



Phenotypic correlates of male reproductive success in western gorillas

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ABSTRACT

Sexual selection is thought to drive the evolution of sexually dimorphic traits that increase male reproductive success. Despite a large degree of sexual dimorphism among haplorhine primates, phenotypic traits that may influence the reproductive success of males are largely unstudied due to long life spans and the difficulties in quantifying such traits non-invasively. Here we employ digital photogrammetry of body length and crest size, as well as ranking of the gluteal muscle size, to test whether these sexually dimorphic traits are associated with long-term measures of male reproductive success in western gorillas. Among 19 adult male gorillas monitored for up to 12.5 years, we found that all three phenotypic traits were positively correlated with the average number of mates per male, but only crest size and gluteal muscle size were significantly correlated with offspring survival and the annual rate of siring offspring that survive to weaning age. We discuss why such sexually dimorphic traits might be under ongoing selection in gorillas and other species.

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Introduction

Sexual dimorphism is generally expected to arise from sexual selection, but it can also arise from other factors such as predation (Darwin, 1871; Andersson, 1994; Plavcan, 2001; Lawler, 2009). Sexual dimorphism is generally considered as evidence that selection has occurred in the past, but it does not indicate whether selection for the dimorphic traits is continuing (Grafen, 1988). Instead, researchers typically test for ongoing selection by examining whether males with more extreme dimorphic traits have higher reproductive success. One of the most comprehensive measures of fitness, lifetime reproductive success, can be expressed as the product of the number of mates per male (N_{MATE}), the fertility of those mates, offspring survival, and longevity (Brown, 1988; Clutton-Brock, 1988). Separate analyses of each component can provide insights into the mechanisms of ongoing selection (reviewed in Breuer et al., 2010).

Examination of morphological and behavioral features of the living great apes and other primates can provide insights into the socioecology, group structure, and social behavior of our ancestors (Plavcan and van Schaik, 1997; Stanford, 2006). Unfortunately, studies of ongoing selection in wild primates have been constrained by the long time needed to collect sufficient demographic

data, difficulties in observing a sufficient number of individuals, and the technical challenges in measuring phenotypic traits (but see for example, Boinski, 1987; Bercovitch, 1989; Lawler et al., 2005; Setchell, 2005; Caillaud et al., 2008; Leigh et al., 2008).

This paper presents evidence of ongoing selection with three sexually dimorphic traits in male western gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, a large swampy forest clearing in the Nouabalé-Ndoki National Park of the Republic of Congo. Western gorillas maintain year-round associations in groups that typically contain one adult male (silverback), an average of three to four adult females, and their immature offspring (Parnell, 2002b; Gatti et al., 2004; Breuer et al., 2010). Subordinate males typically emigrate to become solitary before reaching full maturity (Parnell, 2002b; Stokes et al., 2003; Robbins et al., 2004). While short-term assessments of the social structure have shown that up to 45% of silverbacks are living alone or in non-breeding groups with other males, longer-term measurements suggest that more than 80% of them may eventually acquire females (Parnell, 2002b; Gatti et al., 2004; Breuer et al., 2010), stressing the need for long-term studies to understand the factors influencing male reproductive success. Encounters between adult male gorillas are often limited to threat displays, but they occasionally lead to fatal fights (Watts, 1989; Sicotte, 1993; Robbins, 2003; Levrero et al., 2004; Jeffery et al., 2007; Caillaud et al., 2008). Female dispersal between social units is considered an example of mate choice (Sicotte, 2001; Manson, 2007) and the resident silverback may restrict the transfers of his females through coercion and herding (Sicotte, 1993;

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Parnell, 2002a; Levrero et al., 2004; Robbins et al., 2009). Infanticide by outsider males is considered an extreme form of coercion because it may induce the female to leave the resident silverback who failed to defend her offspring (Fossey, 1984; Watts, 1989). Offspring survival has accounted for more than 50% of the variance in reproductive success among harem holders at Mbeli Bai, so it may be an important variable to consider when examining factors that are potentially influencing selection in this species (Breuer et al., 2010).

Gorillas are among the most sexually dimorphic primates, with silverbacks having twice the total body mass, 20% greater body length, and larger gluteal muscles than adult females (Smith and Jungers, 1997; Breuer et al., 2007). Silverbacks also possess a large pad of fibrous adipose tissue on top of their head, as well as large temporal and nuchal muscles attached to a median sagittal crest and occipital bone crest, so aspects of the head morphology are larger in males than in females (Straus, 1942; Gregory, 1950; Dixson, 1998). In this study, the term ‘crest’ refers to a composite measure of head morphology that may partially reflect the size of both the sagittal crest and the adipose tissue (Fig. 1; Breuer et al., 2007; Caillaud et al., 2008). Our observation methods did not provide a measurement of body mass, but we look for correlations between male reproductive success versus body length, gluteal muscle size, and crest size.

The three measures of reproductive success in this study are N_{MATE} , offspring survival, and the rate of siring offspring that survive to reach weaning age. The siring rate equals the product of N_{MATE} , female fecundity, and offspring survival. N_{MATE} and offspring survival have been major sources of variance in the siring rate (Breuer et al., 2010), whereas female fecundity was relatively unimportant and so is excluded from this study (except for its contribution to the siring rate). When the siring rate is multiplied by adult lifespan, the product equals lifetime reproductive success. Thus the siring rate can help to show how variance in N_{MATE} and offspring survival will affect lifetime reproductive success and ongoing selection. This study was too short to observe the full lifespan of most adults, but we present sensitivity studies to investigate whether any correlations between morphology and reproductive success were influenced by changes in those variables during the observed portions of adulthood. We discuss those correlations within the context of other studies about how such morphological traits may influence male reproductive success in gorillas and other species.

Methods

Study site and population

The study was conducted at Mbeli Bai, a 12.9 ha forest clearing where gorillas come to feed in the south-west of the Nouabalé-Ndoki National Park, Republic of Congo. The gorillas were observed by using telescopes from a 9 m high observation platform overlooking the bai. This study is based on demographic data from February 1995 until July 2007, with an absence from the clearing for two months in 1997 due to civil unrest in the country (Breuer, 2008).

Gorillas groups visit the bai an average of twice per month, so we had to estimate the dates of birth, death, and dispersal for most individuals. Some gorillas have been observed within one to two days after their birth, as confirmed because their group had just been seen without them. When gorillas were first observed beyond that age, their birthdates were estimated by comparing their morphological and behavioral characteristics with other gorillas whose ages were already determined (Parnell, 2002a; Nowell, 2005; Breuer et al., 2009). We believe the precision of those

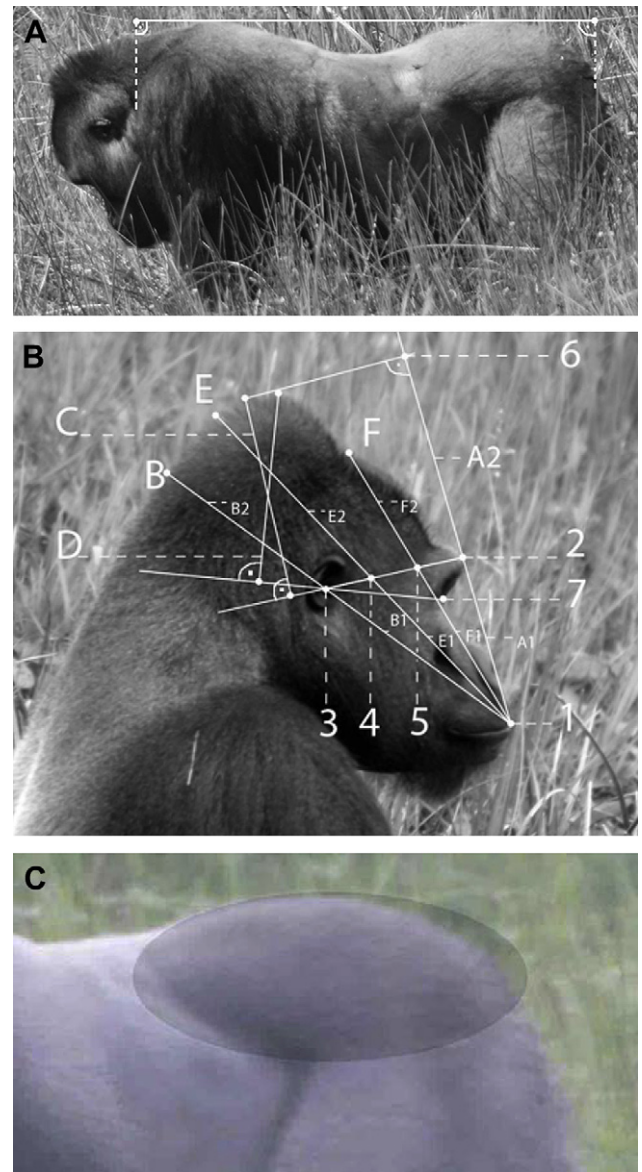


Figure 1. Typical photographs used for assessing for body length (A), crest size (B), and gluteal musculature (C). Based on Spearman rank correlations (ρ), the principal component used for crest size in this study was most highly correlated with measurements ‘E2’ ($\rho = 0.98$) and ‘C’ ($\rho = 0.92$), and it was not highly correlated ($\rho < 0.3$) with measurements such as A1, B1, E1, and F1 (Breuer et al., 2007). In Fig. 1c, the highlighted area in the photo shows the approximate location of the gluteal muscles.

birthdates is within a few weeks for most gorillas who were first observed as infants, and within one to two years for gorillas who were first observed as they approached adulthood. Adulthood was defined to begin at age 10 for females and 18 for males, which is when they began to reproduce. All adult males were fully grown in body size and in the full development of secondary sexual traits such as their silver saddle, sagittal crest, and long arm hair (Breuer et al., 2009).

Dispersal dates were typically determined as the midpoint between visits of the group of origin and the group of destination (Stokes et al., 2003). Dates of death were typically determined as the midpoint between the last time an individual was observed and the first time that the group was seen without him/her. It is unlikely that unweaned infants (<four years) could survive without their mothers (Nowell and Fletcher, 2007; Breuer et al., 2009), so if they

disappeared before that age, we assumed that they had died. Due to the intermittent observations, we might have missed a few infants who were born and died before we saw them.

Measures of reproductive success

Our first measure of reproductive success was the average number of adult females that were with each male throughout his observed years of adulthood (N_{MATE}). For example, if an adult male had no females for two years, and three females for four years, he would have a total of $3 \times 4 = 12$ female-years during six years of observation, for an average value of $12/6 = 2$ adult females.

Our second measure of reproductive success for breeding males was the proportion of offspring born in their group that survived to reach weaning age (four years). Studies of reproductive success often consider offspring survival until their age of first reproduction (Brown, 1988; Strassmann and Gillespie, 2003), but the weaning age should be a reasonable approximation for this study because subsequent mortality until the age of first reproduction is presumed to be minimal, as has been observed for mountain gorillas (Robbins et al., 2011). All analyses involving infant survival were limited to dates in which it could be fully evaluated (i.e., we excluded infants born during the last four years of the study). For example, if four offspring were born in the group of a silverback before July 2003, and three of them survived to reach age four, then his offspring survival would be $3/4 = 75\%$.

Our third measure of reproductive success for each male was his rate of siring offspring that survived to reach weaning age (siring rate). For example, if a male was observed for five years before July 2003 (thus excluding the last four years of the study), and three of the offspring that were born in his group during those years survived to reach age four, his rate of siring offspring that survived to reach age four would be $3/5 = 0.60$ surviving offspring per year.

Morphological measurements

We applied non-invasive digital photogrammetry to measure the body length and crest size of silverbacks (Breuer et al., 2007). We took digital photos of silverbacks from the observation platform and measured the distance of the silverbacks to the camera with a laser range finder. We conducted measurements of pixel length in digital photos with the measure tool in Adobe PhotoShop® CS and calculated a scale factor to convert pixel length to real length. Body length was measured along a tangent of the rump as the distance between the most protruding tip of the shoulder (acromion landmark) and the most caudal tip of the buttock (Fig. 1A; Breuer et al., 2007). Crest size was calculated as the first component of a principal component analysis based on six linear head size measures (Fig. 1B). The crest measurements include soft tissues and hair (similar to how rivals or mates would judge its size). Measurements, such as surface area or perimeter (of torso) have proven to highly correlate with body mass in other species (McFadden et al., 2006), but were impossible to measure in this study due to deviations in body positioning and difficulties in finding appropriate landmarks.

We used qualitative comparisons to rank silverbacks according to the relative size of their gluteal musculature (Caillaud et al., 2008). The comparisons were based on digital photographs taken while the silverback was standing perpendicular to the camera–gorilla axis. The photographs were scaled to make the body lengths of the silverbacks seem identical (so we are essentially evaluating gluteal size relative to body length). Then the photographs were trimmed so body parts other than the gluteal muscle were not visible (Fig. 1C). We presented pairs of photographs to two judges and asked them to select the silverback with the larger

musculature ($n = 18$ silverbacks; 153 pairwise comparisons per trial, two trials per judge). Judges also could score that there was no difference in size. One of the judges was the first author; the other was familiar with the anatomy of gorillas but had no prior knowledge of these study animals. We counted the number of times a silverback was assigned to have the larger musculature and averaged these score from the two trials to calculate an average score for each judge. Since these scores were highly correlated between the two trials and the two judges (minimum Spearman Rank correlation: $r_s = 0.706$, all $p < 0.001$, $n = 18$ silverbacks), we calculated an overall average of the scores from both judges, which was used as a relative measure called the gluteal muscle size.

Analyses

We used exact non-parametric Spearman rank correlation (r_s) (Mundry and Fischer, 1998) of the three morphological variables with our three measures of male reproductive success. We subsequently applied Fisher's omnibus test to take multiple testing into account (all $p < 0.01$). This procedure combines a number of p -values into a single χ^2 -distributed variable with its degrees of freedom equaling twice the number of p -values (Haccou and Meelis, 1992). Tests of Spearman rank correlation (r_s) were done using a macro in Microsoft Excel written by R. Mundry and were either exact ($n \leq 9$) or based on 10,000 permutations.

We ran three sets of sensitivity analyses to investigate whether the correlations between morphology and reproductive success were influenced by changes in those variables throughout the adulthood of each male. First, we re-ran the Spearman rank correlations while excluding four males that were known to be relatively young adults because they had already been observed before reaching adulthood. Second, we re-ran the correlations while including only the nine males that were monitored for more than ten years of adulthood, which was assumed to represent a substantial portion of their entire reproductive careers. Thirdly, we re-tested the correlations for N_{MATE} while including only data from January 2004 to July 2007, which is when all morphological traits were measured. The third set of sensitivity analyses excluded offspring survival and the siring rate because we could not fully evaluate those variables during the last four years of the study.

Results

The 19 silverbacks in this study were observed for an average of 8.6 ± 3.6 SD years (range = 1.3–12.4 years). The number of adult females per adult male averaged 2.4 ± 2.1 (Table 1). Sixteen out of nineteen adult males (84%) were harem holders during this study, and the maximum number of adult females a silverback had at one time was eleven. Offspring survival per male ranged from 0% to 80%, and the siring rate varied from 0.0 to 1.3 surviving offspring per male-year. All three measures of reproductive success showed significant positive inter-correlations, but none of the morphological traits were significantly correlated with each other (Table 2).

Table 1

Summary statistics for the three measures of reproductive success: the average number of adult females for each adult male (N_{MATE}), their offspring survival to age four, and the rate of siring offspring that survived to reach age four.

	N_{MATE}	Offspring survival	Siring rate
Mean	2.39	0.39	0.32
Stdev	2.11	0.29	0.46
Min	0.00	0.00	0.00
Max	6.28	0.80	1.33
Median	2.51	0.43	0.00
n	19.00	11.00	17.00

Table 2

Spearman rank correlations (Rho) among the measures of reproductive success and among the phenotypic traits, along with the sample sizes (n) and p-values (p).

Variable 1	Variable 2	n	Rho	p
Crest size	Body length	17	0.368	0.149
Gluteal size	Body length	18	0.192	0.442
Crest size	Gluteus size	17	0.420	0.089
N_{MATE}	Offspring survival	11	0.890	<0.001
N_{MATE}	Siring rate	17	0.827	<0.001
Offspring survival	Siring rate	11	0.981	<0.001

The Spearman rank correlations consistently showed significantly higher reproductive success for males with larger crests (Table 3). Thus males with larger crests had higher siring rates not only because they had more females (Fig. 2A), but also because those females had higher offspring survival. Results were similar for males with larger gluteal muscles (Fig. 2B). Males with longer bodies had significantly more females, but results for offspring survival and siring rates were not significant.

The Spearman rank correlations between phenotypic traits and reproductive success remained similar when the analyses were limited to males who were observed for at least ten years of adulthood, and when we excluded younger adults who had been observed before reaching full maturity (triangles and circles in Fig. 3). The correlations between phenotypic traits and N_{MATE} also remained similar when we used only data from January 2004 to July 2007, which is when all morphological traits were measured (asterisks in Fig. 3). Thus, despite the possibility that crest size and gluteus muscle size can potentially decline with age, we found no evidence that this impacted our results on phenotypic selection, which leads us to conclude that age had a weaker effect on morphology than variation between adult individuals.

Discussion

This study found several statistically significant correlations among three morphological traits of male western gorillas and components of their reproductive success. Our measures of crest size, body length, and gluteal musculature all showed significant positive correlations with the number of mates per male (N_{MATE}). Those results are consistent with studies of other sexually dimorphic mammals in which larger body size and/or weaponry provides an advantage in male–male competition (e.g., Haley et al., 1994; Setchell et al., 2006; Leigh et al., 2008; Bergeron et al., 2010). Gluteal musculature is associated with locomotor performance such as speed, acceleration, manoeuvrability, and strength; which could be important when silverbacks chase, lunge at each other, or fight (Sigmon, 1974; Stern and Susman, 1981; Kimura, 1992; Demes

Table 3

Spearman correlations (Rho) between each trait versus each measure of reproductive success.

Trait	Reproductive	Spearman Correlations		
	Success	n	Rho	p
Crest size	N_{MATE}	18	0.64	0.004
Crest size	Offspring survival	10	0.75	0.017
Crest size	Siring rate	16	0.58	0.019
Body length	N_{MATE}	18	0.51	0.031
Body length	Offspring survival	10	0.10	0.780
Body length	Siring rate	16	0.35	0.178
Gluteal size	N_{MATE}	18	0.61	0.009
Gluteal size	Offspring survival	10	0.67	0.039
Gluteal size	Siring rate	16	0.50	0.050

Sample sizes (n) and p-values (p) for each analysis.

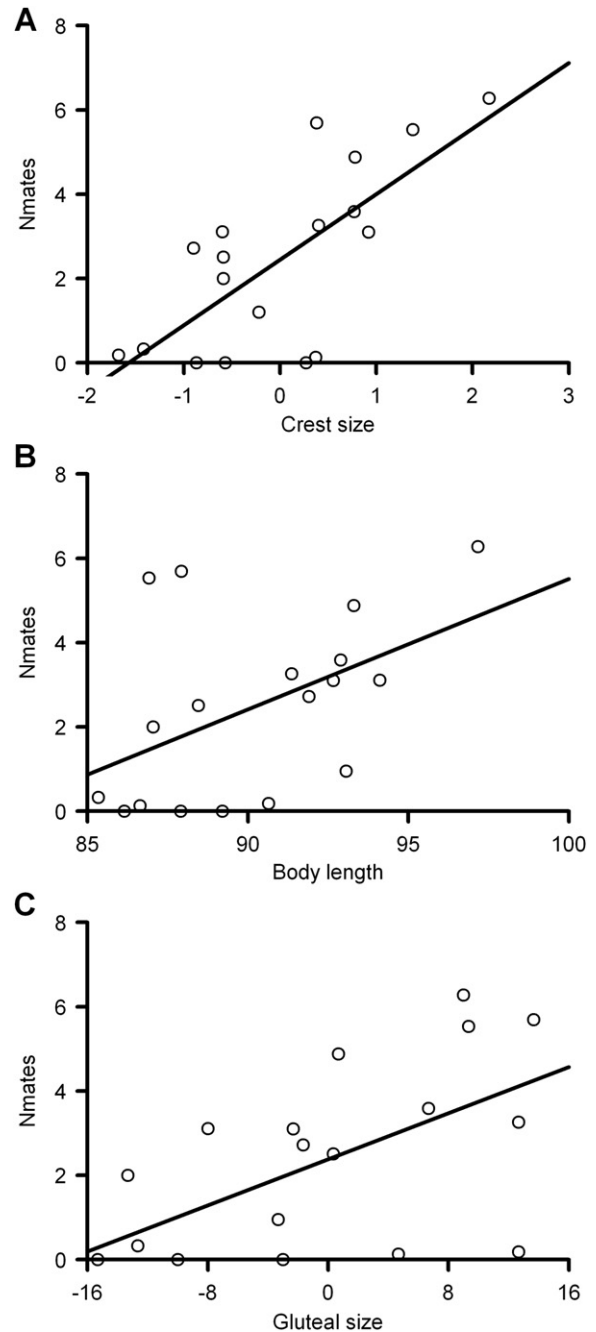


Figure 2. Relationship between the average number of mates per male and crest size (A), body length (B), and gluteal musculature (C). The lines show the best fit of the data by linear regression.

et al., 1994; Lieberman et al., 2006). Longer bodies can be advantageous in species in which males fight by pushing or bipedally (McElligott et al., 2001; Kruuk et al., 2002; Preston et al., 2003). The sagittal crest is associated with biting strength and the adipose tissue has been considered an indicator of overall health status (Parnell, 2002a; Breuer, 2008; Caillaud et al., 2008). The traits that we measured are highly visible, so if they correlate with fighting ability, then they could also be used as ‘status signals’ or ‘badges’ (Guthrie, 1970; Rohwer, 1975; Maynard Smith and Harper, 2003; Wilson et al., 2007). The displays that silverbacks direct toward rivals are also performed toward females, so the sexually dimorphic traits that they highlight may be subject to intersexual selection via

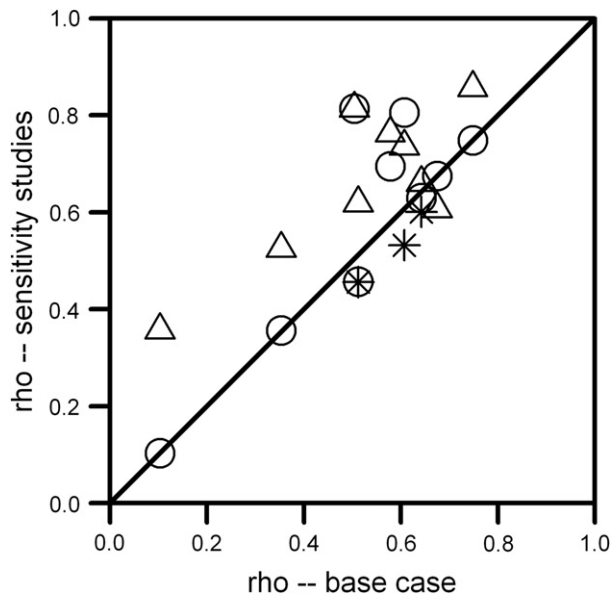


Figure 3. Spearman rank correlation coefficients between phenotypic traits versus reproductive success for the full database (x-axis) and for data subsets (y-axis). The data subsets were; males who were observed for at least ten years of adulthood (triangles); the subset excluding younger adults who had been observed before reaching full maturity (circles) and; the subset including only data from January 2004 to July 2007, which is when all morphological traits were measured (asterisks). Data points above the diagonal line ($y = x$) represent correlations that improved when we focused on a more narrow portion of the database.

female choice (Parnell, 2002a; Robbins, 2003, 2009) and enable him to influence female mating patterns through coercion (Clutton-Brock and Parker, 1995; Muller and Wrangham, 2009; Pradhan and van Schaik, 2009). The relative importance of each type of sexual selection may be difficult to distinguish (Clutton-Brock and McAuliffe, 2009; Hunt et al., 2009).

Our results differ slightly from a study of western gorillas at Lokoué Bai in the Odzala-Kokoua National Park, where harem holders had longer bodies and larger gluteal muscles than non-harem holders, while crest size was mainly related to the number of females belonging to harem holders (Caillaud et al., 2008). In contrast, our study found significant correlations for each trait among all males, which suggests that the same traits which enable a silverback to acquire his first female will also help him to acquire and retain additional females. The contrasting results may arise from our longer-term perspective on whether males were harem holders (longitudinal values of N_{MATE} throughout our 12.5 years of observations, versus ‘snapshot’ values on the date that each trait was measured at Lokoué). The two studies also differed in statistical methodology, and in the way traits were defined and measured, and possibly in the estimated age when males were considered adults. Sample sizes were relatively small in each study (Kingsolver et al., 2001), so meta-analyses of multiple studies may ultimately provide the most rigorous evaluations of ongoing selection in this species.

Offspring survival was significantly higher for males with larger crest size and gluteal muscles, but the results for body length were not significant. Protection against predation and infanticide are considered major influences upon the socioecology of primates, and adult males routinely provide the first line of defense for gorillas (Wrangham, 1980; Fossey, 1984; Stewart and Harcourt, 1987; van Schaik, 1989; Watts, 1989, 2000; Fay et al., 1995; Sterck et al., 1997; Sicotte, 2000; Stokes et al., 2003; Harcourt and Stewart, 2007; Robbins et al., 2007, 2009). From that perspective,

it seems plausible that crest size and gluteal musculature might be correlated with the ability of each male to provide such protection.

Traits that were significantly correlated with both N_{MATE} and offspring survival showed similar correlations with the siring rate. These results are not surprising because the siring rate equals the product of N_{MATE} , female fecundity and offspring survival and because female fecundity shows little variation among silverbacks (Breuer et al., 2010). In addition, our sensitivity studies gave no indication that correlations between morphology and reproductive success were influenced by changes in those variables throughout the adulthood of each male (Fig. 3). Preliminary results suggest that silverbacks with higher siring rates will have longer adult life spans (Breuer et al., 2010), so we expect that traits that were significantly correlated with the siring rate (crest size and gluteal size) will also show significant correlations with lifetime reproductive success.

The correlations between morphological traits and male reproductive success in this study may be considered evidence of ongoing selection, but they do not represent proof of selection. Selection is not a matter of finding correlations between fitness and phenotypes but a matter of understanding how particular phenotypes causally contribute to fitness (e.g., Rice, 2004). We have put forth functional arguments that connect traits to fitness measures, however, our arguments would be enhanced by additional biomechanical, behavioral, and kinematic studies. In addition, the heritable basis of the traits in this study should be determined as phenotype–fitness correlations will not produce any evolutionary change across generations if the traits are not heritable (Pettay et al., 2005; Wilson et al., 2006). Even when traits are heritable, it is possible to have a minimal evolutionary response if selection acts on the environmental variance in phenotypes or the environment deteriorates across generations (Rauscher, 1992; Kruuk et al., 2002; Ozygul et al., 2009). Clearly, more studies are needed to determine the phenotypic correlates of fitness in western gorillas and other long-lived species.

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