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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 nonsires. 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.

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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.

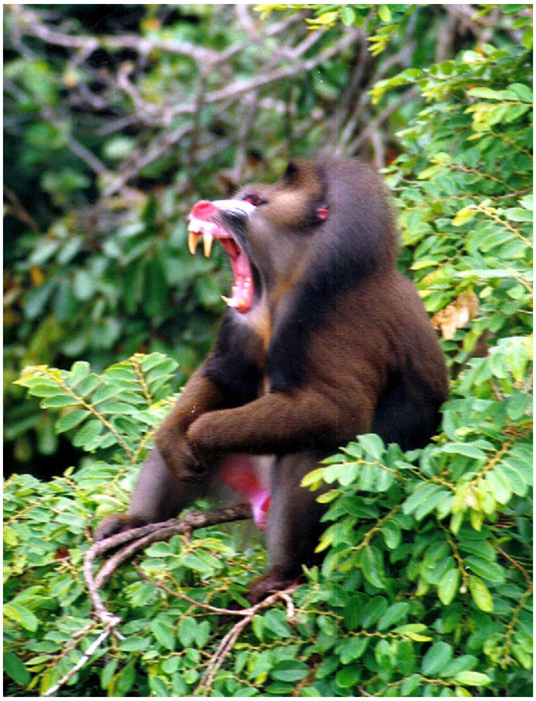

Fig. 1. Canine display or "yawn" by study animal MD12E, ultimately an alpha male. Photograph by J.M. Setchell.

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 nonrenewable 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.

Samples

The Centre International de Recherches Médicales de Franceville, Gabon (CIRMF) maintains the mandrills analyzed for this study as a research colony. The colony was founded with 15 monkeys in 1983, and has grown to over 200 individuals. The CIRMF currently maintains and provisions them as a breeding colony in semi-natural conditions. Animals occupy two enclosed rainforest tracts: E1 (6 ha) and E2 (3.5 ha). DNA samples were available for the founders and 205 of the 231 animals born into the enclosures up to 2002 (Charpentier et al., 2005a). A total of 172 births could be attributed to sires for this study. Offspring sex was known for all animals, except for six neonates, of which we treated four (randomly selected) as males in order to bring the dead infant sex ratio to 1:1 (a biased sex ratio would have no appreciable consequences for our analysis). Birthdates were known for colony animals, giving exact age for calculating conception date (gestation = 175 days).

Females in this colony reach maturity at 4–5 years of age, normally giving birth yearly thereafter (Setchell et al., 2005). The oldest females in the colony now exceed 25 years of age. Males are capable of siring by the time they reach four years of age (Setchell et al., 2005), and the longest-lived males in the sample passed their nineteenth birthdays, nearly reaching their twentieth. Consequently, the potential time period at which males "risk" siring theoretically spans about sixteen years. Reproductive output could be allocated throughout this period.

A total of 63 males (16 sires) exceeding four years of age were available for demographic analyses, but only 38 males (11 sires) could be accessed for morphometric analyses. Morphometrics from this subset were gathered during routine physical examinations, following approved CIRMF protocols. We analyzed canine height (buccal-gingival margin to tip, nearest 1 mm), mass (nearest 100 g), and crown-rump length (nearest 5 mm). Many of these data are repeated measures, but we analyzed the data cross-sectionally in order to assess population-wide patterns of ontogeny. Several analyses focused on "prime" aged males (9–12 yrs). Previous presentations of these canine data included a few erroneous datapoints (Leigh et al., 2005) that have been corrected in the present study (and do not alter previous inferences). We compared alpha or top-ranking males with other males to address possible effects of status on fitness. Social mobility among male mandrills made relative social rank in mandrills difficult to measure, but alpha status was unambiguous. Demographic data were assembled from colony maintenance records. Although data were collected under semi-natural conditions, there are no reasons to assume that these conditions alter normal processes of sexual selection, and, in fact, such circumstances may ameliorate demographic effects of short-term environmental fluctuations on morphology-fitness covariation. We excluded one colony animal not influenced by sexual selection because of management practices. Previous research exhaustively discussed limitations of sexual selection studies on this colony (Wickings, 1995; Setchell and Dixson, 2001a; Setchell et al., 2001, 2005; Charpentier et al., 2005a,b).

Despite strong evidence that sexual selection pervasively affects mandrills, it should be noted that a numerous fitness components can impact the evolution of male morphology. The lack of experimental control forces us to make the relatively safe assumption that sexual selection (i.e., differences in mate acquisition) is primary among these factors. Furthermore, we are unable to fully disentangle the effects of mate choice and intermale competition in our analyses (Setchell, 2005). Male teeth play obvious roles in intermale aggression, but they probably also play a role in attracting females. Finally, we cannot completely rule out life history correlates of tooth wear on other teeth (see King et al., 2005). However, female canine size remains stable once it is fully erupted, and does not appear to covary with lifetime changes in reproductive output. This suggests that males and females differ in the degree to which the tooth relates to life history, implying stronger correlations between canine form and life history in males than in females.

Paternity analyses

Wickings and colleagues reported procedures for DNA extraction and analyses (Wickings, 1995; Charpentier et al., 2005a). A total of eight human microsatellite loci were used for paternity analysis, with other loci used in specific circumstances (Charpentier et al., 2005a). All potential sires were genotyped. Pedigrees were constructed with CERVUS software (Kalinowski et al., 2007), and some assignments were cross-checked with PARENTE software (Cercueil et al., 2002; Charpentier et al., 2005a).

Demographic parameters

Our demographic analyses rely on estimates of the intrinsic rate of increase (r). These estimates are designed to assess population growth, and are usually used to infer fitness differences among populations. However, we test hypotheses about individual fitness based on an adaptation of population-based measures of the intrinsic rate of increase, described by Sade and others (Lenski and Service, 1982; Sade, 1990). The intrinsic rate of increase is estimated from a discrete-time version of the Euler-Lotka equation, calculated through standard life table methods (Stearns, 1992):

$$1 = \sum_{x=0}^{\omega} \mathrm{e}^{-rx} l_x m_x \tag{1}$$

Here, x is age, ω is age at death, l_x is probability of surviving from birth to age x, and m_x is the expected number of conceptions at age x. For comparisons between groups, we estimate l_x from Kaplan-Meier survivorship curves calculated from both sires and nonsires (not shown). Our estimates of m_x do not account for offspring sex ratio as an analytical convenience. Measuring only female births is standard in most analyses of population dynamics (Stearns, 1992) but our objectives do not involve population projections. Therefore, our analyses return higher values for r (and reproductive values) than standard analyses (Alberts and Altmann, 2003).

We employ two kinds of life tables to calculate population-level and individual parameters. First, we calculate vital rates for the entire or aggregate population of sires, based on data grouped by age intervals, as is standard in demographic analyses. Second, we estimate a life table for each individual sire, where $l_x = 1$ until death to estimate "individual r" (Sade, 1990). We then calculate r estimates for both aggregate and individual life tables by satisfying the Euler-Lotka equation, iteratively solving for r with "Goal Seek" tools in Microsoft Excel (Microsoft Corp., 2004). Next, we transform individual r values to λ_i, where $\lambda_i = e^r$. In other words, we calculate the intrinsic rate of increase for the male sample (r), as well as a value of r for each individual male (Sade, 1990). Individual r, or r_i, provides a measure of fitness that can be assessed against morphometric variables for each individual. Measures of individual fitness are desirable because they enable close-grained analyses of how morphologies and behaviors relate to fitness (Sade, 1990). Thus, we expect that individual r values will covary with morphometric variables. It should be noted that analyses of individual fitness also may be heavily influenced by random factors that affect fitness (McGraw and Caswell, 1996).

Investigations of correlations between fitness and morphology are based on estimates of reproductive value (v_x) for the sample of sires. This value calibrates the contribution of an age class to future population growth (Fisher, 1958; Crow, 2002). Reproductive value (v_x) requires calculation of r for the sample of sires (Fisher, 1930). Thus, v_x measures the relative contribution of an age group to population growth (Fisher, 1930; Goodman, 1982; Stearns, 1992; Crow, 2002), where:

$$v_x = \frac{e^{rx}}{l_x}\sum_{x=0}^{\omega} e^{-rx} l_x m_x \tag{2}$$

We interpret the measure as an indication of the degree to which males with a particular morphology impact future population growth. Fisher interpreted v_x as an estimator of the intensity of selection, but such an interpretation remains controversial even today. Finally, we plot number of conceptions against age (m_x), predicting a correspondence between this simple measure of reproduction and canine size. We expect that number of conceptions will provide a rough approximation of fitness and evaluate its performance as such. Finally we measured "relative" values of predicted canine size, reproductive value, and number of conceptions by dividing observed values for these variables by predicted maximum adult size for canines and maximum values for both reproductive value and conception number.

Morphometric and demographic analyses

Hypotheses that associate morphology and fitness require a combination of morphometric and demographic data. First, we expect that conception number and reproductive output show distinct peaks in males, and are not simply distributed evenly across their reproductive lifespan. Second, maximum canine size and body dimensions should correspond with peak reproductive value, reflecting positive correlations with male reproductive parameters and fitness. Third, we expect that a simple count of conceptions will show correlations with morphological variables. Overall, we predict that animals with larger canines and bodies will have higher fitness than animals with smaller canines and bodies, reflecting fitness benefits to larger size. We interpret these correlations as reflecting sexually-selected advantages to big canines, although other fitness components may also play a role in canine size.

In order to test these expectations, we calculated cross-sectional growth curves for canine tooth height using nonparametric distance weighted least-squares (dwls) regression [following procedures similar to Leigh et al. (2005)]. Furthermore, we analyzed correlations between morphology and fitness first by comparing sires ($\lambda_i > 1$; $r_i > 0$) with nonsires ($\lambda_i = 1$; $r_i = 0$). Comparisons utilized canine residuals averaged by individual, effectively age-adjusting data and ensuring that each animal contributed only one datapoint (Moses et al., 1992). In addition, we analyzed pooled data, treating each datapoint independently to cross-check results. Results are consistent, but we report the more conservative results from averaged data. Analyses were conducted when possible for animals that reached "prime age" based on behavioral observations (about 9–12 years of age). Behavioral data are available for 26 prime age males, including 13 sires, while canine measures are available for 24 of these animals (11 sires). We explored multivariate effects of residual canine length, body mass, and body length on fitness (sireship and λ_i), finding no significant multivariate patterns. Thus, unless noted otherwise, we use t-tests for all statistical inferences. Previous analyses by Setchell and colleagues have shown that mandrill adults maintain skeletal dimensions after adult size is reached with body mass diminishing after 17 years of age (Setchell et al., 2006). Consequently, skeletal length does not covary with reproduction. While body mass changes may be relevant, decreases in mass usually occur past the age at which males in this group sire (see below). Changes in the distribution of mass and in coloration with alpha status also occur, and deposed males tend to lose mass (Setchell and Dixson, 2001b).

We expected independent effects of alpha status and canine size on λ_i. Consequently, we tested for correlations between: (1) residual canine size and λ_i and (2) alpha status and λ_i. Alpha status is unambiguous and estimated based on longitudinal observations of the colony. We also attempted to isolate independent effects of canine size, age, and rank on fitness, based on previous analyses of rank among males (Setchell and Dixson, 2001b). Unfortunately, several problems stymied these attempts, including small samples, so this issue requires future analyses featuring more complete rank data. Statistical analyses were conducted with Systat 11 software (Systat Inc., 2004), with a significance level set at 0.05.

Results

Age-related changes in canine morphology and reproduction

The canine tooth erupts between five and nine years of age, and then undergoes rapid size increase in tight correlation with age. The tooth reaches a peak adult value at about nine years of age, maintaining this size until about 11 years. After this age, however, the tooth begins to diminish in size through both breakage and wear. Data also record low age-size correlations among older animals, with considerable residual variation in canine size. Breakage and wear ultimately result in some animals with very small, blunt canines (Fig. 2).

Changes in tooth size correspond very closely with measures of male reproductive performance (Fig. 2). Specifically, the curve for reproductive value (v_x), which is set to 1.0 at birth (Fisher, 1930), rises in close correspondence with the erupting canine tooth, and is nearly superimposed on the canine size curve during the period of eruption (note scalar differences). Reproductive value peaks at the time of maximum canine length, then plateaus until the tooth begins to decline in size. Reproductive value then declines very rapidly, fluctuates in association with a minimal number of conceptions late in life, and ultimately reaches zero. Relative values confirm close temporal correspondence of changes in predicted canine size, reproductive value, and number of conceptions (Fig. 3).

Five males lived to 19 yrs, all dying before their twentieth birthdates, but none older than 19 yrs conceived. For the five oldest males, the time between last conception and death averaged 3.3 yrs (0.8–5.8 yrs). It is important to reiterate that males produce viable sperm as early as four years of age (Setchell et al., 2005). Therefore, in theory, peak reproduction could occur at any time after four years of age, implying a potential reproductive career of about 16 years in this group. The strong peak of the reproductive value curve reveals that reproduction is concentrated in a short time period, rather than distributed evenly throughout the 16-year period of potential reproduction. Minimal reproduction after 15 yrs suggests that male mandrills may experience a lengthy postreproductive period, if they manage to reproduce at all.

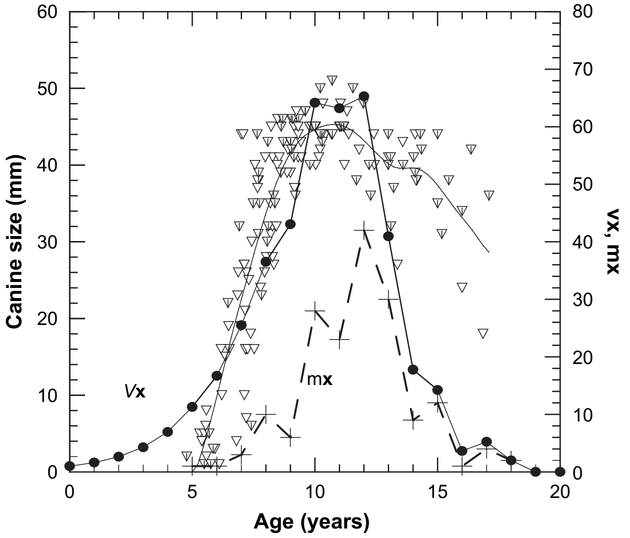

Fig. 2. Canine size (mm, triangle), reproductive value (v_x, circle), and number of conceptions (m_x, +) plotted against age. Triangles with vertical "ticks" designate canine measurements for animals that ultimately sired. Note that left and right vertical axes are on different scales. Reproductive value is constrained to equal 1 at birth.

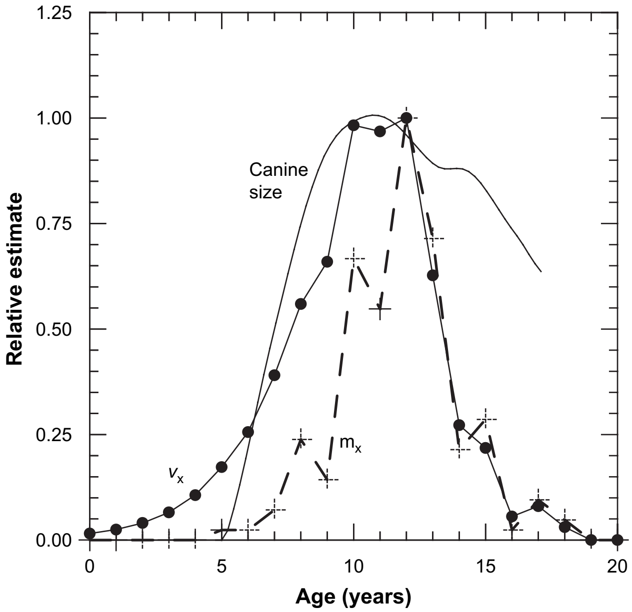

Fig. 3. "Relative" or proportional estimates for canine length, reproductive value, and number of conceptions. Relative estimates are obtained by dividing predicted canine sizes by maximum predicted canine size, reproductive values by maximum observed reproductive value, and conception number by maximum number of conceptions, scaling all maxima to 1.0.

The number of conceptions (m_x) tracks canine size, and because m_x contributes to calculation of reproductive value, conceptions correspond with v_x. Males with canine lengths over two-thirds of maximum predicted length (~45 mm) sired 94% of offspring in this population. Males with predicted canine sizes less than 30 mm sired the remaining infants. Males younger than seven years of age conceived five of these offspring, while the older animals sired the remaining six. A separation in the reproductive value curve and number of conceptions may reveal advantages of earlier reproduction.

Adult body dimensions for mass and length are stable after attainment of adult sizes (Setchell et al., 2001), but mass does decline in the teen years (Setchell et al., 2006). Therefore, these parameters do not change in the same way as the canine with reproductive performance, although we cannot discount late effects of diminished body mass.

Comparisons of sires and nonsires

Each sire's estimate of the individual intrinsic rate of increase (r_i) is, by virtue of sireship, greater than zero ($\lambda_i > 1$). In addition, sires possess significantly larger canines than nonsires (where $\lambda_i = 1$; Table 1). Residuals measured from

Table 1
Summary statistics for morphometrics from averaged residuals

Measurement	Sires			Nonsires		
	n	Mean	s.d.	*n*	Mean	s.d.
Residual canine length (mm)	11	2.13*	2.82	27	−1.15	5.06
Residual body mass (kg)	11	0.47	1.44	21	0.13	1.43
Residual body length (cm)	12	−0.46	6.47	18	1.86	2.40

*Denotes a significant difference between sires and nonsires, $p = 0.016$.

nonparametric regression of canine size against age (Fig. 2) for the entire samples of sires and nonsires indicate that sires have canines that are, on average, about 3.28 mm longer than nonsires, a significant difference ($p < 0.016$). Sires have canine teeth (age-adjusted) approximately 8% larger than nonsires. Although sire canines significantly exceed the size of nonsire canines, individual fitness among sires is uncorrelated with canine residual size. This may be a consequence of small sample size, but it also suggests that, for sires, factors other than canine size influence fitness. Thus, our significant t-test comparing sires and nonsires establishes a selection differential between sires and nonsires, suggesting that a selection gradient would depend on canine teeth plus other factors. Finally, in contrast to the canine tooth, other morphometric variables show no significant differences between these sires and nonsires (Table 1). Residuals show that, although sires are slightly heavier than nonsires, they are marginally shorter than nonsires.

Comparisons of “prime age” animals also reveal statistically significant canine residual size differences between sires ($n = 11$) and nonsires ($n = 13$; $p < 0.020$). Only 30% of males over four years of age sired offspring (16/53; Setchell et al., 2005), with 13 reproducing between 10–12 years of age. Among sires, λ_i ranges widely (mean = 1.16, s.d. = 0.10), reaching 1.33 in the most prolific animal, who sired a total of 42 offspring, peaking with 13 offspring in his 12th year. It is important to note that the total offspring sired for each animal correlates strongly with λ_i (Pearson $r = 0.91$), indicating that conception or offspring counts provide good fitness estimates. However, using λ_i as a fitness measure assigns higher fitness to animals that sire at young ages, accounting for the contribution of offspring that reproduce sooner than offspring of older sires. Thus, males that sired at early ages realized higher fitness by this measure than old sires among those with equal numbers of conceptions.

Male social rank

Social rank may be interrelated with canine size and fitness. However, rank shifts in this colony, sometimes dramatically (Setchell and Wickings, 2005), precluding attempts to analyze these relations in a quantitative manner. Canines of six males that reached alpha status are not significantly larger than those of other sires, but mean λ_i for alphas exceeds that of other sires ($p < 0.012$). Moreover, alphas with larger canines have higher λ_i values, suggestive of positive correlations between trait (canine) size and fitness. However, this tendency does not reach statistical significance, perhaps as a consequence of the small sample of alpha males.

Discussion

General patterns

Analyses of demographic and morphometric data yield a detailed understanding of how a single aspect of morphology relates to fitness through life history scheduling. Ontogenetic analyses of mandrill canine size show that the tooth has a dynamic history throughout the life course (Fig. 2; Leigh et al., 2005). Numerous factors affect male mandrill fitness, including age, demography, behavior, and genealogy (Charpentier et al., 2005a; Setchell et al., 2005). The present study confirms the hypothesis that canine tooth ontogeny and adult canine size correlate with fitness of male mandrills, implying the operation of sexual selection on canine size. These results contribute to our understanding of male fitness by documenting a tight temporal correspondence between the size of canine weaponry and male reproduction. The canine relates to fitness in two ways. First, and most importantly, correspondences between the eruption schedule and conception timing demonstrate that the canine tooth plays an important role in facilitating access to females. Second, sires have larger teeth than animals that fail to reproduce. Associations between fitness and canine size appear to have pervasive effects on the male life course, unlike somatic dimensions. These findings fit the expectations of sexual selection theory, and are the first to tie male canine size and its ontogeny directly to reproductive success in a primate population. These results have important implications for understanding mandrill morphology and behavior. Support for hypotheses linking tooth size to reproduction and fitness have far more general implications, including consequences for concepts central to theories of sexual selection, demography, and aging.

Male reproductive scheduling

The adult canine tooth is present only after five years of age, and is simply too small to support intermale competition until about 9 years of age, even though males can reproduce about five years prior to attainment of adult canine size. The canine in mandrills erupts more rapidly than in other anthropoids (Leigh et al., 2005), and from about nine to 12 years of age, reaches maximum size, corresponding to a time when sires are most prolific. We suspect that the mandrill canine verges on a limit for primates in terms of formation and eruption rates. After about 12 years of age, male reproductive output decreases precipitously. Marked declines in reproduction following 12 years of age, along with reproductive cessation in the oldest males, points to the potential for a long postreproductive period. We can isolate the canine as a morphological feature, perhaps singular in this regard, that is interwoven with reproductive scheduling. On the other hand, somatic dimensions (especially length) change little during adulthood. Some aspects of mass may relate to reproductive performance among adults by distinguishing alphas from nonalphas, but mass itself does not differentiate between sires and nonsires. In essence, the canine relates to reproductive scheduling by proving adequate as a weapon only for a short timespan. The length of a male's reproductive period is determined by both how long it takes for the tooth to erupt and by its resistance to wear and breakage once adult size is attained. A sire's greatest contribution to future population size is expected at maximum canine length, apparently compensating for low reproduction during both young and old ages. The need for canine adequacy effectively compresses what could be a reproductive career spanning from four to 20 years of age to a brief period of a few years between about nine and 13 years of age. Males may be reproductively viable for only about 20% of maximum lifespan. It is clear from behavioral observations that adequate canine weaponry is a prerequisite to reproduction, as fights lead to serious injuries, usually from parallel canine slashes (J. Setchell, pers. obs.). Consequently, canines that erupt rapidly serve to enable reproduction at the earliest possible ages. The effects of rapid eruption may be further enhanced if the tooth serves as a mate choice characteristic in females (but unfortunately, we cannot currently test this possibility).

After attaining full adult size, the mandrill canine tooth diminishes, as does male reproductive output. The mandrill canine tooth, like all anthropoid primate canines, is nonrenewable: once worn, it cannot be regenerated. The diminution of canine size, through normal wear, breakage, or both, presages rapid reproductive decline in males. These results suggest that canine size plays a major role in determining fitness (λ_i) by allowing males to compete effectively during certain life periods.

The strict time constraints on reproductive scheduling determined by the canine tooth have important implications for sexual selection theory. The effects of secondary sexual characteristics on the scheduling of reproduction have not received detailed investigation in analyses of sexual selection in primates. However, interspecific studies usually point to the intensity and frequency of male intersexual competition as major factors in the evolution of male canine weaponry (Kay et al., 1988; Plavcan and van Schaik, 1992; Plavcan, 1993, 2001). Constraining reproduction to a brief time period may influence both of these variables. The intensity of intermale competition may be quite high, but only for a relatively brief period of time, with that period of time reflected by the duration of the tooth's maximum length. We predict lower intensity interactions for animals with smaller teeth. Similarly, the temporal patterning of the frequency of interactions might be affected by the canine, with lower frequencies characteristic of animals with smaller teeth. These features suggest that some method of accounting for the timespan during which males can reproduce, or are at peak canine dimensions, may help explain variation in dimorphism across species. Finally, the present results support the analytical decision to base canine dimorphism size measures on relatively unworn adult teeth (Plavcan and van Schaik, 1992): peak canine size is associated closely with sexual selection, despite the transience of full tooth size.

Adult tooth size

The significant difference between the canine size among animals that sired and those that did not indicates that size differences, apart from eruption scheduling, influence reproductive success. This implies the potential for several different kinds of selective forces operating on mandrill canines. The adult canine may reflect a compromise between several different selective forces, including selection for rapid eruption, large adult size, and resistance to wear and breakage. Enhanced sizes of sire canines may suggest that effects of slight differences in timing of tooth eruption may not matter, provided that eruption delays lead to larger teeth. However, eruption rates do not vary substantially, with little interindividual dispersion around regressions that describe eruption patterns (Leigh et al., 2005). Whether or not animals that reach the largest size the earliest realize reproductive advantages cannot be established by these data. Several sires did reach maximum size very early, and those with high positive residuals early may realize increased fitness. These early maturers may also realize benefits from extending the timespan during which the canine is at maximum length.

The benefits of large size are obvious in relation to intrasexual competition. The average advantage sires hold in terms of age-adjusted canine size is about 8%. This value is consistent with weaponry advantages in other species, such as bighorn sheep (*Ovis canadensis*), in which horns of highly successful rams were more than 5.5% larger than those of competitors (Coltman et al., 2002). This 8% difference, either in displays of the canine tooth, biting, or as a female mate choice characteristic, seems to be functionally significant.

Rank and canine weaponry

The canine may have important consequences for rank attainment and maintenance in this colony. Alpha males achieved higher fitness than other males, and there may be a correlation among alphas between fitness and canine size. On the other hand, alpha canines are not uniformly larger than those of other sires. This finding suggests that the canine is not the sole determinant of alpha status. Contributions and interactions of several factors influencing status probably affect fitness. Although the quantitative effects of these factors cannot be analyzed independent of canine size at present, these results are sufficient to exclude the canine as the sole determinant of alpha status. Female mate choice may select for noncanine morphologies or behaviors related to alpha status (Setchell et al., 2005).

Evolution of weaponry

Comparative assessments of fitness and sexual selection in mammals, although limited currently to only a few species, point to important distinctions among different types of sexually-selected weaponry. The canine deteriorates with age through normal occlusal wear. In this population, males also break teeth relatively frequently. Breakage accounts for high variance in older males, with broken teeth no longer functional as weapons. Primate dental weaponry contrasts starkly with other kinds of sexually-selected mammalian weaponry, notably horns, antlers, and body mass, which renew either continually or periodically (Short and Balaban, 1994) and are sometimes polymorphic (Robinson et al., 2006). Renewable weaponry either reaches a constant adult size and shape, or becomes increasingly large, imposing, and elaborate with age (e.g., antler size in cervids). For example, red deer (*Cervus elaphus*) stags realize maximum annual breeding success just as antlers attain adult size, but reproduction declines after this age in spite of annual antler regeneration and maintenance or enhancement of size (Kruuk et al., 2002). Neither body size (Bercovitch et al., 2003) nor renewable weaponry (Kruuk et al., 2002) seem to show consistently strong correlations with fitness through life history scheduling across mammals. In red deer, sexual selection on antlers interacts with selection on body condition and nutritional status (Kruuk et al., 2002). In bighorn sheep, however, relations to weapons may be more straightforward. Male fitness increases nonlinearly with age-related increases in horn size until death (Coltman et al., 2002). In contrast to these examples, selection on nonrenewable weaponry in mandrills is tied to weapons that actually fade with advancing age. Male mandrills apparently lose competitive abilities, attractiveness as mates, or both, as the canine diminishes. They also have no prospects for improvement in the presence of competition, even under optimal nutritional circumstances such as those afforded to this colony. Dependence on nonrenewable weaponry appears to entrain morphology, life history, and fitness. Consequently, advances in sexual selection theory may need to account for renewability of weapons, as well as life history correlates of weaponry (Robinson et al., 2006).

Reproductive value and fitness

The centrality of the canine in mandrill life history scheduling has important theoretical implications for interpreting reproductive value. First, these results empirically support the theoretical notion that v_x plays a major role in life history scheduling (Goodman, 1982). In this case, the association between v_x and age-related changes in weaponry reveals a morphological basis to changes in reproductive value. Canine weaponry may be a life history pacemaker in mandrills, helping to determine an optimal life history, theoretically achieved upon maximizing v_x in each age class (Schaffer, 1979; Goodman, 1982). An optimum is clearest in the absence of parental care and discrepancies in resource allocations amongst age classes (Fisher, 1930; Schaffer, 1979), both of which probably hold for male mandrills. A male mandrill's greatest impact on future generations occurs at maximum canine size, with negligible contributions at other ages. In addition, theoretical considerations predict that male v_x influences female mate choice (Kokko et al., 2002). Therefore, the male canine tooth may advertise reproductive value, amplifying its fitness consequences through female mate choice. Consequently, viewing mandrill male life histories through the lens of reproductive value suggests that an optimal mandrill male life history requires rapid canine eruption, large canines at prime ages, and gradual wear. Hypotheses about optimal life histories are crucial to testing morphological predictions about selection, and relating these predictions to patterns of genetic variation. Canine developmental biology and mechanical properties of the adult tooth define when and how readily males can reproduce, offering morphological ties to the evolution of an optimal life history.

The relations between morphological features and v_x may present special circumstances consistent with Fisher's biological interpretation of v_x. Fisher reasoned that "the direct action of Natural Selection [sic] must be proportional" (1930: 27) to the contribution of an age class to future generations, implying that the force of natural selection could be inferred from reproductive value. Many authors, following Hamilton (1962), regard this interpretation as an oversimplification (Schaffer, 1979; Goodman, 1982; Kokko et al., 2002). Because the force of mortality increases with age, a premium on early selection should almost always be expected, with the efficacy of selection throughout the lifespan declining with age (Williams, 1957; Hamilton, 1962; but see Baudisch, 2005). This expectation raises questions about whether or not reproductive value measures intensity of selection.

We suggest that relating reproductive value to selection intensity is most feasible when an aspect of morphology corresponds directly to reproductive value, linking morphology, performance, and fitness (Arnold, 1983). While the efficacy of selection does decline with age through the action of mortality, the canine tooth establishes an aging schedule independent of other somatic systems because it erupts late, then declines in size. Therefore, the tooth determines a new relation between selection and mortality not present in juvenile animals. The inability of strictly demographic analyses to account for correlations between morphology and life history may explain persistent theoretical controversy regarding v_x. The association of sexually-selected weaponry and v_x presents the opportunity to infer the strength of selection, especially when such features alter the pattern of mortality so dramatically.

Life history and aging

The canine's role in life history scheduling means that it offers insights into aging (Williams, 1957; Hamilton, 1962). Sexual selection has favored large size produced by rapid canine eruption. However, selection against wear among geriatric mandrills must have trivial effects, given their sometimes-lengthy postreproductive periods. These attributes establish the necessary conditions for life history tradeoffs. In this case, attributes of the canine tooth that are selectively favored early in life (rapid eruption of a large tooth) grant males early access to mates. On the other hand, these same attributes probably compromise the tooth's ability to resist wear and breakage later in life. The absence of late reproduction precludes selective counterbalances to the effects of early selection, producing a tradeoff. Senescence of the tooth, and with it declines in reproduction, may be an outcome of a selective "trade" for a large, rapidly formed canine tooth that breaks easily once worn. The main attribute under selection may be length, produced through rapid eruption, as a result of a selective premium on early reproduction. We predict that this comes at the cost of enamel thickness, which we assume is an energetically expensive component of the tooth that constrains tooth development time. For example, in *Papio* baboons, male enamel relative to crown size tends to be thinner than female enamel (Hlusko et al., 2004), which may suggest selection for thicker enamel and higher costs of enamel development in males. Moreover, we also expect that great length may reduce cross-sectional area and, thus, increase bending moments. A long thin canine tooth with thin enamel and small cross-sectional area would result in a tooth with low bending resistance and, thus, may be susceptible to breakage (Hylander, pers. comm.). Normal wear of a thinly enamelled tooth may further reduce cross-sectional area or alter canine shape, affecting resistance to bending. Low reproductive output later in life cannot counterbalance this by offering the chance to respond to selection for increased bending strength on a worn tooth.

The possibilities for life history tradeoffs have important implications beyond mandrills in two directions. First, formation of teeth during the prenatal and lactation periods suggests that maternal effects and investment could play a surprisingly large role in determining the mechanical properties of the tooth. Well-nourished and high-ranking mothers should produce offspring with better teeth, producing variation in the raw material responsive to sexual selection. Higher-quality teeth may develop more rapidly, resist wear or bending, or some combination of these features. In any case, the possibility of strong maternal effects reveals interesting and important new dimensions to sexual selection theory (Kruuk et al., 1999; Qvarnstrom and Price, 2001; Kotiaho et al., 2003; Delph, 2005), especially when weaponry is nonrenewable. Second, these results indicate that species with nonrenewable weaponry offer simple mammalian systems for testing aging models (Williams, 1957; Hamilton, 1962). Aging models remain controversial (Hughes et al., 2002; Hughes and Reynolds, 2005), particularly in mammals, but the possibilities offered by analyzing teeth in terms of life history tradeoffs are significant. Specifically, genes involved in tooth development are becoming well-known (Thesleff, 2006), providing opportunities to investigate directly the consequences of tradeoffs for the evolution of both genetic and morphological diversity.

Canines and the fossil record

Connections between canine morphology and life history have broad implications for interpreting the fossil record. Analyses of hominoids have gleaned life history data directly from tooth histology (Dean et al., 2001; Mahoney et al., 2007). Our results suggest that the canine could harbor detailed information about male fitness in extinct species. Pending analyses of females, this result probably applies best to fossil taxa with strong sexual dimorphism. Associations between male fitness, life history, and canine development that might be inferred from fossils have significant implications for human evolution. A wide range of dimorphism among primates as well as within the human lineage (Plavcan et al., 2005) implies variation in the degree to which canines associate with life history scheduling. Reduced canine dimorphism could correspond with expanded male reproductive periods, allowing a response to selection favoring longevity. Such factors could also be important in human evolution.

Conclusions

Analyses of male mandrills indicate that a single morphological feature, the size of the canine tooth, is strongly correlated with reproductive success. Reproductive output corresponds closely with the size of the adult canine tooth. Both variables change dramatically during life as the tooth erupts, and later suffers wear and breakage. The vast majority of conceptions occur during a relatively brief period of maximum canine length, with conceptions at other ages both rare and sporadic. In addition to corresponding to the timing of conceptions, canines are significantly larger in sires than in nonsires, providing certain individuals with a clear competitive edge.

These results are the first to demonstrate close ties between fitness and weaponry in male primates. The relations between weaponry and fitness in species with nonrenewable weapons, such as primate canines, may be exceptional in comparison to other sexually selected weapon systems. Specifically, the nonrenewability of the canine tooth could entrain weaponry and life history, contrasting with species that rely on renewable weapons (e.g., horns, antlers, and body mass). The mechanical properties of the canine tooth may largely define an optimal male mandrill life history. Theoretically, these results help resolve longstanding controversies about the meaning of Fisher's reproductive value, possibly by illustrating a case in which reproductive value reflects the intensity of (sexual) selection. The close ties between morphology and aging offer insights into theories of aging. Finally, analyses of dimorphic canines among fossils provide opportunities to recover detailed information about the scheduling of male life histories.

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