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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.

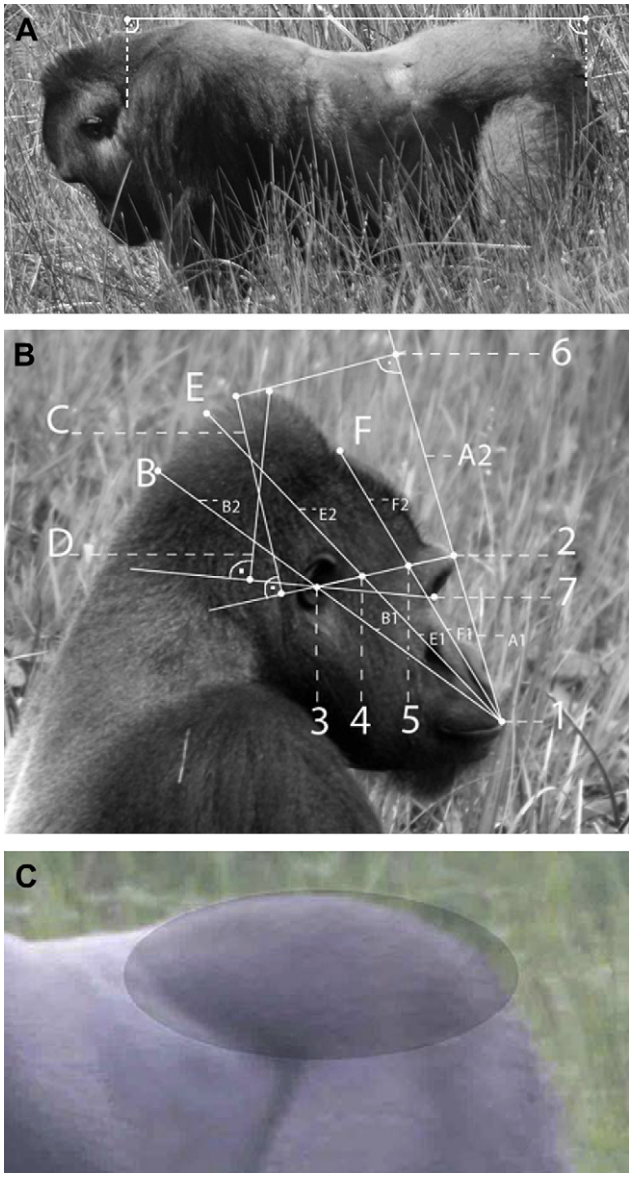

Figure 1. Typical photographs used for assessing for body length (A), crest size (B), and gluteal musculature (C). Based on Spearman rank correlations (rho), the principal component used for crest size in this study was most highly correlated with measurements 'E2' (rho = 0.98) and 'C' (rho = 0.92), 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.

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 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

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