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Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*)

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Abstract

Sexual selection theory explains the evolution of exaggerated male morphologies and weaponry, but the fitness consequences of developmental and age-related changes in these features remain poorly understood. This long-term study of mandrill monkeys (*Mandrillus sphinx*) demonstrates how age-related changes in canine tooth weaponry and adult canine size correlate closely with male lifetime reproductive success. Combining long-term demographic and morphometric data reveals that male fitness covaries simply and directly with canine ontogeny, adult maximum size, and wear. However, fitness is largely independent of other somatometrics. Male mandrills sire offspring almost exclusively when their canines exceed approximately 30 mm, or two-thirds of average adult value (45 mm). Moreover, sires have larger canines than non-sires. The tooth diminishes through wear as animals age, corresponding with, and perhaps influencing, reproductive senescence. These factors combine to constrain male reproductive opportunities to a brief timespan, defined by the period of maximum canine length. Sexually-selected weaponry, especially when it is nonrenewable like the primate canine tooth, is intimately tied to the male life course. Our analyses of this extremely dimorphic species indicate that sexual selection is closely intertwined with growth, development, and aging, pointing to new directions for sexual selection theory. Moreover, the primate canine tooth has potential as a simple mammalian system for testing genetically-based models of aging. Finally, the tooth may record details of life histories in fossil primates, especially when sexual selection has played a role in the evolution of dimorphism.

Keywords: Male reproductive success; Male life history; Tooth development

Introduction

Darwin eloquently solved the evolutionary problem of exaggerated sex-biased characters, determining that reproductive advantages, garnered either through intrasexual competition or by mate preferences, could explain seemingly maladaptive secondary sexual characteristics (Darwin, 1871). Sexual selection can account for variability in both fitness and morphology throughout the animal kingdom by controlling weaponry evolution in complex ways (Darwin, 1871; Andersson, 1994; Plavcan, 2001; Kruuk et al., 2002; Robinson et al., 2006). Among dimorphic primates, canine teeth are among the most obvious products of sexual selection, primarily functioning as formidable weapons of intermale sexual competition (Plavcan and van Schaik, 1992; Plavcan, 2001). Unfortunately, previously intractable problems have precluded population-based analyses of exactly how sexual selection operates in these species. Consequently, explanations of primate sexual dimorphism and sexual selection have relied on broad-

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scale interspecific correlational analyses (Ralls, 1977; Kay et al., 1988; Plavcan and van Schaik, 1992; Plavcan, 1993, 2001; Leigh, 1995) mainly because calibrating primate fitness necessitates several distinct and rare forms of data (King et al., 2005; Lawler et al., 2005). Most importantly, male fitness estimates require connecting paternity data with demographic information collected on the timescale of decades (Buchan et al., 2003; Charmantier and Sheldon, 2006). Fitness measures must then be merged with morphological ontogenetic measurements of male weaponry. Myriad obstacles hinder primate sexual selection studies, not the least of which include promiscuous mating, sex-biased dispersal, protracted ontogenies, long lifespans, comparatively high male mortality, adverse field conditions, and the near-impossibility of experimentation (Plavcan, 2001; Setchell and Dixson, 2001a; Charpentier et al., 2005a).

We surmount many of these problems by analyzing male fitness and canine weaponry across the life course in one of the most dimorphic terrestrial mammals, the mandrill (*Mandrillus sphinx*; Plavcan, 2001; Setchell and Dixson, 2001a; Charpentier et al., 2005a; Fig. 1). We test hypotheses about relations between male fitness and canine weaponry using long-term data from a semi-captive, provisioned mandrill colony (Wickings, 1995). The main hypothesis tested is that canine tooth eruption and wear directly correlate with male mandrill fitness through the allocation of reproductive effort during the lifespan. More specifically, we evaluate the hypotheses that canine tooth ontogeny, adult canine size, and measures of body size relate directly to measures of fitness. To test these hypotheses, we articulate morphometric measures with two kinds of fitness indicators. First, we estimate reproductive values for the group of males that sired offspring (v_x), a parameter interpreted as a measure of the genetic contribution of each age class to future generations (Fisher, 1930) by measuring how many total offspring an animal may "expect" at a given age (Newton and Rothery, 1997). We hypothesize that reproductive values for sires reach maximum values when canine length is maximized. Second, we employ a direct measure of fitness for each male to determine how morphology (especially canine size) correlates with reproductive achievements of individual males. For this we calculate λ_i, a rate-sensitive measure of individual reproductive output for each sire (Sade, 1990; Brommer, 2004). Overall, we expect that canine eruption and wear affect fitness through impacts on life history scheduling, indicating that canine tooth morphology, especially its ontogenetic trajectory, plays a major role in male fitness. Thus, we hypothesize that elevated fitness in animals with large canines ultimately accounts for the high level of canine tooth size dimorphism in the species.

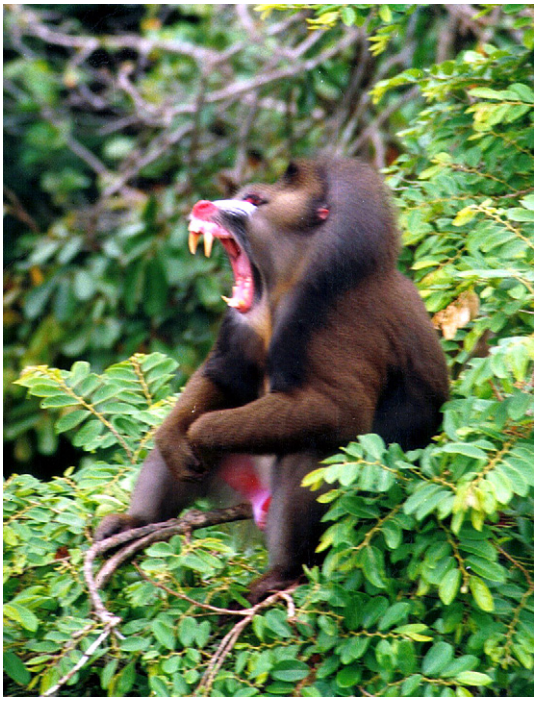

Fig. 1. Canine display or "yawn" by study animal MD12E, ultimately an alpha male. Photograph by J.M. Setchell.

Analyses of fitness in mandrills have important theoretical repercussions beyond primates. Most importantly, our results have implications for refining sexual selection theories by showing that these theories must incorporate life history parameters to understand population-level processes. In addition, our analyses of the canine tooth strongly suggest that different types of weapons have various consequences for sexual selection. Previous analyses of male fitness in large-bodied terrestrial mammals have focused on species with renewable weaponry (e.g., horns, antlers, and body mass), unlike the non-renewable canine tooth of primates. Furthermore, our analytical techniques contribute to resolution of longstanding controversies regarding different measures of fitness (Fisher, 1930; Grafen, 2006), and have important implications for approaches to aging (see Charmantier et al., 2006). Finally, ties between the attributes of the canine tooth and fitness may provide direct insights into demographic parameters of fossil species.

Materials and methods

Mandrill biology

Mandrills (*Mandrillus sphinx*, Cercopithecoidea) are large-bodied, terrestrial monkeys, indigenous to the rainforests of Central Africa (Gabon, Cameroon, Republic of Congo, and Equatorial Guinea; Grubb, 1973), and listed as "vulnerable" by the IUCN. Stable matrilines form the core of groups, but males become solitary during adolescence (Setchell and Dixson, 2002). Groups ranging from 50 to 600 individuals have been recorded in the wild (Rogers et al., 1999; Abernethy et al., 2002). Mandrills are the most dimorphic of all primate species: males reach about 31 kg, or are about 3.4 times the size of females (Setchell et al., 2001). Full-sized male canine teeth (~45 mm) greatly exceed those of females (~10 mm; Darwin, 1871; Leigh et al., 2005). Darwin (1871) himself extensively discussed sexual dimorphism in mandrill coloration and canine weaponry.