscles recruited during leaping. The force (f) generated by a muscle is proportional to its cross-sectional area (a), or $a \propto f$ (Swartz, 1993). Although we did not measure muscle cross-sectional area, we did measure circumference (c). Circumference at the midpoint of the thigh provides an approximation of muscle force because circumference itself is proportional to area, noting that $c^2/4\pi = a$, and by extension: $c^2/4\pi \propto f$. Limb length also contributes to loco-motor performance. The velocity and distance of a leap depends on the distance over which the propulsive force is applied to the substrate. Longer limb elements can apply propulsive forces over greater distances (Swartz, 1993). This results in a longer acceleration time, which translates into a greater leaping distance. Consequently, longer limbs enable longer leaps and provide longer periods to dissipate landing forces (Preuschoft, 1985; Biewener, 2003). Given this, our definition of leg shape can be linked to the major biomechanical factors that influence locomotor performance in sifaka. Our analysis of selection shows that directional selection acts on leg shape, favoring males with relatively longer legs and a greater thigh circumference. Increased leg length and muscle mass, on the whole, increases both the distance and efficiency of a leap (Biewener, 2003). It is likely that males who possess these attributes have a locomotor advantage during the intrasexual arboreal chases. Quantitative studies of sifaka positional behavior during the mating season are needed to confirm this possibility.

The result for stabilizing selection acting on body mass and torso shape may also relate to locomotor performance. We suggest that selection favors intermediate values of body mass in sifaka because leaping ability is hindered by relatively larger body mass. This suggestion is based on the following kinematic and biomechanical conclu-sions derived from interspecific studies: 1) leaping is energetically costly in primates (Alexander, 1991; Crompton et al., 1993; Demes et al., 1999); 2) leaping imposes high compressive and bending stresses on sifaka long bones (Demes et al., 1991; Terranova, 1996); 3) indriid long bones scale isometrically with body mass implying low safety factors (i.e., increases in body mass are not "over-compensated" for by increases in bone robusticity) (Demes et al., 1991; Terranova, 1996); 4) larger-bodied leaping prosimians have less propulsive muscle mass per unit body mass than smaller ones (Demes et al., 1998); and 5) leaping animals may be locomoting at the upper limits of their performance capabilities (Crompton et al., 1993; Demes et al., 1999). Because of these factors, heavier animals often make behavioral adjustments during a leap (Demes et al., 1995). These behavioral adjustments include reducing leaping distance, using preparatory "to and fro" movements, optimizing take-off angle, and timing jumps with elastic rebound of swaying branches (Crompton, et al., 1993; Demes, et al., 1995). If mating competition in an arboreal environment is dependent on leaping ability related to arboreal chases, selection may favor males of a particular optimum weight because heavier males must make these behavioral adjustments during intrasexual contests. Detailed field observations are needed to confirm this proposal, particularly because our interpretation rests on the assumption that in-terspecific allometric patterns can be applied to intraspecific variation in our population.

The idea that body mass can limit locomotor performance in arboreal primates is supported indirectly by comparative studies of sexual di-morphism. These studies show that arboreal species are less sexually dimorphic in body mass than terrestrial species. The lack of highly di-morphic arboreal species suggests an upper limit to male body mass, given the challenges of maneu-vering on relatively small branches (Harvey et al., 1987; Plavcan and van Schaik, 1997; Lindenfors and Tullberg, 1998). Our results support this interpretation, showing that stabilizing and not directional selection acts on male body mass in the sifaka. However, allometric factors confound this interpretation: terrestrial primates tend to be larger than arboreal primates and body mass itself is positively correlated with the degree of sexual size dimorphism (Smith and Cheverud, 2002). In this regard, positive directional selection pressures acting on male body mass would result in more sexual dimorphism in a terrestrial species than the same selection pressures acting on an arboreal species.

Finally, it is necessary to discuss the role of canine size. Positive directional selection does not operate on upper canine size. Intuitively, it might be supposed that longer canines cause more serious wounds; afterall, there is a strong interspecific association between canine length and intensity of male-male combat in anthropoid primates (Plavcan and van Schaik, 1992). Given the ferocity of male-male competition during the mating season in sifaka (Richard, 1992), longer canines would seemingly be advantageous in vanquishing sexual rivals. However, canine size (or length) per se is not directly related to the ability to inflict serious wounds. The ability of a pointed object to puncture a compliant material (as when a canine is used to bite into flesh) is a function of *both* force and the area of the point or tip (Frazzetta, 1988). Because of this, a reduced or dulled point area, coupled with a sufficient bite force, can still puncture a compliant material. More colloquially, even dull upper canines can puncture skin and cause bloody wounds. For selection to act on canine size, canines must be effective in precluding sexual rivals from mating, either through agonistic signaling or overt physical combat. Although contests between male sifaka can be bloody, canine size is not positively related to variation in male fertility in this population. Also, sifaka do not use their teeth to signal agonistic intent (Richard, 1978). Taken together, male canine size does not appear to be an intrasexually selected trait in our population.

After reviewing hypotheses regarding the selective basis for sexual dimorphism in primates, Lindenfors (2002: 604) concluded: "the present study leaves selection for male agility as the only factor left to explain strepsirrhine monomorphism in sexually selected species." Our results overlap with this conclusion, although we suggest that further studies are required to determine the specific manner in which sifaka males use locomotion to achieve a reproductive advantage. Do reproductively successful males rely on agility, endurance, speed, and/or jumping power to outcompete their sexual rivals during bouts of arboreal leaping and chasing? Answering this question will shed light as to how our results can be generalized to sexually monomorphic but non-VCL lemurs. The question as to why sifaka males fight at all remains elusive, but suggests simply that fighting is sometimes a successful strategy to pursue. Bouts of fighting can be nested within episodes of chasing, and we show that selection targets traits implicating the latter rather than the former. Fighting may be a successful tactic for displacing sexual rivals, but such displacement does not always guarantee the victor a mating partner (Richard, 1992). A more decisive, albeit ambitious, test of our results would be to follow numerous males during the mating season and develop robust associations between particular behaviors (e.g., number of fights won, frequency of "successful" chases, ratio of chases to fighting, etc.) and reproductive output. Given the pattern of phenotypic selection observed in this study, we would expect to see a strong correlation between chasing behaviors and male fitness.

Sexual monomorphism in sifaka and other gregarious lemurs

Comparative studies on sexual dimorphism in primates have noted the lack of dimorphism in body mass and canine size in lemurs and other strepsirrhines despite conspicuous male-male competition (Kappeler, 1990, 1996; Plavcan et al., 1995; Leigh and Terranova, 1998; Lindenfors and Tullberg, 1998; Plavcan, 2001; Smith and Cheverud, 2002). Numerous socioecological, genetic, and/or environmental factors have been invoked to explain this discordance. We briefly outline them here. They are: 1) genetic correlations between the sexes constrain levels of sexual dimorphism (Kappeler, 1990, 1996; Plavcan, 1998); 2) variance in reproductive success is equal between males and females due to similar selection pressures (van Schaik and Kappeler, 1993; Plavcan et al., 1995); 3) sexual monomorphism is an atavism due to a recent shift in activity pattern in non-nocturnal lemurs (van Schaik and Kappeler, 1993, 1996); 4) various female socio-reproductive strategies operate to reduce male-male conflicts and variation in paternity (e.g., Pereira and Weiss, 1991; Richard, 1992; Pereira and McGlynn 1997); 5) climatic factors linked to resource availability constrain growth parameters in males

(e.g., Ravosa et al., 1993; Leigh and Terranova, 1998; Overdorff et al., 1999; Wright, 1999); and 6) sperm competition precludes positive directional selection on body mass (Pochron and Wright, 2002). This study brings proximate, selection-based data to bear on this subject. We provide a direct explanation that reconciles intrasexual aggression and sexual monomorphism: positive directional selection does not target male body mass or male canine size in our population. Our analysis demonstrates that a sexually monomorphic population can experience substantial intrasexual selective pressures in seemingly non-obvious ways. The degree to which other factors, such as female choice, sperm competition, and ontogeny, overlay and/or further contribute to sexual monomorphism in sifaka and other lemurs requires further study. Clearly female mate preferences can shape male reproductive success in this population (Brockman, 1999), and an integrated study of male and female reproductive strategies will likely reveal the myriad selective forces that create and constrain inter- and intrasexual phenotypic patterns in this population (see Plavcan, 2004).

It is important to emphasize that although positive directional selection does not act on body mass or canine size, this does not preclude the possibility that a strong genetic correlation exists among the sexes for these traits. In this study, we have only measured the strength of intrasexual selection acting on male traits, not how intrasexually selected traits will respond to selection in males and females. The mean phenotypic change for a vector of selected traits (Δz) (i.e., the response to selection) is the product of two factors: a vector of selection gradients ($\boldsymbol{\beta}$) (i.e., the strength of selection) and an additive genetic variance-covariance matrix ($\mathbf{G}$), which governs the transmission of trait values across generations (Fairbairn and Reeve, 2001):

$$\Delta z = \boldsymbol{\beta}\mathbf{G} \qquad (2)$$

As Equation (2) shows, if $\boldsymbol{\beta}$ is negligible or negative—as in the case for body mass and canine size—traits will not respond positively to selection, independent of whether a strong genetic correlation exists between the sexes. If selection pressures shift to positive values and begin to act on male

traits, a strong genetic correlation can greatly extend the time it takes to evolve sexual dimorphism (Lande, 1980, 1987). Therefore, a complete quantitative genetic analysis of sexual dimorphism requires longitudinal information on selection pressures acting on both males and females, as well as an estimation of the genetic correlation between them. To this end, our analysis cannot rule out time-scale effects, as in a disequilibrium hypothesis (see van Schaik and Kappeler, 1996), or that genetic correlations also contribute to the sexual monomorphism we see in the present day Beza Mahafaly population.

Conclusions

Given the overall pattern of selection acting on the five traits described in this study, we conclude that male-male competition is more dependent on traits related to locomotor performance rather than on traits related to fighting ability. If fighting were a major determinant of male fertility, then we would expect to find directional selection targeting body mass and canine size. Instead, directional selection targets leg shape and stabilizing selection acts on body mass and torso shape. Our discussion reveals how positive directional selection enhances locomotor performance by increasing thigh circumference and lengths of leg elements. Biomechanically, this pattern of directional selection translates into greater thigh muscle mass and longer distances over which muscle forces can be applied. Further, we showed that stabilizing selection acting on body mass can be related to energetic and allometric constraints related to leaping behaviors. The most reproductively successful males in our population possess relatively long and muscular legs and an intermediate (i.e., optimum) body mass. These direct measurements of selection reveal how sexual monomorphism in body mass and canine size can be maintained in the population in spite of overt male-male competition.

Acknowledgements

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