# LIFE HISTORY IN MALE MANDRILLS (*MANDRILLUS SPHINX*): PHYSICAL DEVELOPMENT, DOMINANCE RANK, AND GROUP ASSOCATION

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# ABSTRACT

We assess life history from birth to death in male mandrills (*Mandrillus sphinx*) living in a semi-free-ranging colony in Gabon, using data collected for 82 males that attained at least the age of puberty, including 33 that reached adulthood and 25 that died, yielding data for their entire lifespan. We describe patterns of mortality and injuries, dominance rank, group association, growth and stature and secondary sexual character expression across the male lifespan. We examine relationships among these variables and investigate potential influences on male life history including differences in the social environment (maternal rank and group demography) and early development, with the aim of identifying characteristics of successful males. Sons of higher-ranking females were more likely to survive to adulthood than sons of low-ranking females. Adolescent males varied consistently in the rate at which they developed, and this variation was related to a male's own dominance rank. Males with fewer peers and sons of higher-ranking and heavier mothers also matured faster. However, maternal variables were not significantly related to dominance rank during adolescence, the age at which males attained adult dominance rank, or whether a male became alpha male. Among adult males, behavior and morphological development were related to a male's own dominance rank, and sons of high-ranking females were larger than sons of low-ranking females. Alpha males were always the most social, and the most brightly colored males, but were not necessarily the largest males present. Finally, alpha male tenure was related to group demography, with larger numbers of rival adult males and maturing adolescent males reducing the time a male spent as alpha male. Tenure did not appear to be related to characteristics of the alpha male himself.

## KEYWORDS

mandrill; maturation; ontogeny; individual variation; maternal influence

Primate growth and development strategies differ from those of many other animals. Relative to predictions made according to their body size, primates are characterised by a lengthy pre-reproductive period (Roff, 1992). Physical development and behavior change with age, as individuals pass through the developmental phases of infancy, juvenescence, adolescence, early adulthood, prime adulthood and senescence, each with differing life history priorities and each requiring different tactics to maximise fitness (Pereira and Fairbanks, 1993; Pereira and Leigh, 2003; Setchell and Lee, 2004). Comparative studies usually treat life history variables as species specific (e.g. Promislow and Harvey, 1990). However, life histories may also vary greatly among individuals of a single species and the study of individual variation is important for our understanding of life history evolution (Borries et al., 2001; Lee, 1996). Differing circumstances during immaturity influence the ontogenetic trajectory adopted, leading to differences in adult morphology, physiology, and behavior (Pereira and Leigh, 2003; Roff, 1992; Schlichting and Pigliucci, 1998; Stearns, 1992).

Growth and development, and changes with age, are relatively understudied in primates, due to their slow life histories and long life-spans. Few long-term studies have tracked the development of individuals over all, or most, of their lifespan. Reports of age-specific mortality and reproduction are more common (references in Richard et al., 2002), but studies linking experiences during development to reproductive tactics and fitness are relatively rare (Altmann, 1991; Pereira and Leigh, 2003). The influence of social and demographic variables on reproduction has been better studied, particularly in terms of maternal rank. In species with matrilineal rank inheritance, maternal rank clearly influences daughter's reproductive success (e.g. Altmann et al., 1988; Bercovitch and Strum, 1993; Setchell et al., 2002; e.g. van Noordwijk and van Schaik, 1999). Among males, high maternal rank promotes high male rank, and increased mating success, in macaques (*Macaca mulatta*, *M. fuscata*: references in Alberts and Altmann, 1995b; *M. fascicularis*, van Noordwijk and van Schaik, 2001), but not in baboons (Johnson, 1987; Packer et al., 2000; Pereira, 1989). Sons of high-ranking rhesus macaques (Bercovitch, 1993) and baboons (Alberts and Altmann, 1995b) also reach maturity earlier than sons of low-ranking mothers. This may result in an important fitness advantage, particularly in species where a large proportion of a male's lifespan is pre-reproductive. Finally, male dispersal decisions may also be influenced by maternal factors. In baboons, early dispersal is related to maternal death before the male's sixth birthday, while late dispersers had young mothers (Alberts and Altmann, 1995a). In rhesus macaques, sons of high-ranking mothers delay dispersal when compared to sons of low-ranking mothers (Berard, 1990).

Here we assess life history from birth to death in male mandrills (*Mandrillus sphinx*, Cercopithecidae), and explore factors that influence growth and development, as well as adult size, morphology, and dominance rank. Mandrills live in multi-male, multi-female groups, and are one of the most sexually dimorphic primate species. Adult males are far larger than females, with long canine teeth; brightly colored skin on the face, rump and genitalia; boney supra-maxillary swellings; a yellow beard; a long cape of hair and an epigastric fringe of white hair (Hill, 1970). Mandrills inhabit the dense rain-forest of Gabon, Equatorial Guinea, southern Congo, and southern Cameroon, and it has as yet proved impossible to habituate and follow known individuals in the wild (Abernethy et al., 2002; Harrison, 1988). Most of our knowledge of mandrill behavior and reproduction comes from a semi-free-ranging colony at the Centre International de Recherches Médicales, Franceville (CIRMF), Gabon. Male reproductive success in this colony is strongly associated with dominance rank, with the top-ranking male siring 33-100% (mean 75%) of offspring born during a single birth season (Setchell et al., 2005a).

To be reproductively successful, a male mandrill must (i) survive the long pre-reproductive period; (ii) pass through the long period of adolescence to adulthood, then (iii) successfully challenge for alpha rank to gain high reproductive success, and (iv) retain the top position to sire and continue to sire offspring. Finally, (v) if he survives his fall from alpha rank, then he will no longer sire many offspring, but may invest in his existing offspring, for example by protecting them from potentially infanticidal rivals (e.g. Palombit et al., 2000) (strong evidence for infanticide exists in the CIRMF mandrill colony). We have previously reported basic patterns of male growth and development from birth to adulthood, and dominance rank-related variation in both adolescent and adult male development for these mandrills (Setchell and Dixson, 2001a; 2001b; , 2002; Wickings and Dixson, 1992a; 1992b). However, the earlier reports concern animals of estimated age, while the later reports include animals of known age only up to the age of 11 yr (n=13) and are based on a short-term study (21 months) relative to the 20 year lifespan of some male mandrills (Setchell et al., 2005b). As of April 2005, we are able to update these previous reports with data for 82 males that reached at least the age of puberty, including 33 that reached adulthood. Twenty-five of these subjects died and provided data for their entire lifespan.

The purpose of this paper is to update previous reports, and to describe age-related patterns of mortality and injuries, dominance rank, group association, growth in mass and stature, and secondary sexual character expression across the entire lifespan in male mandrills. We also examine relationships among these variables, and test the hypothesis that social environment influences male life history, especially with regard to maternal rank and group demography. These analyses aim to identify characteristics of successful males. Although the semi-free colony lacks predation and male migration, limiting our study of demographics and intragroup dynamics, studies of such captive animals yield long-term data concerning individual phenotype, which are impossible to collect in the wild.

## METHODS

### Study population

The mandrill colony at the Centre International de Recherches Médicales in Franceville, Gabon (CIRMF), was established in 1983/4, when 15 animals (7 males, 8 females) originating from the wild were released into a 6.5 ha naturally rain-forested enclosure (E1). All further additions to the group are due to reproduction of the founder animals; some animals have been removed. A second semi-free-ranging group was established in 1994 (in E2, 3.5 ha) by transferring 17 mandrills (including 4 adult males and 6 adult females) from E1. The animals forage freely in the enclosures, and receive daily supplements of monkey chow and seasonal fruits; water is available *ad libitum*. Breeding in the colony is moderately seasonal, with 63% of female peri-ovulatory periods occurring between July and September (Setchell and Wickings 2004). A corresponding birth peak occurs in January to March (Setchell et al. 2002).

The date of birth is recorded for all individuals born into the colony. The age of founder animals was estimated using dental status on arrival at CIRMF (based on comparisons with data from animals of known date of birth) and their previous history (Wickings and Dixson, 1992a). Infants are tattooed with their identification number while still carried ventrally by their mother, and animals over the age of 2.5 yr are given ear-tags to aid identification. Veterinary intervention is limited to animals that are severely injured. Daily observations are made of female reproductive status, births, male sociality, dominance ranks (based on *ad libitum* records of avoidance), injuries and disappearances. Monthly photographs are also taken of males for subsequent coloration measurements.

Data used for this study were collected from records kept since the beginning of the colony (capture data, dates of birth, disappearance or removal), daily observations of dominance ranks and male sociality (since 1996), photographs (mainly since 1996) and digital images (2003 onwards). The study ended with a final capture during April 2005, after which the colony was reorganised. A total of 135 males contributed data to the study, including 7 founder males of estimated age. Eighty-two males attained at least the age of 3.8 yr (estimated puberty, Setchell and Dixson, 2002). Of these, 25 disappeared, 2 escaped, 13 were removed from the enclosures and 42 were still present at the end of the study. Only six of the 25 animals that disappeared were confirmed deaths (the carcass was found). However, animals that disappeared are assumed to have died, as it is very unlikely that they escaped but were not observed in the surrounding area, and carcasses are often impossible to locate in the enclosures.

Data concerning female reproductive status, male sociality (males aged 4+ yr) and dominance ranks (males aged 6+ yr) were available for Mar-96 to Nov-97, Jun-02 to Mar-03, and Sep-03 to Apr-05 (total 51 months). Data concerning female reproductive status, male sociality (males aged 10+ yr) and dominance ranks (males aged 10+ yr) were available for 36 months of the intervening periods (no data were available for 23 months, distributed in blocks of 1-5 months, mean 2 months). All data were collected by JMS and EJW; inter-observer reliability was verified and maintained by regular simultaneous observations. Group sizes increased from 15 initially to a maximum of 104 animals in 2002, corresponding to smaller groups observed in the wild (Hoshino et al., 1984; Rogers et al., 1996). Group composition during the study is summarised in Table 1. The population was expanding for most of the study.

The testes descend at a mean age of 3.8 yr in male mandrills (Setchell and Dixson, 2002), and we considered males to be 'adolescent' – i.e. reproductively competent but not yet of adult size, appearance or status – from the age of 4 yr to 9 yr. Males were considered males to be 'adult' at 9 yr, when they typically reach adult size (Setchell and Dixson, 2002), and can dominate older males (this study).

## Dominance rank and sociality

The top ranking male in a group was ranked 1, the second 2, and so on. To account for the different numbers of males present in the study groups over time, we expressed dominance ranks as the percentage of males over six years of age dominated per month. All other males consistently avoided a male ranked 100 %, while a male ranked 0 % consistently avoided all other males aged 6+ yr. Systematic rank data for younger males were not available, but where data were available, males aged 6+ yr always dominated younger males. Although not stable over long periods, rank relationships were always linear and transitive; circularities were not observed. Attainment of adult dominance rank was defined as the first unreversed win by an adolescent male over any adult male in an agonistic interaction (Alberts and Altmann, 1995b).

Male group association was scored during daily observation periods as "group associated": travelling, feeding, and interacting as part of the social group; "peripheral": travelling and feeding on the edge of the group, often more than 100 m from all other group members; or "solitary": travelling and feeding alone (Wickings & Dixson, 1992). Male sociality was expressed as % days group associated and % days solitary per month. The measurement of days spent "peripheral" meant that % days solitary was not equal to 100 minus % days in centre of group.

## Color measurements

The color of the red skin on the nose is closely related to circulating levels of testosterone and to the degree of expression of other secondary sexual traits in male mandrills (Setchell and Dixson, 2001a; 2001b), and was used as a measure of secondary sexual development. Color was measured for males over the age of 4 yr using photographic records scanned into a computer (1989-2003, 782 images), and digital images captured using a Nikon Coolpix 5700 digital camera saved as fine quality jpegs (2003-2005, 737 images). All images used were of males when they were in either an open grassy area (not in the shadow of the forest margin), or in an open feeding pen.

Images required calibration, to account for exposure and light drift (Gerald et al., 2001). Colony conditions and the use of historical photographs meant that it was impossible either to obtain images of animals in the same frame as a photographic white and black standard, or to place a standard in the same position as the animal and capture a second image immediately following that of the subject. We therefore used only images where color ranged the full spectrum from white to black, and used the “Autolevels” command in Adobe Photoshop 6.0 (Image Mode set to RGB) to define the lightest and darkest pixels in each color channel as white and black. Once calibrated, the midnasal strip was outlined in a standard fashion using the polygonal lasso tool in Adobe Photoshop 6.0. The mean luminosity and the mean red intensity value (mean number of pixels at each intensity level) of the highlighted area were measured using the “Image > histogram” command. Red intensity divided by luminosity of the image best described the red color of an image, and was highly and significantly positively correlated with previous measures made using quantified color charts (Setchell and Dixson, 2001a).

## Morphological measurements taken at capture

Males were captured annually for veterinary examination. Additional captures have occurred for research purposes in some years. Anaesthesia was accomplished using a “Telinject” blowpipe to deliver a syringe containing “Imalgene1000” (10 mg / kg. Rhone-Mérieux, Lyon, France). Body mass (nearest 100 g), crown rump length (CRL, nearest 5 mm), and the length (L) and width (W) of the left testis (1mm) were measured during captures. One founder male that was missing a leg was removed from the data-set for body mass. The volume of the left testis was calculated using the formula for a regular ellipsoid: $TV = \pi / 6.W^2.L$. In two males the left testis had atrophied following injury and the right testis was measured. Maximum tail width, measured using callipers (nearest 1mm) was used as a measure of “fattedness” (Setchell and Dixson, 2002).

## Potential influences on male life history

Potential influences on male life history included two maternal variables, four demographic variables, and a measure of early development:

Maternal variables:

1. Maternal rank at birth. Female dominance ranks are stable in mandrills, with daughters acquiring a rank just below their mothers (Setchell, 1999). Female rank at each conception was therefore expressed as the percentage of females over three years of age dominated to account for demographic changes over time. Females were also divided into high (top quartile), medium (25-75%) and low-ranking (bottom quartile).
2. Maternal mass at the closest capture to birth of the male (excluding mass at more than 2 months gestation). This was not correlated with maternal rank (r=0.049, p=0.679, n=74 males).

We were unable to investigate the influence of maternal death on male development, as the mothers of all except the founder males were present to at least the age of 2 yr, and very few males lost their mothers during the study.

Demographic variables:

1. The number of adult males in the group when a male reached 9 yr. This was highly positively correlated with the number of reproductive females available when a male reached 9 yr, and this second variable was therefore not used in analyses. There were always more reproductive females in the group than there were males present, but the number of sexually attractive females present on any one day was always less than the number of males. The number of adult males in a group was also positively correlated with alpha male rank stability (see results).
2. The number of males belonging to the same birth cohort and maturing simultaneously.
3. The age of the alpha male when a male reached 9 yr.
4. The age distribution of adult males in the group when a male reached 9 yr, measured as the age of the eldest male. An alternative measure, mean age differences of the three top-ranking

males (Alberts et al., 2003), was highly positively correlated with both the age of the alpha male and the number of adult males present, and was therefore not used.

The size of a male's matriline and the number of older and younger siblings may also influence a male's development, as larger matrilines may offer more kin support. However, it is difficult to make predictions concerning matriline size since mature brothers are both competitors and potential coalition partners, while mature sisters reduce a male's reproductive opportunity (Alberts and Altmann, 1995b).

We measured early development using mass-for-age during infancy for the subset of males for whom this information was available. Infancy was defined as birth to eight months, based on the median inter-birth interval less the length of gestation (405-175 days, Setchell et al., 2002). To determine relative mass for males that were measured at different ages we used locally weighted least squares regression (lowess, f=0.3, 10 iterations) to fit a curve to the body mass records for all males (Moses et al., 1992; Setchell et al., 2001). 123 data points were available for 105 males aged 0-8 months (1-3 points per male). 'Residuals' were computed for each data point as the natural logarithm of the ratio of the observed value to the average value given by the lowess curve for that age (Moses et al., 1992). Where two or more data points were available for a male, the mean was used as a measure of its relative mass-for-age. Early development was positively correlated with maternal rank (r=0.283, p=0.051, n=48), confirming previous results for a smaller sample of males in the colony (Setchell et al., 2001).

All of the above variables were considered as potential influences on (i) the age at which a male first reversed an adult male, and (ii) adolescent male development. Maternal rank and mass, as well as a male's own mean rank-for-age residual during adulthood, were considered as potential influences on variation in behavior and morphology during adulthood. The number of rival adult males present in a group and maternal variables were considered as potential influences on alpha male tenure. Finally, to compare the characteristics of alpha males with those of other males present we identified 12 stable periods (seven in E1, five in E2) where the ranks of males aged 8+ yr had not changed during the three previous months, and did not change for at least six months, and examined mean values for behavior and morphology for each male during each stable period.

## Statistical analyses

We used Kaplan-Meier survival analyses to examine age at disappearance (presumed mortality), to take into account males that were still alive at the end of the study or who were removed. Log rank test statistics (L) were used to test for equality of survival distributions. Survival analyses were also used to examine the age at which males first out-ranked an adult male and the age at which males attained alpha status, because some males had not attained these milestones by the end of the study.

All data available for all males were treated as a mixed longitudinal and cross-sectional sample to examine general patterns of behavior and development vs. age. Data were grouped into 6-month age-classes, using the mean value at each age-class for each male where more than one value was available. Previous studies have shown that males do not show circannual change in secondary sexual traits, with the exception of testicular volume (Setchell and Dixson, 2001c). The majority of captures occurred during the non-mating season, but excluding the few mating season data points for testicular volume did not substantially alter results.

The incomplete nature of the data set was such that males contributed to multiple age-classes, but not to all. Intervals between data points for individual males and the variation observed in adult male morphology meant that it was not possible to determine the age at which individual males attained adult size and appearance. We therefore compared the development of each male with the average curve for each morphological and behavioral variable using standardised residuals, calculated using a univariate general linear model with the trait as the dependent variable, and age-class as the predictor. Individual identity significantly influenced all behavioral and morphological variables during adolescence (ANOVA, controlling for age-class, $p<0.001$ in all cases), implying that within individual variance was lower than variation among individuals, while inspection of the data for males contributing multiple data points also indicated that an individual male’s residuals were relatively consistent over time. We therefore concluded that data points for an individual could usefully be summarised to a single mean value describing a male’s phenotype-for-age (see also Altmann and

Alberts, 2005). Similar mean residuals were calculated for males aged >9 yr, to describe adult development for age.

Relationships between residuals for different morphological and behavioral variables were examined using principle components analysis (PCA) on the mean residual for each male for each variable, enabling us to define "general maturity" factors for adolescent males (Setchell and Dixson, 2002). We based this analysis on males aged 6-9 yr because males begin to develop secondary sexual characters and to become peripheral to the social group at 6 yr (Setchell and Dixson, 2002 and this study), and because our data concerning dominance rank began at this age.

We used stepwise multiple linear regressions with a forward selection procedure to examine the effect of independent variables on male phenotype. In no case was tolerance <0.1, meaning that collinearity was not a serious problem in these analyses (Quinn and Keough, 2002). We investigated early development separately, because this information was available for only a subset of males. With the exception of alpha male tenure, all variables were normally distributed (skew / standard error of skew <3, Zar, 1996). All statistical analyses were performed using SPSS 11.0, and all tests were two-tailed. Means are quoted ± standard errors. Sample sizes vary, as not all information was available for all males.

## RESULTS

### Mortality and injury

Males lived for 14±0.9 yr (95% CI 12.4–15.8 yr, median 17 yr). Seventy-one percent of males survived to 10 yr, and none lived longer than 20 yr (Fig. 1a). Mortality increased from puberty at about 4 yr, with a plateau at 13-17 yr. If males attained 13 yr, then they were likely to survive several more years. Injuries increased from age 5 yr (minor injuries only) to a peak at 11-12 yr (Fig. 2). Sixteen of 65 injuries (25 %) and 11 (31%) of 35 serious injuries were to alpha males; the remaining injuries occurred in males ranked 2-20. Forty-eight injuries (74 %) and 35 (78 %) serious injuries were observed during months when sexually attractive females were available. Scoring males that required veterinary treatment for serious injury as "dead" did not change the patterns of mortality substantially.

Males born to low-ranking mothers were less likely to survive than those born to high- or medium-ranking females (Fig. 1b). However, these differences are non-significant, perhaps due to the small number of events observed (24 disappearances in total, $L$ = -0.69, p = 0.708). Males that were small for their age as infants did not live as long (11.0±1.1 yr, 95% CI 8.76-13.21 yr, 8 events, 19 censored cases) as large infants (16.1±1.1 yr, 95% CI 13.9-18.3 yr, 3 events, 20 censored cases) but this difference showed only a trend towards significance ($L_1$=3.40, p=0.065).

## Dominance rank

Dominance rank increased with age from 6-11 yr, peaked from 11-16 yr, and fell again from 16-20 yr (Fig. 3). Mean rank-for-age during adolescence was not significantly correlated with either maternal rank (r=0.146, p=0.382, n=38) or maternal mass (r=-0.057, p=0.739, n=37). Nor was mean rank-for-age during adulthood significantly correlated with either maternal rank (r=0.131, p=0.593, n=19) or maternal mass (r=0.051, p=0.836, n=19).

Males attained adult dominance rank (first reversed an adult male) at 9.1±0.2 yr (n=18 males, range 7.8-11.4 yr), and males that reached 9 yr (n=27) attained at least third position in the hierarchy. The only significant predictor of age at first reversal was the age of the alpha male (Table 2). As the age of the alpha male increased, so did the age at which males first reversed an adult male. This relationship was driven by three males that matured in the presence of only an alpha male, with no lower ranking adult males. To reverse an adult male these maturing males therefore had to reverse the alpha male himself. Excluding these three males from the analysis resulted in no significant predictors of age at first reversal. The age at which a male first reversed an adult male was not significantly correlated with his early development (r=0.398, p=0.264, n=10).

Seven males in E1 and two males in E2 attained alpha rank during the study. Seven of these nine dominance take-overs involved death (n=4) or serious injury (n=3) to the previous alpha male. Fights were never observed, and it is unknown whether the new alpha males were responsible for the injuries to the defeated alpha male. In one case, the alpha and beta males were severely injured, and the third-ranking male became alpha male via succession. Two further beta males also became alpha through succession: one because the alpha male was removed from the colony, and the other when the alpha male fell out of a tree and died of his injuries. One take-over involved a male that jumped into E2 from E1 and overthrew the reigning alpha male. There was no evidence of male-male coalitions to overthrow alpha males.

The probability of becoming alpha male at some point during a male's career increased from 0 at 8.5 yr to 0.44 at 12.5 yr, and was highest in males aged 11.5 yr. Males that gained alpha status were aged 10.8±0.4 yr (range 8.8-12.6 yr, n=10); males that lost alpha status did so at 13.7±1.0 yr (range 10.5-19.0, n=9). New alpha males were previously beta males (n=6), or rose quickly through the ranks during the three months prior to takeover (n=3). Defeated alpha males that did not die as a result of their wounds ranked 2-6 during the six months following take-over (mean 3.5±0.7, n=5). In only one case did a defeated alpha male regain top rank, via succession, after an interim period of 10 months at rank 2. Although no infanticide has been witnessed in the colony, circumstantial evidence of infanticide occurred following the removal of all males aged 6+ yr from E1 and the introduction of two novel males in April 2005, when three of 22 nursing infants died (aged approx. 4 months), one of whom showed signs of canine wounds from an adult male (Olivier Bourry, pers. comm).

Of nine males that attained alpha status, seven were sons of high-ranking females, while only two were born to low-ranking females. The survival distributions for age at attainment of alpha rank were not significantly different ($L_1$=0.39, p=0.512). Of six males that became alpha, and for whom data concerning early development were available, three were small-for-age, and three were large-for-age.

Tenure as alpha male ranged 1-96 months, with a mean of 24.5±12.9 months (n=6). Ninety-six months was exceptional and the second longest tenure was 42 months. Tenure was significantly negatively correlated with the number of rival adult males present in a group and negatively correlated with the number of adolescent males maturing while a male was alpha (Table 3). It was not significantly correlated with maternal rank or mass, or with infant mass-for-age (Table 3).

### ***Group association vs. age***

Although males in the colony cannot normally emigrate from their natal group or immigrate into another group, they peripheralise from the social group during adolescence. Mean % days males spent in the centre of the social group fell from 5.5 yr to a minimum at 9 yr (Fig. 4a). Mean group association was 40-60 % in males aged 10-14 yr, increased in males aged 14.5-17.5 yr, and fell again in elderly males. Mean % days solitary increased from 6-9 yr, with a maximum at 9 yr (Fig. 4b). Mean solitariness ranged 28-43 % in males aged 10-14 yr, decreased at age 14.5 yr, remained low until 18 yr then increased in elderly males.

### *Morphology vs. age*

Mass increased from birth, with growth accelerating at 3.5 yr, and decelerating at 9 yr. Males reached a maximum mass of 31-32 kg at age 10-12 yr (Fig 5a). Mass decreased to ~30 kg in males aged 12-17 yr, then fell again, and males aged 19 yr were equivalent in mass to 7 yr old males. Male CRL increased to the age of 9 yr (Fig. 5b) (the slight rise in CRL in elderly males was due to the few individuals that attained this age being slightly larger than average). Red color began to increase after 6 yr, reached a plateau between 10-17.5 yr, and decreased slightly in the oldest males (Fig. 6a). TV increased from age 5.5 yr (Fig. 6b), reaching a maximum at 13-15 yr, after which it declined to the equivalent of early adult values. Variation in TV was high at all ages during adulthood. “Fattedness”, measured as the maximum width of the tail, continued to increase beyond 10 yr, peaked at 14.5 yr, and decreased in males aged 18+ yr (Fig. 6c).

## Variation during adolescence

PCA of six morphological (mass, CRL, TV, fattedness, canine height and red coloration) and two behavioral (time spent with the group, time spent solitary) variables for adolescent males aged 6-9 yr identified three factors that accounted for 72 % of the total variance (Table 4). Body mass, CRL, TV, canine height and time spent solitary loaded positively on the first axis, while time spent with the group loaded negatively. All but CRL loaded positively on the second axis, with red coloration, fattedness and canine height loading highest. Body mass and CRL loaded highest on the third axis. Factor 1 was best predicted by maternal rank and the number of males in a cohort, with males that scored higher having higher ranking mothers and fewer peers (Table 2). Factor 2 was best predicted by a male's own rank-for-age and maternal mass, with males scoring higher being higher ranking for their age and having heavier mothers (Table 2). Factor 3 was best predicted by a male's own rank-for-age, again with males scoring higher for this factor being higher ranked for their age (Table 2).

None of the three adolescent development factors was significantly related to early development (n=19, factor 1 r=0.105, p=0.668; factor 2 r=-0.068, p=0.781; factor 3 r=0.014, p=0.954). Factor 3 (but not factors 1 or 2) was significantly related to the age at which males attained adult dominance rank, with males scoring positively (i.e. larger males) first reversing an adult male at a younger age than males scoring negatively (survival analysis comparing males scoring positively and negatively for each factor: factor 1 $L_1$=1.28, p=0.257, factor 2 $L_1$=0.05, p=0.815; factor 3 $L_1$=6.71, p=0.010). None of the three factors was significantly related to whether a male became alpha male (factor 1 $L_1$=0.10, p=0.757, factor 2 $L_1$=0.10, p=0.926, factor 3 $L_1$=0.87, p=0.352).

### Variation during adulthood

Variation in dominance rank, time spent with the group, time spent solitary, body mass, CRL, and secondary sexual development between adult males and within individual adult males across their lifespan is summarised in Table 5. PCA of time spent with the group, time spent solitary, mass, CRL, TV, fattedness, canine height and red coloration for males aged >9 yr identified three factors that accounted for 72% of the total variance (Table 6). Red coloration, time spent with the group, mass, CRL and TV loaded positively on the first axis, while time spent solitary loaded negatively, and fattedness and canine height were neutral. Time spent solitary, mass, TV and fattedness loaded positively on the second axis, while time spent with the group loaded negatively and red coloration and CRL were neutral. Time spent solitary, CRL and canine height loaded positively, and fattedness negatively on the third axis. The best predictor of factor 1 was a male's own mean rank residual, with higher-ranking males scoring higher. None of the variables tested (rank, maternal rank and maternal mass) predicted factor 2, but both maternal rank and maternal mass predicted factor 3, with sons of higher-ranking mothers, and sons of smaller mothers scoring higher (Table 2). Early development was not significantly related to any of the factors (n=10, Factor 1: r=-0.021, p=0.955; Factor 2: r=-0.200, p=0.579; Factor 3: r=0.427, p=0.219). Nor was tenure as alpha male related to any of the factors (Table 2).

During stable periods for which data were available the alpha male was always the most social and the least solitary male (males aged >9 yr, 11 stable periods, alpha male mean 92±2% group, 3±1% solitary). Alpha males also scored highest for red coloration, but were not necessarily highest scoring for mass, CRL, TV, fattedness or canine height (Table 7).

# DISCUSSION

## Patterns with age

The relationship between dominance rank and age formed an inverted U-shape, starting low among adolescent males, rising to a maximum in prime age animals, and falling with increasing age. This is related to changes in reproductive potential and fighting ability with age and is similar to other primate species where males compete for access to receptive females (Cowlishaw and Dunbar, 1991; Dunbar, 1988; Sprague, 1998; van Noordwijk and van Schaik, 1985; van Noordwijk and van Schaik, 1988b). Dominance rank in these mandrills showed less of a peak than reported for baboons where rank peaks in early adulthood, then falls immediately (Alberts et al., 2003; Packer et al., 2000). This difference may be due to lack of males immigrating from other groups, and low mortality among older males in this study. As expected, given that alpha males sire the majority of offspring, the pattern of dominance rank with age closely matches that for male reproductive output with age, both peaking from age 10-16 yr (Setchell et al., 2005b). Male decisions relating to group membership and transfer also appear to be influenced by age-related changes in competitive ability and reproductive potential in long-tailed macaques (van Noordwijk and van Schaik, 2001; van Noordwijk and van Schaik, 2004). Male mandrills peripheralise during adolescence, when they are competitively inferior, and may or may not rejoin the social group when they reach their prime. Variation in group association occurs both between and within individual males across their adult lifespan.

This larger data set confirms previously described patterns of development to adulthood in mandrills (Setchell and Dixson, 2002) and shows that physical condition continued to change with age as individuals move from young adulthood, through their prime, to senescence. Statural growth ceased at 9-10 yr, due to epiphyseal closure, but body mass peaked, then decreased slightly, before declining markedly in the oldest males, as in other species (Leigh, 1992). The curve for body mass closely matched that for dominance rank. Males attained adult rank at 9 yr, when they were reaching peak mass. They became alpha at about peak mass, and the decrease in body mass matched a decrease in dominance rank. Canine height also peaked at 9-11 yr, when males attain adult rank, and may also attain alpha rank (Leigh et al., 2005). Canine height decreased more rapidly than body mass as males passed their prime, due to both wear and breakage, in a close parallel of male reproductive value (Leigh et al., in prep). In very old age, wear of the entire dentition may negatively affect body mass (Phillips-Conroy et al., 2000), which may partly explain the decline in mass observed in older animals. Secondary sexual character expression also changed during the adult phase and was closely related to dominance rank. Testicular size and fattedness peaked later than any other character, including body mass, suggesting that males continue to invest in testes mass and fat rumps longer when they have attained their maximum body mass. Patterns of red coloration with age were similar to those for rank and body mass, decreasing only in the oldest males.

## What makes a successful male mandrill?

***(i) Survival:*** Mortality was very low in the mandrill colony in comparison with natural primate populations, where most individuals die before reaching adulthood, and at least half of these deaths occur during infancy (Pereira and Altmann, 1985). However, sons of higher-ranking females seemed more likely to survive to adulthood than sons of low-ranking females, as also found in rhesus (Vessey and Meikle, 1987) and long-tail macaques (van Noordwijk and van Schaik, 2001). Smaller infants may also be less likely to survive than larger ones, although our dataset is indequate to confirm this.

***(ii) Development during adolescence:*** Males that develop, and attain maturity, faster should experience a fitness advantage, as long as earlier maturation does not entail higher mortality. Our data were insufficient to test whether faster development was more risky, but they do confirm previous findings that adolescent males vary consistently in the rate at which they develop and that this variation is positively related to a male's own dominance rank (Setchell and Dixson, 2002). The larger sample of males also revealed that males with fewer peers mature faster. Previous work has also suggested that males that develop in the absence of adult males grow faster (Setchell et al., 2001), although the number of adult males present did not significantly predict adolescent development in this study. Adolescent male development was also related to maternal variables, with sons of higher-ranking mothers maturing faster. Similar findings have been reported for rhesus macaques (Bercovitch, 1993) and baboons (Alberts and Altmann, 1995b). Males born to heavier mothers also matured faster. Surprisingly, we found no link between early development and later maturation. Males that were large for their age as infants did not develop more quickly during adolescence, nor did they attain adult dominance rank earlier than males that were small for age as infants. This may be due to limitations of the method used to estimate early development, i.e. using only one, or a few, data points for individual males. Alternatively, other variables that influence growth and development may intervene during the long maturation process, disguising or over-riding any influence of early development.

***(iii) Attaining top rank:*** Males gained top rank via both aggressive challenge and via succession when higher-ranking males were injured, died or were removed. Rank acquisition appears to be mainly a result of male-male competition, but females may have some control over male group membership, rank and tenure, forming coalitions to chase and attack adult males (Setchell et al., 2005c). Although larger males first reversed adult males and entered the adult hierarchy at a younger age than smaller males, whether a male became alpha male seemed to be related to group demography rather than to his own characteristics. Males that developed more quickly as adolescents were not more likely to become alpha male, and sons of high ranking mothers did not attain adult dominance rank earlier than sons of low ranking mothers. However, there was some evidence suggesting that sons of high-ranking female mandrills may be more likely to become alpha male. Similarly, in wild Amboseli baboons, high maternal rank can lead to a developmental advantage, but demography determines the age at which males attain adult rank and first consortship (Alberts and Altmann, 1995b). Male rank in both natal (aged 5-9 yr) and new troops (age 6-15 yr) is also independent of maternal rank in baboons at Gombe National Park, Tanzania (Packer et al., 2000).

The major correlate of adult behaviour and morphology was male dominance rank, which was positively related to red coloration, group association, mass, CRL and TV (adult factor 1). However, the developmental advantage accruing to sons of higher-ranking females during adolescence also persisted into adulthood. Sons of higher ranking mothers scored higher for adult factor 3 (i.e. higher for CRL and canine height, but lower for group association), although this factor explained only 14 % of variance between males. Surprisingly, sons of smaller females also scored higher for this factor, in contrast to results for adolescent males, where sons of heavier females scored higher for canine height.

Alpha male mandrills were the most brightly colored, but this red coloration develops following attainment of alpha status rather than prior to a rank challenge (Setchell and Dixson, 2001b). Despite the overall relationship between male rank and adult behaviour and morphology, alpha male mandrills were not necessarily the heaviest, longest, or fattest adult males present in the group. Nor did they have the longest canine teeth. A lack of a clear relationship between body size and dominance rank has also been shown for chacma baboons (Kitchen et al., 2003). Kitchen et al (2003) suggest that this is because dominance rank is a more transient variable than body size. It seems likely that differences in recent experience (e.g. defeat in male-male interactions depresses testosterone levels, Raleigh and Macquire, 1990; Rose et al., 1975; Sapolsky, 1987), or in personality (Sapolsky and Ray, 1989), may be more important than small differences in body size when males decide whether or not to attempt a dominance take-over.

***(iv) Alpha male tenure:*** Our sample size of alpha male tenures was small, but the finding that tenure was negatively related to the number of males present suggests that increased group size led to decreased stability, as in baboons (Alberts et al., 2003). This is likely due to increased numbers of males meaning more males that are close in fighting ability (Cowlishaw and Dunbar, 1991). Alpha male tenure was less related to a male's own characteristics or to his mother's than to those of the group. Tenure was not related to maternal variables, a male's early development or to his adult development. Average tenure was longer than that reported for savannah (8 months, Alberts et al., 2003) or chacma baboons (5 months, Palombit et al., 1997). This may be because male mandrills in this colony face limited options, as they are unable to transfer to groups where opportunity is better, and they may be less likely to attempt to take-over their natal group than a non-natal group.

***(v) Post-reproductive males:*** Fallen alpha males lose most, if not all, future reproductive opportunities, and may also lose existing offspring to infanticide. New alpha males should benefit from infanticide, as they are unlikely to have sired existing infants, but are very likely to sire the next infants (Hrdy, 1979; van Schaik, 2000). Death of an infant reduces the inter-birth interval from an average of 405 to 305 days (Setchell et al., 2002). Infanticide was not observed during the study, probably because all but one males that attained alpha status were already living in the same enclosure and could therefore have mated sneakily with females prior to take-over. Interestingly, the only male that could not have already sired infants when he became alpha male, because he jumped from one enclosure to the other, was viciously attacked by females (Setchell et al., 2005c). The three suspected cases of infanticide that occurred after this study ended took place when both adult males present had been introduced into the enclosure when the females were already pregnant, and when no potential sires were available to protect the infants.

Although male mandrills appear to show little parental care, males that lose rank and survive may continue to contribute to their offspring's fitness by protecting them from new alpha males. Lactating females show a clear preference for proximity to the likely sire of their offspring, even when he is no longer alpha male (Setchell, 1999). Further, as in long-tail macaques, where alpha males only begin to associate closely with mothers and infants when infants sired after their take-over are born (van Noordwijk and van Schaik, 1988a), older adult male mandrills are most likely to respond to screams from juveniles with agonistic support (unpublished data). Quantitative data are lacking here however, and play-back experiments would be useful to determine whether these males selectively support their offspring (true parental care, as shown for baboons, Buchan et al., 2003), or simply respond non-selectively to screams from any offspring that they may have sired.

## CONCLUSIONS

Studies of mandrills of estimated age, and a shorter-term study of 13 males have described patterns of development to adulthood in mandrills (Setchell and Dixson, 2001a; 2001b; , 2002; Wickings and Dixson, 1992a; 1992b). This study used 23 years of morphological and demographical data, and ten years of behavioral data, to confirm these patterns for a larger sample size of known-age males. We also show that physical condition continues to change with age as individuals move from young adulthood, through their prime, to senescence. Social environment influenced male life history in profound ways. Sons of higher-ranking females were more likely to survive to adulthood than sons of low-ranking females, matured faster during adolescence, were longer (but not heavier) as adults, and may have been more likely to become alpha male, and thus to sire many offspring. Sons of heavier mothers also matured faster during adolescence, although they were not larger as adults. Dominant males, and those with fewer peers, also matured faster during adolescence. Adult behavior and morphological development were related to dominance rank. Alpha males were always the most social, and the most brightly colored males. However, they were not necessarily the largest males present. Finally, tenure as alpha male was related to group demography rather than to characteristics of individual males, with larger numbers of rival adult males and maturing adolescent males reducing the time a male spent as alpha male (and therefore his reproductive success). These results demonstrate the importance of long-term, intensive studies of animals of known age for understanding individual variation in life history, and the factors that modulate development and thereby influence adult outcomes.

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# LITERATURE CITED

Abernethy KA, White LJT, and Wickings EJ (2002) Hordes of mandrills (*Mandrillus sphinx*): Extreme group size and seasonal male presence. J Zool *258:*131-137.

Alberts SC, and Altmann J (1995a) Balancing costs and opportunities - dispersal in male baboons. Am Nat *145:*279-306.

Alberts SC, and Altmann J (1995b) Preparation and activation - determinants of age at reproductive maturity in male baboons. Behav Ecol Sociobiol *36:*397-406.

Alberts SC, Watts H, and Altmann J (2003) Queuing and queue jumping: Long term patterns of dominance rank and mating success in male savannah baboons. Anim Behav *65:*821-840.

Altmann J, and Alberts SC (2005) Growth rates in a wild primate population: ecological influences and maternal effects. Behav Ecol Sociobiol *57:*490-501.

Altmann J, Hausfater G, and Altmann SA (1988) Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In TH Clutton-Brock (ed.): Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems. Chicago: University of Chicago Press, pp. 403-418.

Altmann SA (1991) Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. Proc Natl Acad Sci USA *88:*420-423.

Berard JD (1990) Life History Patterns of Male Rhesus Macaques. PhD, University of Oregon, Eugene.

Bercovitch FB (1993) Dominance rank and reproductive maturation in male rhesus macaques (*Macaca mulatta*). J Reprod Fertil *99:*113-120.

Bercovitch FB, and Strum SC (1993) Dominance rank, resource availability, and reproductive maturation in female savanna baboons. Behav Ecol Sociobiol *33:*313-318.

Borries C, Koenig A, and Winkler P (2001) Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). Behav Ecol Sociobiol *50:*391-402.

Buchan JC, Alberts SC, Silk JC, and Altmann J (2003) True paternal care in a multi-male primate society. Nature *425:*179.

Cowlishaw G, and Dunbar RIM (1991) Dominance ranking and mating success in male primates. Anim Behav *41:*1045-1056.

Dunbar RIM (1988) Primate Social Systems. Ithaca, N.Y.: Comstock Press.

Gerald MS, Bernstein J, Hinkson R, and Fosbury RAE (2001) Formal method for objective assessment of primate color. Am J Primatol *53:*79-85.

Harrison MJS (1988) The mandrills in Gabon's rain forest: Ecology, distribution and status. Oryx *22:*218-228.

Hill WCO (1970) Primates, Comparative Anatomy and Taxonomy, Vol 8, Cynopithecinae, Papio, Mandrillus, Theropithecus. Edinburgh, UK: Edinburgh University Press.

Hoshino J, Mori A, Kudo H, and Kawai M (1984) Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. Primates *25:*295-307.

Hrdy SB (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol *1:*13-40.

Johnson JA (1987) Dominance rank in juvenile olive baboons, *Papio anubis*: the influence of gender, size, maternal rank and orphaning. Anim Behav *35:*1694-1708.

Kitchen DM, Seyfarth RM, Fischer J, and Cheney DL (2003) Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). Behav Ecol Sociobiol.

Lee PC (1996) The meaning of weaning: Growth, lactation and life history. Evol Anthropol *5:*87-96.

Leigh S, Setchell JM, and Buchanan LS (2005) Ontogenetic basis of canine dimorphism in Anthropoid primates. Am J Phys Anthropol *127:*296-311.

Leigh SR (1992) Patterns of variation in the ontogeny of primate body size dimorphism. J Hum Evol *23:*27-50.

Moses LE, Gale LC, and Altmann J (1992) Methods for analysis of unbalanced, longitudinal growth data. Am J Primatol *28:*49-59.

Packer C, Collins DA, and Eberly LE (2000) Problems with primate sex ratios. Philos Trans R Soc Lond Ser B-Biol Sci *355:*1627-1635.

Palombit RA, Cheney D, Fischer J, Johnson S, Rendell D, Seyfarth RM, and Silk JB (2000) Male infanticide and defense of infants in chacma baboons. In CP van Schaik and CH Janson (eds.): Infanticide by Males and its Implications. Cambridge: Cambridge University Press, pp. 123-152.

Palombit RA, Seyfarth RM, and Cheney DL (1997) The adaptive value of 'friendships' to female baboons: experimental and observational evidence. Anim Behav *54:*599-614.

Pereira ME (1989) Agonistic interactions of juvenile savanna baboons. 2. Agonistic support and rank acquisition. Ethology *80:*152-171.

Pereira ME, and Altmann J (1985) Development of social behaviour in free-living non-human primates. In ES Watts (ed.): Nonhuman Primate Models for Human Growth and Development. New York: Alan R Liss Inc, pp. 217-309.

Pereira ME, and Fairbanks LA, eds. (1993) Juvenile Primates: Life History, Development and Behavior. New York; Oxford: Oxford University Press.

Pereira ME, and Leigh SR (2003) Modes of primate development. In PM Kappeler and ME Pereira (eds.): Primate Life Histories and Socioecology. Chicago: University of Chicago Press, pp. 149-176.

Phillips-Conroy JE, Bergman T, and Jolly CJ (2000) Quantitative assessment of occlusal wear and age estimation in Ethiopian and Tanzanian baboons. In P Whitehead and C Jolly (eds.): Old World Monkeys. Cambridge: Cambridge University Press, pp. 321-340.

Promislow DEL, and Harvey PH (1990) Living fast and dying young: a comparative analysis of life history variation among mammals. J Zool *220:*417-438.

Quinn GP, and Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.

Raleigh MJ, and Macquire MT (1990) Social influences on endocrine function in male vervet monkeys. In TE Ziegler and FB Bercovitch (eds.): Socioendocrinology of Primate Reproduction. New York: Wiley-Liss, pp. 95-111.

Richard AF, Dewar RE, Schwartz M, and Ratsirarson J (2002) Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). J Zool *256:*421-436.

Roff DA (1992) The evolution of life histories. New York: Chapman and Hall.

Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, and Tutin CEG (1996) Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. Am J Primatol *40:*297-313.

Rose RM, Bernstein IS, and Gordon TP (1975) Consequences of social conflict on plasma testosterone levels in rhesus monkeys. Psychosom Med *40:*60-70.

Sapolsky RM (1987) Stress, social status, and reproductive physiology in free-living baboons. In D Crews (ed.): Psychobiology of Reproductive Behavior. New Jersey: Prentice Hall, pp. 292-322.

Sapolsky RM, and Ray JC (1989) Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*). Am J Primatol *18:*1-13.

Schlichting CD, and Pigliucci M (1998) Phenotypic Evolution: A Reaction Norm Perspective. Sunderland, Massachusetts: Sinauer.

Setchell JM (1999) Socio-sexual development in the male mandrill (*Mandrillus sphinx*). PhD Thesis, University of Cambridge, Cambridge, UK.

Setchell JM, Charpentier M, and Wickings EJ (2005a) Mate-guarding and paternity in mandrills (*Mandrillus sphinx*): Factors influencing monopolisation of females by the alpha male. Anim Behav *70:*1105-1120.

Setchell JM, Charpentier M, and Wickings EJ (2005b) Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). Behav Ecol Sociobiol *58:*474 - 485.

Setchell JM, and Dixson AF (2001a) Arrested development of secondary sexual adornments in subordinate adult male mandrills (*Mandrillus sphinx*). Am J Phys Anthropol *115:*245-252.

Setchell JM, and Dixson AF (2001b) Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. Horm Behav *39:*177-184.

Setchell JM, and Dixson AF (2001c) Circannual changes in the secondary sexual adornments of semifree-ranging male and female mandrills (*Mandrillus sphinx*). Am J Primatol *53:*109-121.

Setchell JM, and Dixson AF (2002) Developmental variables and dominance rank in male mandrills (*Mandrillus sphinx*). Am J Primatol *56:*9-25.

Setchell JM, Knapp LA, and Wickings EJ (2005c) Violent coalitionary attack by female mandrills against an injured alpha male. Am J Primatol *68:*411-418.

Setchell JM, and Lee PC (2004) Development and sexual selection in primates. In PM Kappeler and CP van Schaik (eds.): Sexual Selection in Primates. Cambridge: Cambridge University Press.

Setchell JM, Lee PC, Wickings EJ, and Dixson AF (2001) Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). Am J Phys Anthropol *115:*349-360.

Setchell JM, Lee PC, Wickings EJ, and Dixson AF (2002) Reproductive parameters and maternal investment in mandrills (*Mandrillus sphinx*). Int J Primatol *23:*51-68.

Sprague DS (1998) Age, dominance rank, natal status, and tenure among male macaques. Am J Phys Anthropol *105:*511-521.

Stearns SC (1992) The Evolution of Life Histories. Oxford: Oxford University Press.

van Noordwijk MA, and van Schaik CP (1985) Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Anim Behav *33:*849-861.

van Noordwijk MA, and van Schaik CP (1988a) Male careers in sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour *107:*24-43.

van Noordwijk MA, and van Schaik CP (1988b) Male strategies of migration and rank acquisition in wild *Macaca fascicularis*. Aggress Behav *10:*177-177.

van Noordwijk MA, and van Schaik CP (1999) The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. Primates *40:*105-130.

van Noordwijk MA, and van Schaik CP (2001) Career moves: transfer and rank challenge decisions by male long-tailed macaques. Behaviour *138:*359-395.

van Noordwijk MA, and van Schaik CP (2004) Sexual selection and the careers of primate males: paternity concentration, dominance acquisition tactics and transfer decisions. In PK Kappeler and CP van Schaik (eds.): Sexual Selection in Primates: New and Comparative Perspectives. Cambridge: Cambridge University Press, pp. 208-229.

van Schaik CP (2000) Infanticide by male primates: the sexual selection hypothesis revisited. In CP van Schaik and CH Janson (eds.): Infanticide by Males and its Implications. Cambridge: Cambridge University Press, pp. 27-60.

Vessey SH, and Meikle DB (1987) Factors affecting social behaviour and reproductive success of male rhesus monkeys. Int J Primatol *8:*281-292.

Wickings EJ, and Dixson AF (1992a) Development from birth to sexual maturity in a semi-free-ranging colony of mandrills (*Mandrillus sphinx*) in Gabon. J Reprod Fertil *95:*129-138.

Wickings EJ, and Dixson AF (1992b) Testicular function, secondary sexual development, and social status in male mandrills (*Mandrillus sphinx*). Physiol Behav *52:*909-916.

Zar JH (1996) Biostatistical Analysis. Upper Saddle River, NJ: Prentice-Hall.

Fig. 1. Cumulative survival curves for (a) all males, including males of estimated age; (b) males born to high (solid lines), medium (dashed) and low (dotted line) ranking females.

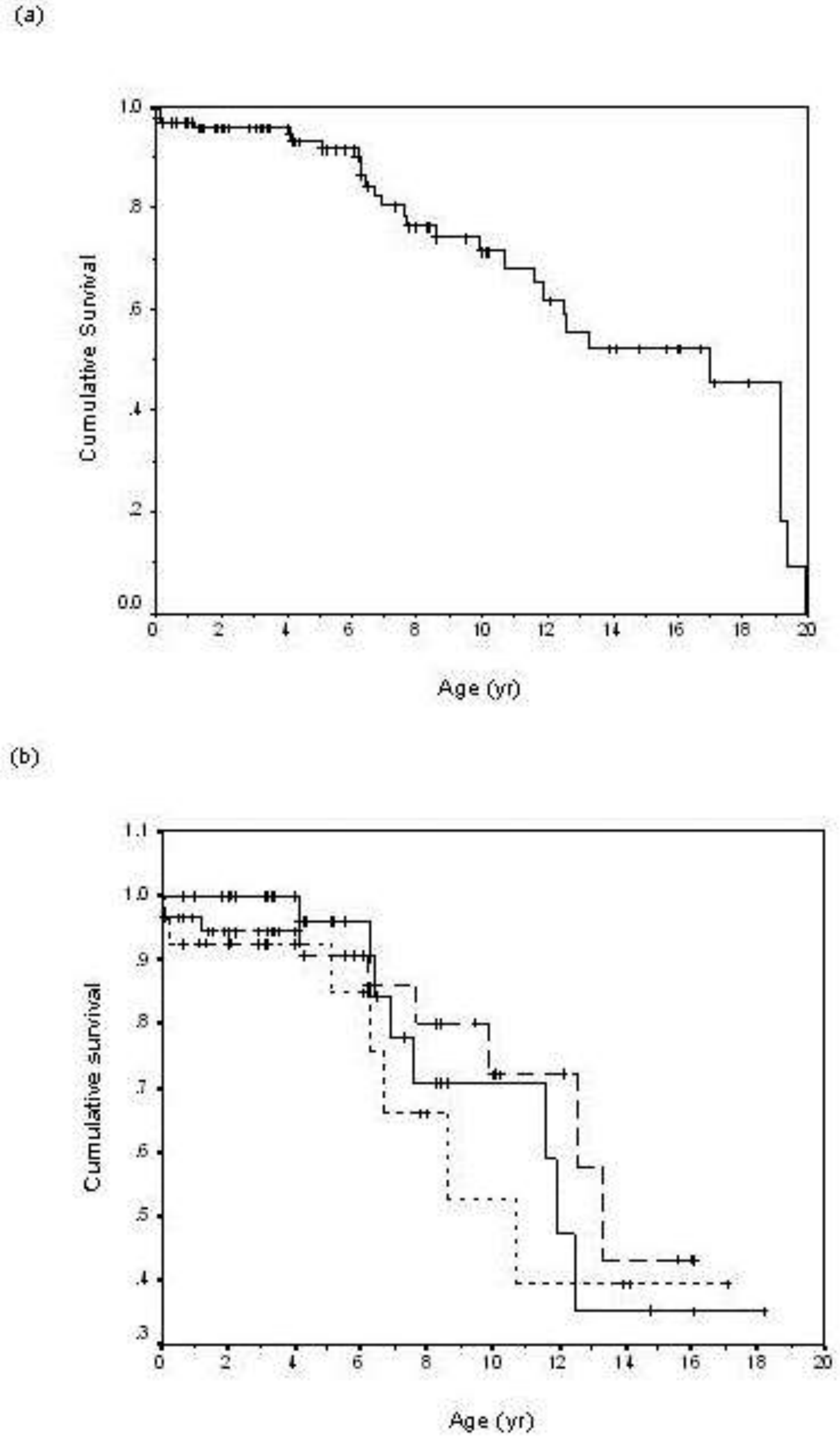

Fig. 2. Injuries observed vs. age. Injury rate is number of observations divided by the number of males observed at that age. Black bars represent serious injury (serious bite wounds), grey bars superficial injuries (scratches, grazes, minor bite wounds). Sample sizes are in parentheses below each age-class.

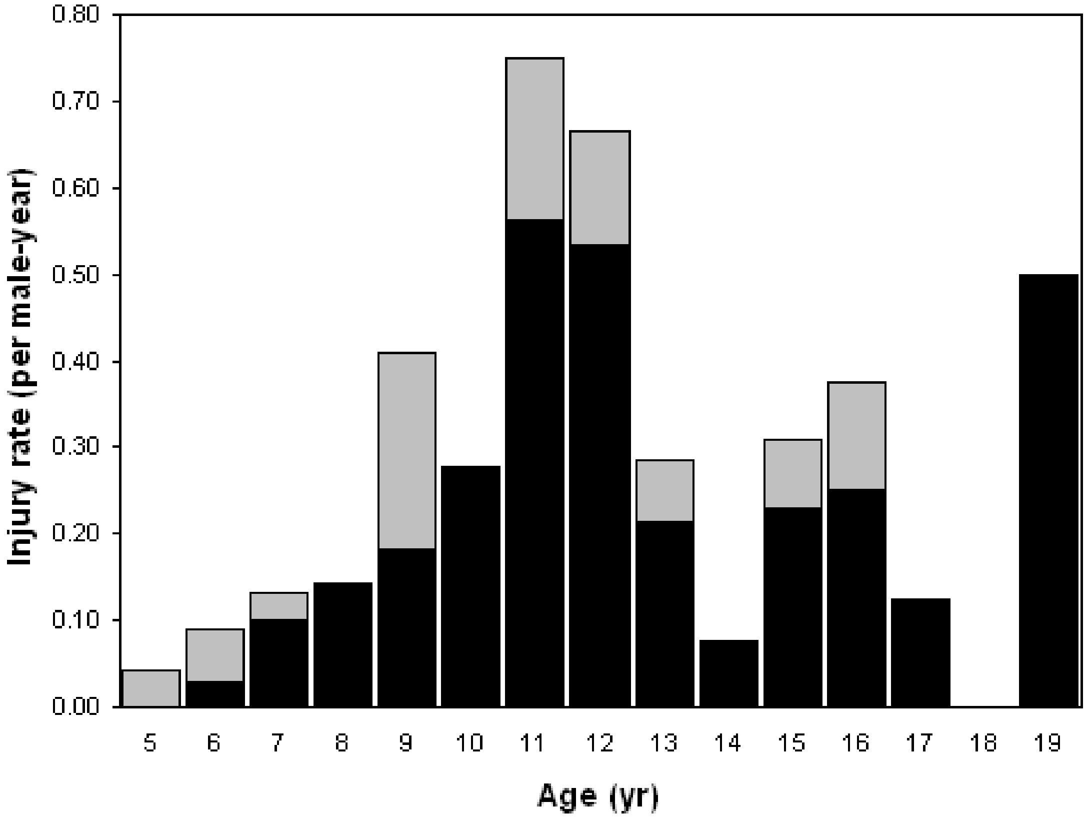

Fig. 3. Dominance rank vs. age. Mean±sem % males aged 6+ yr dominated for 6 month age classes. Sample sizes are shown below the x-axis. Individual males (n=44) contributed 1-19 data points (mean 8.1±0.8)

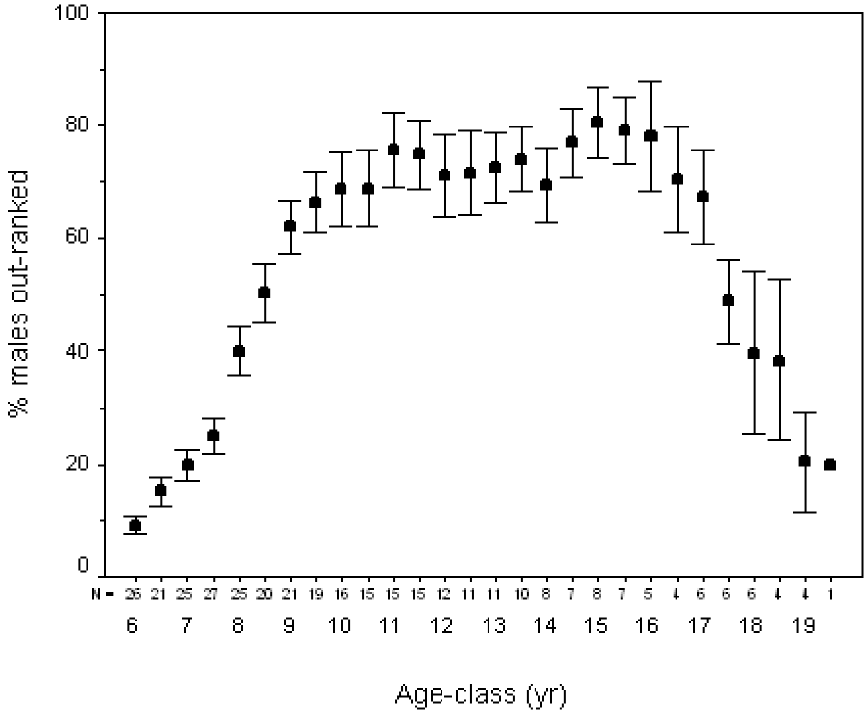

Fig. 4. Group association vs. age. Mean±sem % days (a) social and (b) solitary for 6 month age classes. Sample sizes are shown below the x-axis. Individual males (n=55) contributed 1-19 data points (mean 7.2± 0.8)

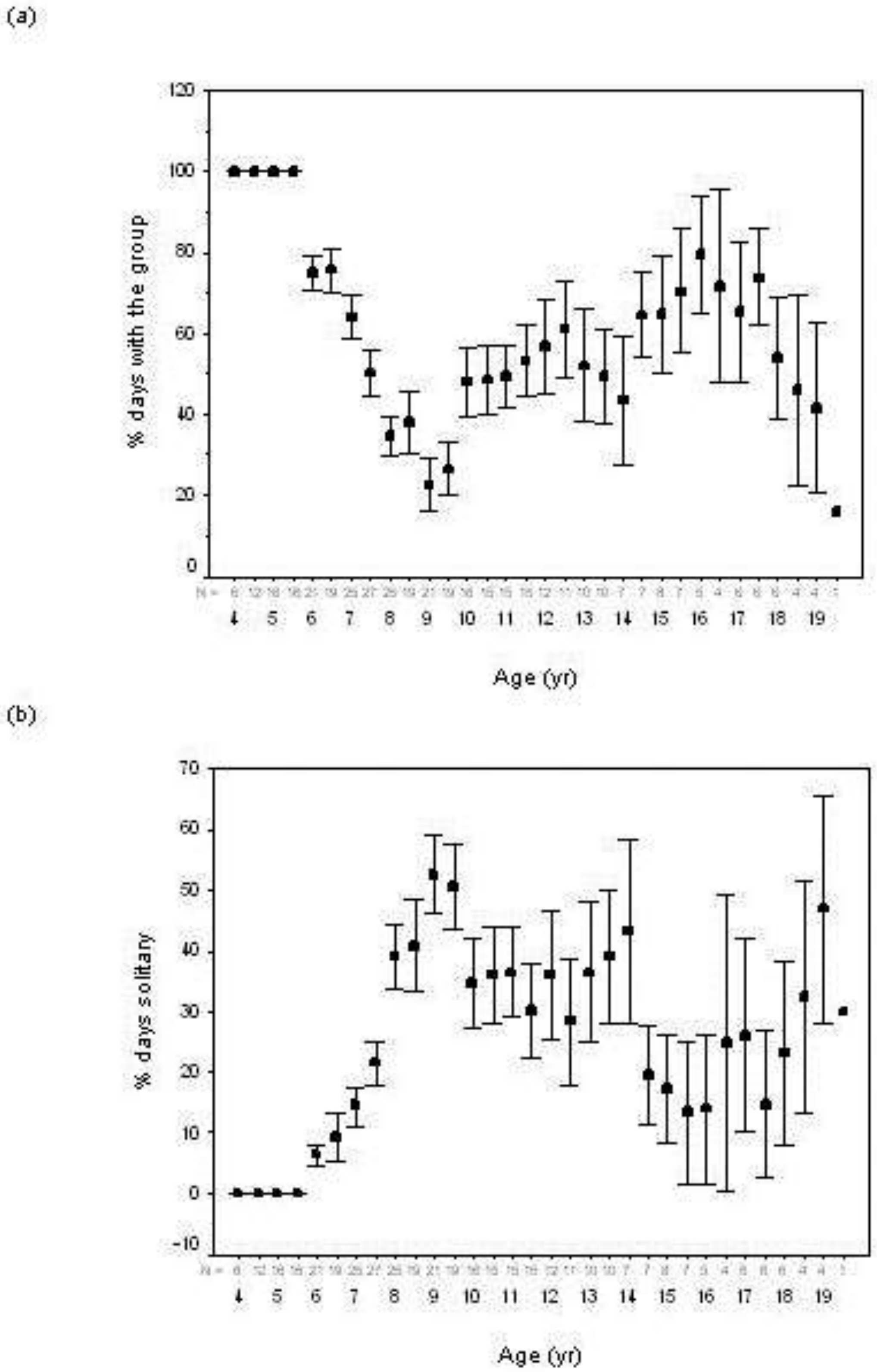

Fig. 5. Body size vs. age. Mean±sem body mass (a) and crown-rump length (b) for 6 month age classes. Sample sizes are shown below the x-axis. Individual males contributed 1-41 data points for mass (138 males, mean 7.1±0.6), and 1-25 data points for CRL (126 males, mean 5.3±0.4)

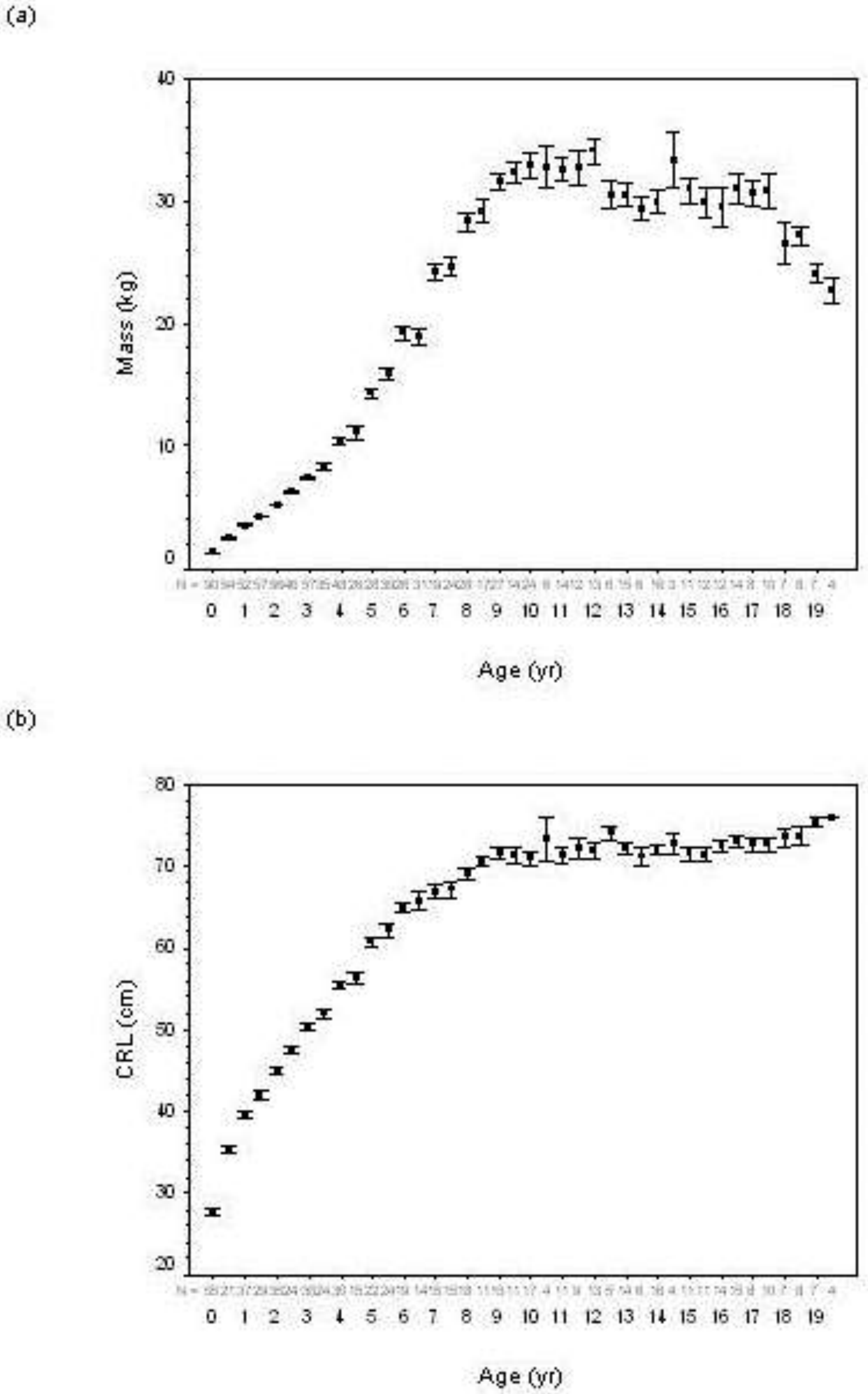

Fig. 6. Secondary sexual characters vs. age. Mean±sem red coloration (a), TV (b) and fattedness (c) for 6 month age classes. Sample sizes are shown below the x-axis. Individual males contributed 1-19 data points (67 males, mean 4.8±0.5) for red coloration, 1-25 data points (94 males, mean 4.9±0.5) for TV, and 1-10 data points (102 males, mean 3.5±0.2) for tail width.

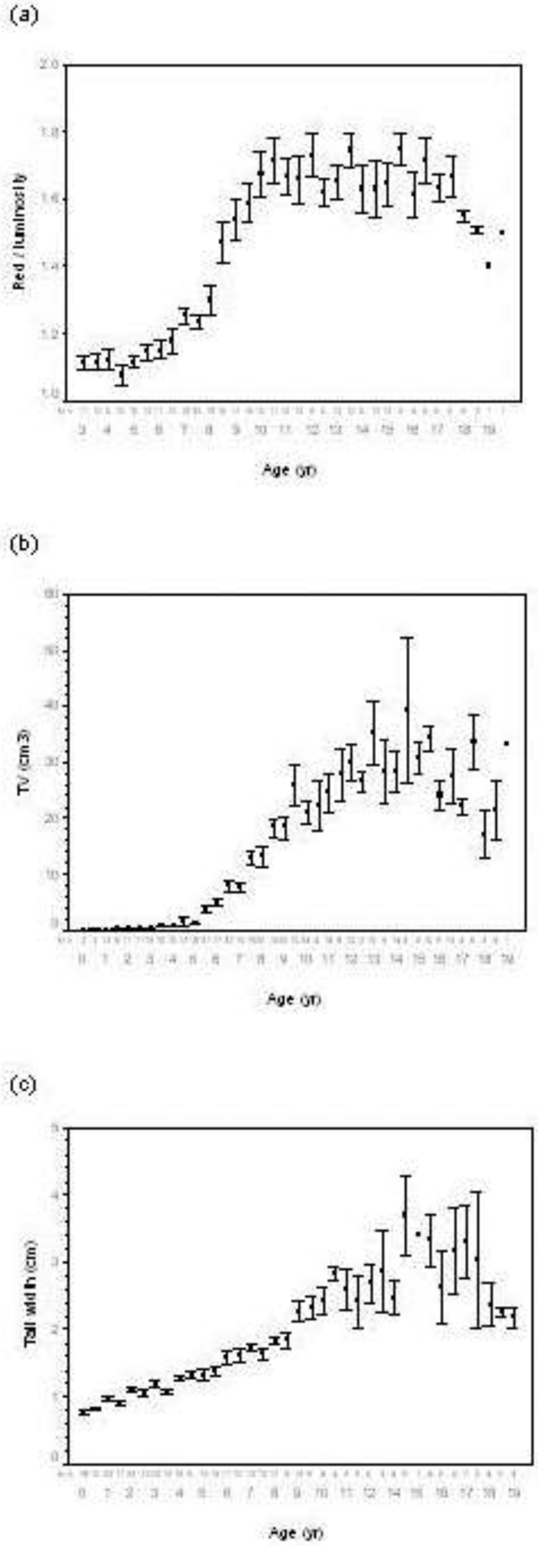

Table 1: Group composition during the study period

| | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Enclosure 1** | | | | | | | | | | | | | | | | | | | | | | | |
| Total | 15 | 47 | 57 | 48 | 49 | 59 | 69 | 80 | 86 | 67 | 73 | 79 | 75 | 47 | 57 | 48 | 49 | 59 | 69 | 80 | 86 | 67 | 79 |
| All females | 8 | 9 | 9 | 11 | 10 | 16 | 18 | 19 | 21 | 25 | 34 | 37 | 28 | 31 | 22 | 22 | 30 | 34 | 40 | 43 | 35 | 42 | 47 |
| Reproductive females | 2 | 5 | 6 | 7 | 7 | 9 | 10 | 11 | 14 | 16 | 18 | 19 | 16 | 16 | 13 | 13 | 15 | 17 | 22 | 23 | 20 | 20 | 26 |
| All males | 7 | 9 | 9 | 12 | 13 | 15 | 17 | 20 | 26 | 33 | 36 | 38 | 19 | 26 | 26 | 27 | 29 | 35 | 40 | 43 | 32 | 31 | 32 |
| Adolescent males | 4 | 5 | 6 | 6 | 4 | 4 | 3 | 3 | 5 | 6 | 11 | 14 | 11 | 11 | 11 | 10 | 12 | 13 | 17 | 15 | 12 | 8 | 13 |
| Adult males | 1 | 1 | 1 | 1 | 3 | 5 | 5 | 6 | 6 | 6 | 7 | 7 | 1 | 2 | 3 | 5 | 8 | 9 | 10 | 8 | 6 | 5 | 5 |
| **Enclosure 2** | | | | | | | | | | | | | | | | | | | | | | | |
| Total | | | | | | | | | | | | | 25 | 25 | 28 | 32 | 33 | 37 | 41 | 47 | 51 | 61 | 60 |
| All females | | | | | | | | | | | | | 13 | 13 | 12 | 14 | 15 | 18 | 21 | 25 | 29 | 36 | 36 |
| Reproductive females | | | | | | | | | | | | | 6 | 9 | 8 | 9 | 10 | 12 | 12 | 13 | 15 | 16 | 22 |
| All males | | | | | | | | | | | | | 12 | 12 | 16 | 18 | 18 | 19 | 20 | 22 | 22 | 25 | 24 |
| Adolescent males | | | | | | | | | | | | | 6 | 5 | 5 | 5 | 5 | 4 | 8 | 9 | 11 | 12 | 11 |
| Adult males | | | | | | | | | | | | | 4 | 4 | 4 | 4 | 4 | 5 | 4 | 4 | 3 | 3 | 4 |

Group composition in January of each year
Reproductive females are females old enough to show sexual swellings during the year concerned
Adolescent males are aged 4-9 yr
Adult males are aged 9+ yr

Table 2: Results of multiple regressions investigating the influence of various predictor variables on the age that males attained adult rank, and PCA factors describing adolescent and adult development for age.

| Dependent variable | $R^2_{adj}$ | Mean square |  | F | p | Predictor variables | ß | t | p |
|---|---|---|---|---|---|---|---|---|---|
|  |  | regression (df) | residual (df) |  |  |  |  |  |  |
| Age attained adult rank | 0.248 | 5.722 (1) | 0.866 (16) | 6.604 | 0.021 | Maternal rank | 0.224 | 0.984 | 0.341 |
|  |  |  |  |  |  | Maternal mass | 0.088 | 0.381 | 0.708 |
|  |  |  |  |  |  | N$^o$ adults when 9 | -0.137 | -0.588 | 0.565 |
|  |  |  |  |  |  | Age of eldest male when 9 | -0.355 | -1.694 | 0.110 |
|  |  |  |  |  |  | N$^o$ males in cohort | 0.320 | 1.560 | 0.138 |
|  |  |  |  |  |  | Age of alpha when 9 | 0.541 | 2.570 | **0.021** |
| Adolescent factor 1 | 0.577 | 7.000 (2) | 0.587 (14) | 11.916 | 0.001 | Maternal rank | 0.788 | 4.439 | **0.001** |
|  |  |  |  |  |  | Maternal mass | 0.077 | 0.391 | 0.702 |
|  |  |  |  |  |  | N$^o$ adults when 9 | 0.333 | 1.641 | 0.125 |
|  |  |  |  |  |  | N$^o$ males in cohort | -0.647 | -3.644 | **0.003** |
|  |  |  |  |  |  | Age alpha when 9 | 0.028 | 0.126 | 0.902 |
|  |  |  |  |  |  | Rank | -0.027 | -0.158 | 0.877 |
| Adolescent factor 2 | 0.397 | 3.136 (2) | 0.501 (14) | 6.263 | 0.011 | Maternal rank | -0.121 | -0.593 | 0.564 |
|  |  |  |  |  |  | Maternal mass | 0.476 | 2.452 | **0.028** |
|  |  |  |  |  |  | N$^o$ adults when 9 | 0.025 | 0.103 | 0.919 |
|  |  |  |  |  |  | N$^o$ males in cohort | 0.147 | 0.695 | 0.499 |
|  |  |  |  |  |  | Age alpha when 9 | 0.161 | 0.759 | 0.462 |
|  |  |  |  |  |  | Rank | 0.497 | 2.557 | **0.023** |
| Adolescent factor 3 | 0.284 | 5.004 (1) | 0.681 (15) | 7.350 | 0.016 | Maternal rank | -0.239 | -1.138 | 0.274 |
|  |  |  |  |  |  | Maternal mass | -0.058 | -0.265 | 0.795 |
|  |  |  |  |  |  | N$^o$ adults when 9 | -0.028 | -0.113 | 0.912 |
|  |  |  |  |  |  | N$^o$ males in cohort | -0.005 | -0.021 | 0.984 |
|  |  |  |  |  |  | Age alpha when 9 | 0.248 | 1.149 | 0.270 |
|  |  |  |  |  |  | Rank | 0.573 | 2.711 | **0.016** |
| Adult factor 1 | 0.379 | 6.523 (1) | 0.606 (15) | 10.765 | 0.005 | Maternal rank | 0.159 | 0.796 | 0.439 |
|  |  |  |  |  |  | Maternal mass | 0.247 | 1.276 | 0.223 |
|  |  |  |  |  |  | Rank | 0.646 | 3.281 | **0.005** |
| Adult factor 2 | -0.126 | 0.322 (3) | 0.796 (13) | 0.405 | 0.752 | Maternal rank | -0.106 | -0.376 | 0.713 |
|  |  |  |  |  |  | Maternal mass | -0.228 | -0.812 | 0.432 |
|  |  |  |  |  |  | Rank | -0.060 | -0.227 | 0.824 |
| Adult factor 3 | 0.367 | 1.910 (3) | 0.467 (13) | 4.086 | 0.030 | Maternal rank | 0.550 | 2.614 | **0.021** |
|  |  |  |  |  |  | Maternal mass | -0.507 | -2.403 | **0.032** |
|  |  |  |  |  |  | Rank | -0.311 | -1.557 | 0.144 |

Table 3: Results of Spearman rank correlations between alpha male tenure and group demography, maternal variables, early development and adult development

|  | Number of adult males present | Number of adolescent males maturing | Maternal rank | Maternal mass | Early development | Adult factor 1 | Adult factor 2 | Adult factor 3 |
|---|---|---|---|---|---|---|---|---|
| $r_s$ | -0.851 | -0.794 | -0.529 | 0.232 | -0.359 | -0.051 | -0.667 | -0.616 |
| p | 0.032 | 0.059 | 0.280 | 0.638 | 0.553 | 0.935 | 0.219 | 0.269 |
| n | 6 | 6 | 6 | 6 | 5 | 5 | 5 | 5 |

Application of the sequential Bonferroni correction does not influence the significance of the results

Table 4: Component matrix for residuals for age for adolescent males

|  | Factor (% variance explained) |  |  |
|---|---|---|---|
|  | 1 (30%) | 2 (22%) | 3 (20%) |
| Red coloration | -0.140 | 0.876 | -0.204 |
| Time spent with group | -0.834 | 0.075 | 0.356 |
| Time spent solitary | 0.743 | -0.021 | -0.517 |
| Mass | 0.487 | 0.095 | 0.729 |
| CRL | 0.468 | -0.227 | 0.626 |
| TV | 0.718 | 0.012 | 0.141 |
| Fattedness | -0.015 | 0.741 | 0.464 |
| Canine height | 0.424 | 0.621 | -0.212 |

Table 5: Variation during adulthood

|  | Mean | Range | N | Max variation within an individual male | Mean age at max (range) (yr) |
|---|---|---|---|---|---|
| Max. time with group | 78% | 5-100% | 16 | 1-99 % | 12.1 (10.0-17.5) |
| Max. time solitary | 55% | 0-100% | 16 | 1-91% | 11.0 (10.0-13.5) |
| Mass | 36.3 kg | 27.4-45.0 kg | 21 | 21-43 kg (22 kg) | 11.7 (9.3-15.6) |
| CRL | 72.0 cm | 66-79cm | 21 | N/A | N/A |
| Max color attained | 1.9 | 1.5-2.2 | 23 | 1.4-2.2 (0.8) | 12.2 (9.5-17.0) |
| Max TV attained | 37 $cm^3$ | 15-100 $cm^3$ | 26 | 19.7-99.7 $cm^3$ (80 $cm^3$) |  |
| Maximum canine height | 4.5 cm | 4.1-5.1cm | 18 | 1.2-5.1 cm (3.9 cm) | 9.9 (9.1-10.7) |
| Max fattedness | 3.3 cm | 1.8-7.7 cm | 12 | 1.7-7.7 cm (6 cm) | 13.2 (10.2-16.6) |

Table 6: Component matrix for residuals for age for adult males

| | Factor (% variance explained) | | |
|---|---|---|---|
| | 1 (31%) | 2 (27%) | 3 (14%) |
| Red coloration | 0.495 | 0.090 | 0.128 |
| Time spent with group | 0.756 | -0.478 | -0.393 |
| Time spent solitary | -0.669 | 0.514 | 0.468 |
| Mass | 0.611 | 0.495 | 0.256 |
| CRL | 0.754 | 0.267 | 0.401 |
| TV | 0.435 | 0.763 | -0.091 |
| Fattedness | -0.277 | 0.593 | -0.423 |
| Canine height | 0.018 | -0.635 | 0.556 |

Table 7: Comparison of alpha and other adult males for behavioral and morphological variables during stable periods

| | Alpha scores highest | Another male scores highest | Insufficient data |
|---|---|---|---|
| Time spent with group | 11 | 0 | 1 |
| Time spent solitary | 0 | 11 | 1 |
| Red coloration | 11 | 0 | 1 |
| Mass | 3 | 5 | 4 |
| CRL | 4 | 4 | 4 |
| TV | 3 | 5 | 4 |
| Fattedness | 4 | 3 | 5 |
| Canine height | 1 | 6 | 5 |