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Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*)

Abstract In sexually dimorphic, polygynous species, where males provide little parental care and competition between males for access to fertile females is high, sexual selection theory predicts sex differences in age-specific reproductive output and mortality profiles, and greater variance in lifetime reproductive success in males than in females. We examined age-specific reproductive output, mortality patterns and the extent and causes of variation in reproductive success for a semi-free-ranging colony of mandrills (*Mandrillus sphinx*, Cercopithecidae) in Franceville, Gabon, using long-term (20 year) demographic records and microsatellite parentage analysis. Although differences in the demography and feeding ecology of this closed, provisioned colony, in comparison with wild mandrills, limit interpretation of our results, sex differences in reproductive output and mortality showed the patterns predicted by sexual selection theory. Mortality was higher in males than in females after sexual maturity, and lifespan was significantly shorter in males (mean 14 year) than in females (>22 year). Age at first reproduction was signif-

icantly earlier in females (mean 4.2 year) than in males (11.6 year), and male reproductive output declined earlier. All females of breeding age produced offspring; while only 17 of 53 sexually mature males (32%) sired. Males sired a maximum of 41 offspring, versus 17 in females, and variance in male reproductive output was significantly greater than in females at all ages. The most important influence on variation in lifetime reproductive output in both sexes was joint variation between length of the breeding period and reproductive rate, due to lower reproductive rates in younger animals. Finally, social rank significantly influenced reproductive output in both sexes: high-ranking females began their reproductive careers earlier and had a higher subsequent reproductive rate than low-ranking females, while males that achieved top rank during their career sired far more offspring than males that did not.

Keywords Age at first reproduction · Lifetime reproductive success · Intra-sexual competition · Dominance

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Introduction

Sexual selection arises from "the advantages that certain individuals have over others of the same sex and species, in exclusive relation to reproduction" (Darwin 1871, p. 256). In polygynous species, sex differences in parental investment and potential rates of reproduction lead to different reproductive priorities in males and females (Trivers 1972; Clutton-Brock and Vincent 1991). Although female reproductive success is mainly limited by access to resources, and the time required to transfer those resources to offspring during gestation and lactation, male reproductive success is primarily determined by access to fertile females (Bateman 1948; Trivers 1972). Thus sexual selection is more intense in males than in females, with competition between males for access to fertile females (intra-sexual selection) favouring the evolution of aggressiveness, larger body size and weaponry; and female mate choice (inter-sexual selection)

leading to the evolution of extravagant male ornaments (Darwin 1871).

Sex differences in the nature of competition and the intensity of sexual selection predict differences in patterns of reproductive output versus age in males and females. Female reproductive output is expected to show an inverted U-shaped curve, beginning at a relatively young age, increasing after the first few breeding attempts, reaching a plateau as females reach adult size, and continuing at a constant level until females reach old age, at which point output decreases again with physical decline in the ageing female (Clutton-Brock 1988). Variation in female reproductive output is likely to be best explained by variation in breeding lifespan. By contrast, male reproductive output is expected to show more individual variation, and to be more closely related to competitive ability. Male age at first reproduction should be delayed in comparison to females, as young males are competitively inferior to males in their prime. Reproductive output should peak during early adulthood, when males reach prime competitive ability, then decline with age and body condition, producing a condensed breeding lifespan in comparison to that of females (Clutton-Brock 1984; Maher and Byers 1987; Dunbar 1988). Finally, polygynous mating systems also predict that male survival should be lower than in females, due to the costs of intra-sexual competition and large body size (Ralls et al. 1980; Promislow 1992).

Long-term studies of reproductive success are relatively rare for large mammals, due to their requirement for continuous, longitudinal observations of identified individuals that reproduce slowly over long life spans. However, some notable studies exist for red deer (*Cervus elaphus*, Clutton-Brock et al. 1988; Kruuk et al. 1999), Soay sheep (*Ovis aries*, Coltman et al. 1999), lions (*Panthera leo*, Packer et al. 1988), elephant seals (*Mirounga angustirostris*, le Boeuf and Reiter 1988), baboons (*Papio anubis*, Packer 1979; *P. cynocephalus*, Alberts and Altmann 2003; Altmann et al. 1996) and macaques (*Macaca fuscata*, Fedigan et al. 1986; *M. fascicularis*, van Noordwijk and van Schaik 1999; *M. sylvanus*, Kuester et al. 1995; *M. mulatta*, Bercovitch et al. 2003). Assessing male reproductive output is particularly difficult in species where females mate with multiple males per receptive period (e.g. in the multi-male, multi-female societies of many primate species). Although the development of molecular techniques has allowed accurate paternity assignment, many of the available assessments of lifetime reproductive success use behavioural estimates of male mating success to estimate reproductive success (e.g. Packer 1979; Fedigan et al. 1986), which can result in biases due to surreptitious and nocturnal mating behaviour (e.g. Drickamer 1974). In addition, male mating success is not necessarily equal to fertilisation success for a variety of reasons, including the timing of mating in relation to ovulation, sperm competition, and cryptic female choice (Parker 1970; Eberhard 1996). Finally, social rank changes over an individual male's career and short-term cross-sectional studies (e.g. over one or two mating seasons) may therefore artificially inflate estimates of male reproductive skew, by providing a "snap-shot" image of a single stage in each male's life-history (Hausfater 1975; Altmann et al. 1996). Collection of long-term genetically determined paternity data is further impeded for species in which males disperse away from study groups, and where the previous history of immigrating males is unknown (e.g. Alberts and Altmann 1995). It is thus not surprising that such data are still extremely rare.

Mandrills (*Mandrillus sphinx*, Cercopithecidae) live in multi-male, multi-female groups, and are one of the most sexually dimorphic species of land mammal, typifying the sex differences that prompted Darwin to develop his theory of sexual selection. Male body mass is 3.4 times that of females (Setchell et al. 2001), and male canine teeth measure 44 mm, versus 10 mm in females (Setchell and Dixson 2002; Leigh et al. 2005). Adult males also possess a variety of exaggerated secondary sexual adornments, including brightly coloured 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). This adult sexual dimorphism is reflected in patterns of growth and development: while females reach adult size at the age of 7 year, males do not attain adult size and appearance until 9–10 year (Setchell et al. 2001; Setchell and Dixson 2002). Differences between males and females are thought to have evolved due to intense male–male competition in this species (Wickings and Dixson 1992b; Setchell and Dixson 2001), although female choice for large, ornamented males may also be involved (Setchell 2005).

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 (Harrison 1988). Most of our knowledge of mandrill behaviour and reproduction therefore comes from a semi-free-ranging colony at the Centre International de Recherches Médicales, Franceville (CIRMF), Gabon. Studies of this colony show that mandrills have typical cercopithecid matrilineal inheritance of rank (Setchell 1999). Breeding is moderately seasonal, with 63% of peri-ovulatory periods occurring between July and September, and only 6% between December and April (Setchell and Wickings 2004), and a corresponding birth peak in January to March (Setchell et al. 2002). Preliminary data from the wild suggest a similar pattern, with tumescent females observed from May to November (Abernethy et al. 2002). Previous paternity studies have shown that variance in male reproductive output is extremely high in the CIRMF colony, with the top-ranking male siring 70–100% of offspring born during a single birth season (Wickings et al. 1993; Wickings 1995). However, no study has yet examined the relationship between male reproductive output and age, or compared this with female reproductive careers.

In this study we present 20 years of demographic and paternity data for the CIRMF mandrill colony, to examine age-specific patterns of reproductive output and mortality in the two sexes; variation in total reproductive output and the contribution of non-breeders, length of the breeding period and reproductive rate to that variation; and the influence of maternal and social rank on reproductive output. Although

this semi-free colony lacks predation and male migration, these are the best estimates of reproductive success that we can currently make for mandrills, as reproductive data remain impossible to collect for wild mandrills.

Methods

Study population

The semi-free-ranging breeding colony of mandrills at CIRMF, Gabon was established in 1983 when 15 animals (8 females and 7 males) were released into a naturally rain-forested enclosure 6.5 ha in area (Enclosure 1). A second semi-free-ranging group was established in 1994 (Enclosure 2, 3.5 ha) by transferring 17 mandrills (including 6 adult females and 4 adult males) from the first enclosure. In addition to the founder animals, a total of 228 individuals (115 females, 105 males, 8 sex unknown) had been born into the colony by September 2002, when data collection for this study ended. Fifty-one individuals (8 females, 29 males, 14 sex unknown) have died or disappeared (presumed dead), 45 (26 females aged 0–10 year, 19 males aged 0–17 year, including representatives of all matrilines) have been removed to provide subjects for medical research at the CIRMF (n=43), and to prevent the spread of naturally occurring lentiviral infection in Enclosure 1 (n=2). At the end of the study 147 animals (83 females, 64 males) remained in the enclosures. The animals forage naturally in the enclosures, and receive daily provisions of monkey chow, fruits and vegetables. Water is available *ad libitum*. The date of birth is recorded for all individuals born into the colony. The age of founder animals was estimated using dentition (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 year are given coloured and numbered ear-tags to aid identification. Veterinary intervention is limited to animals that are severely injured, but may artificially increase survival.

The numbers of females and males contributing to each age-class in this study are listed in S1 (individuals contributed to multiple age-classes as they aged). To examine female reproductive output, we included all conceptions that resulted in the birth of an infant (early abortions may have been missed). Data concerning male reproductive output were obtained using genetic paternity determination for 193 of the 228 infants born into the enclosures during the study period. Sires were unknown for 35 offspring, either because no blood sample was available, or because sires could not be identified with confidence. As paternity is concentrated in the alpha male during any one mating season (Wickings et al. 1993; Wickings 1995; Charpentier et al. 2005), unknown sires are most likely to be the alpha male. The missing data are therefore likely to reduce variation in male reproductive output, if they introduce any bias into the analyses. We did not include offspring survival in analyses of reproductive success, as mortality rates were extremely low. Only 15 of 228 mandrills born into the colony died before the age of 1 year (6.6%) and paternity could be determined for only five of these offspring.

Age-classes

The testes descend at an average of 3.8±0.3 year (n=15) in male mandrills (Setchell and Dixson 2002) and males were therefore considered as potential sires from this age. Males aged 3.8–9.0 year, who were sexually mature but not yet fully grown (Setchell and Dixson 2002), were classed as adolescent. Males aged 9+ year may be of adult size and appearance (Setchell and Dixson 2002), and may out-rank older males (Setchell 2003), and were classed as adults. Females were termed sexually mature once they had conceived their first offspring.

Dominance hierarchies

Rank relations between males and between females were determined using *ad libitum* records of avoidance behaviour made during daily observation periods. Female dominance ranks are stable in mandrills (Setchell 1999), and female rank at each conception was expressed as the percentage of females over 3 years of age dominated (no changes in rank have been observed after this age, unpublished data) to account for demographic changes over time (Cheney et al. 1988). Females were grouped into high (upper quartile), mid (25–75%), and low rank (lower quartile) classes, and the median rank of each female over her breeding life span was also calculated for some analyses.

The identity of the dominant male (alpha) was always clear from avoidance interactions between males (all other males avoided this individual, who never avoided other males). Where changes in alpha male occurred, these were clear and occurred from one day to the next. For the purposes of this study males were divided into those that became alpha at some stage during the study (alpha males and those that did not (non-alpha males).

Mortality

Individuals that disappeared from the enclosures were used to examine sex differences in patterns of mortality. These animals are presumed to have died; disappearances could not be due to transfer into another group, as this is not possible in the CIRMF colony.

Paternity analysis

Blood samples were obtained during annual captures when animals were anaesthetized using blowpipe intramuscular injections of ketamine (Imalgène 1000;10 mg/kg body weight). DNA was extracted from blood samples as previously described (Wickings 1995). Maternity was

Table 1 Characteristics of the eight microsatellite loci used for paternity analyses

Locus	Number of alleles	Frequencies (range)	Observed heterozygosity
D18S536	8	0.014–0.470	0.731
D3S1768	10	0.007–0.293	0.798
D12S67	16	0.002–0.160	0.939
D13S765	8	0.002–0.329	0.819
D8S1106	6	0.062–0.529	0.705
D5S1457	9	0.005–0.289	0.853
D2S1326	6	0.033–0.372	0.699
D5S1470	10	0.005–0.205	0.899

verified and paternity assigned using eight microsatellite loci (Table 1). Genotypes were available for all potential sires, and paternity was assigned using two methods: CERVUS 2.0 (http://helios.bto.ed.ac.uk/evolgen/cervus, Marshall et al. 1998) and PARENTE (Cercueil et al. 2002).

CERVUS 2.0 is based on the likelihood-based approach described in Marshall et al. (1998). Simulations were carried out to estimate the critical difference in log-likelihood score between the most likely and the second most likely candidate father. Simulation input parameters were 2.4% rate of typing errors, 92.6% of loci typed and 10,000 cycles. Estimation of the frequency of null alleles did not reveal any deviation from Hardy–Weinberg equilibrium. In 177 cases CERVUS assigned a sire with a 95% confidence level, and for the remaining 28 cases sires were attributed at only a relaxed level (80%).

PARENTE (Cercueil et al. 2002) was used to confirm paternity in cases where CERVUS attributed sired at a relaxed level. PARENTE uses a Bayesian method to calculate the probability of paternity for each sire using information from all possible sires. For each individual, PARENTE verifies the genetic and age compatibilities for all potential triads (individual, potential mother, potential father), and calculates the probability that a parentage link is correct using the allelic frequencies and the sampling rate of the population, taking into account incompatibilities and the error rate (estimates of the error rate in the data and mean proportion of loci typed were the same as for CERVUS).

Using a combination of CERVUS and PARENTE, paternity could be assigned for 193 (94%) of 205 infants for whom blood samples were available (for more details see Charpentier et al. 2005).

Statistical analysis

Kaplan–Meier survival analyses were used to examine age at first reproduction (conception in females, fertilisation in males) and age at disappearance (presumed mortality). Log rank test statistics were used to test for equality of survival distributions. Founder females were excluded from examination of age at first conception, as their early reproductive career may have been compromised by their captive conditions. Founder males were included in the sample (there

was no significant difference in the distribution of age at first reproduction for founder and colony-born males, log-rank statistic=0.00, df=1, p=0.966).

Age-specific reproductive output curves were plotted using the number of individuals present in each age-class (S1) and the number of conceptions (females) or offspring sired (males) per individual. Results are presented as offspring produced per year and total number of offspring produced versus age.

The proportion of variance in lifetime reproductive output attributable to non-breeders, breeding lifespan (L) and the average number of offspring produced per year of reproductive lifespan (F) were examined using methods developed by Brown (1988). According to these methods, the overall variance in lifetime reproductive success (LRS) among breeders and non-breeders is given by the expression:

$$pV(\mathrm{LRS}) + p(1 - p)\, m_{\mathrm{LRS}}^2$$

$V(\mathrm{LRS})$ and m_{LRS} are the sample variance and mean of LRS, respectively, calculated only for breeders. p is the proportion of breeders. The first term in this expression is the proportion of variance due to variation among animals that successfully bred, while the second is the proportion of the overall variation due to failure to breed (Brown 1988, p. 448).

As our measure of LRS does not include offspring survival, LRS is equal to the product of L and F. Variation in LRS among those animals that bred could therefore be partitioned into variation in L (defined as the number of years since first conception in females; number of years since sexual maturity in males), F (defined as the offspring produced per year of breeding period), and joint variation in L and F (Brown 1988). The percentage variance in LRS accounted for by variation in the individual variables L and F and their product can be calculated as follows (Brown 1988):

Standardised variances (G values) are calculated for L and F as the square of the coefficient of variation as $G(L) = V(L)/m_L^2$ and $G(F) = V(F)/m_F^2$, where m_L and m_F are the means, and $V(L)$ and $V(F)$ the variances of L and F, respectively. Standardised variance in LRS is calculated as $G(LF)=V(LF)/(m_L m_F)$, where $V(LF)$ is variance in total reproductive output. $G(L)$ and $G(F)$ expressed as a percentage of $G(LF)$ then give the percentages of $V(LF)$ accounted for by variation in the individual variables L and F, respectively, while the remaining percentage is accounted for by joint variation between L and F.

Strictly, the above analyses should only take into account individuals for whom the entire reproductive career is known. However, primates have long lifespans, and no study has yet been able to cover the whole reproductive career for a large sample of individuals. We therefore present analyses using all females and males in the sample, as well as estimating lifetime reproductive output for each sex. Too few females died naturally during the study to allow us to examine lifetime reproductive output. We therefore used six of the founder cohort of females (one founder female

was removed from the analysis because she died accidentally) to estimate lifetime reproductive output, reasoning that these females were approaching the end of their reproductive careers. Sufficient males died during the study period (n=24) to allow us to examine their lifetime reproductive output (note that this introduces a sampling error, as the majority of males were still alive at the end of the study).

Statistical analyses were performed with SPSS for Windows release 11.0.0 (SPSS Inc. Chicago, Illinois, 2001). Means are quoted $\pm$ SE; all tests are two-tailed.

Results

Age-specific mortality

Mortality was generally low, but a marked sex difference was observed (Fig. 1; log-rank test statistic=11.44, df=1, p<0.001). The two sexes were indistinguishable until the age of 4 year, but sex differences became marked at 6 year. Of 111 females, only eight disappeared (7%): seven before 5 year, and one after 19 year. Females lived to 22$\pm$1 year (95% CI 21–24 year, median survival could not be calculated for females, due to the small number of disappearances), although the data were limited to 25 year, meaning that females may survive longer than this. Male survival was 14$\pm$1 year (95% CI 13–16 year, median 17 year); no male lived longer than 20 year. Males that disappeared prior to reaching adulthood (n=14) simply disappeared from one day to the next. However, of the 10 adult males that disappeared, four were seriously wounded prior to disappearance (likely as a result of male–male combat); three of these were alpha male at the time.
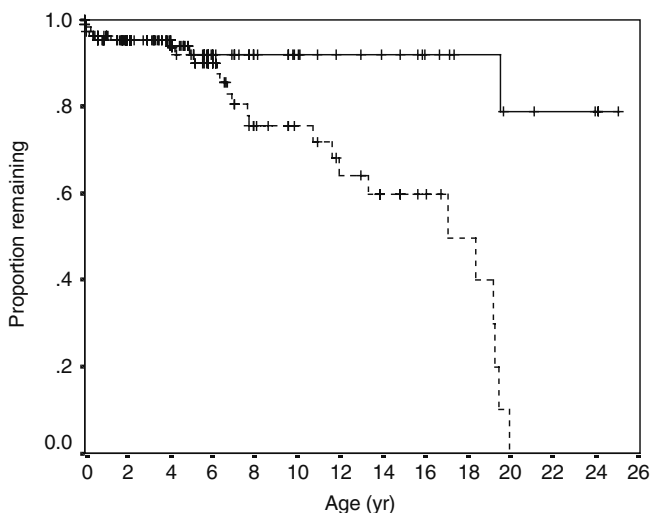

Fig. 1 Age-specific survival in female (*solid line*) and male (*dashed line*) mandrills. Curves were produced using survival analysis to examine patterns of disappearances. Crosses represent censored cases
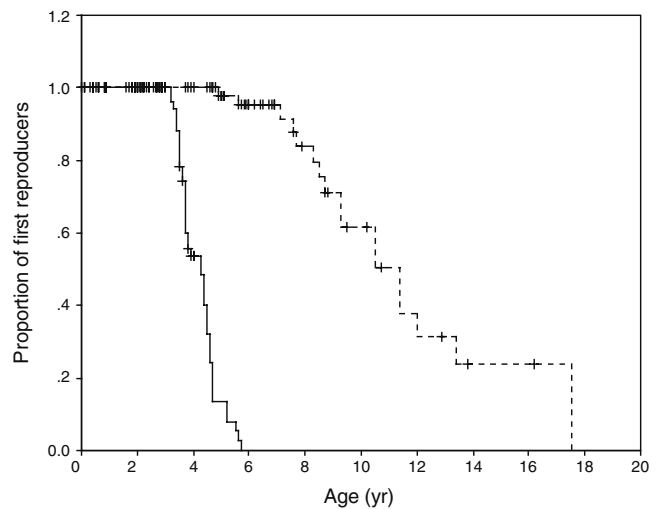

Fig. 2 1-cumulative survival curve showing age at first reproduction in female (*solid line*) and male (*dashed line*) mandrills. Crosses indicate censored cases

Age at first reproduction

Females conceived their first offspring at 4.3$\pm$0.3 year, significantly earlier than males sired for the first time, at 11.4$\pm$1.0 year (Fig. 2; log-rank test statistic=107.58, df=1, p<0.001). Females were thus pre-reproductive for a mean of 22% of their lifespan, versus 83% in males. Variance in age at first reproduction was significantly greater in males than in females ($F_{1,58}$=30.66, p<0.001). The youngest sire was aged 4.9 year, although this fertilisation occurred when no adult males were associated with the social group. The youngest male to sire in the presence of multiple adult males was aged 5.6 year.

All surviving females conceived by the age of 5.7 year (Table 2). Among sexually mature males, the probability of becoming a sire increased significantly with age (logistic regression: sire vs. non-sire, B=0.78, standard error of B=0.21, Wald statistic=13.25, df=1, p<0.001, exp(B)=2.18). Fifty-two percent (11 of 21) of males sired at least one offspring by the time they reached adulthood, and the probability of siring at least one infant reached 1.0 in males aged 18 year (Fig. 2). However, few older males were present in the study sample.

Age-specific reproductive output

Female output increased from age 3–5 year, remained relatively constant from 5–22 year, and dropped to zero at 24 year (Fig. 3). Although this is possible evidence for a decrease in output with age, few aged females contributed to the study (see table in S1). Sexually mature females conceived 0.8$\pm$0.0 infants per year. Maximum female output was one infant per year, with one exception (in 353 female-years, females older than 3 year), when a female bore two surviving infants in the same year.

Mean male reproductive output was <0.1 offspring per year until the age of 7 year, rose steeply to peak at age

Table 2 Age at first conception (females) and sirehood (males)

	Number of events	Number censored	Range	Median±SE	95% CI for median	Mean±S.E	95% CI for mean
Females	43	49	3.2–5.7 year	4.3±0.3 year	3.7–4.9 year	4.2±0.1 year	4.0–4.4 year
Males	17	53	4.9–17.5 year	11.4±1.0 year	9.5–13.3 year	11.6±0.8 year	10.0–13.3 year

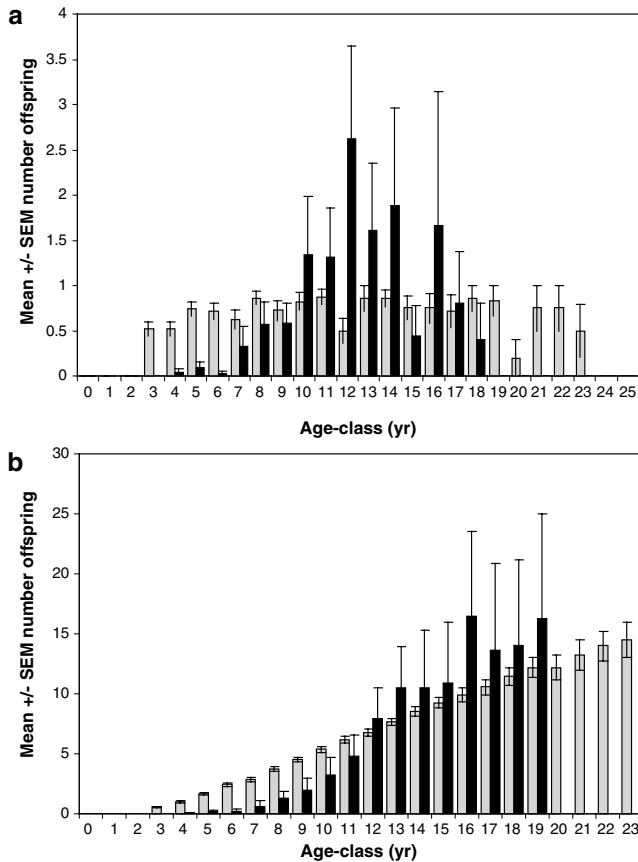Censored cases are those where females had not yet conceived, and males had not yet sired by the end of the study

Fig. 3 Age-specific reproductive output (**a**) and age-specific cumulative reproductive output (**b**) in female (*grey bars*) and male (*black bars*) mandrills. Sample sizes for each age-class can be found in S1 (individuals contribute to several age-classes, age-classes with only one individual are not shown)

12 year, and decreased again to 0 by 19 year (Fig. 3a). Seventy-five percent of infants (146 of 193) were sired by males aged 10–16 year. Maximum male output was 13 offspring in any 1 year. Variance in male reproductive output was large, and greater than in females, at all ages between 7 and 18 year (Fig. 3a).

Variation in total female reproductive output

The total number of offspring produced by females increased steadily with age (Fig. 3b). The 51 sexually mature females produced a total of 1–17 offspring, with a variance of 19.8 (Table 3). Inclusion of the seven females (12%) that died before reaching sexual maturity did not alter variance in female output, with non-breeders accounting for 11.9%,

and breeders 88.1% of the variance. Partitioning the variance among breeding females showed that joint variation between L and F accounted for 75.2% of this variance, due to the low numbers of offspring produced per year in younger females. L (0.3–20.0 year, Table 3) accounted for 23.7% of variance in female output, while F (0.4–1.0 offspring per year, Table 3) accounted for only 1.1%.

The six founder females produced 13.2±1.2 offspring (Table 3). This underestimates lifetime output, as five of these females were still alive at the end of the study (all aged >20 year). Variance in lifetime reproductive output was low among these females (6.6), with no non-breeders. Partitioning this variance showed that, again, joint variation in L and F was by far the most important influence on female output (90.9%), while L (14.6–20.0 year, Table 3) accounted for 3.2%, and F (0.6–0.9 offspring per year, Table 3) accounted for 5.9%.

Social rank and female reproductive output

Age at first conception was significantly correlated with female rank ($n=43$, $r_s=0.598$, $p<0.001$, Fig. 4), and with maternal rank ($r_s=-0.692$, $p<0.001$). On average, high-ranking females had a 1.3 year advantage in age at first conception (3.7±0.1 year, $n=23$) when compared to low-ranking females (5.0±0.2 year, $n=7$).

Reproductive rate correlated significantly with a female's median social rank during her breeding career ($n=35$ multiparous females, $r_s=0.501$, $p=0.002$; Fig. 4), and with maternal rank at conception ($n=29$, $r_s=0.483$, $p=0.008$). This translated to a mean of 0.26 extra offspring per year in high-ranking females when compared with low-ranking females.

Variation in total male reproductive output

Mean male output equalled that of females at 12 year, after which it was equal to or greater than female output (Fig. 3b). Variance in the total number of offspring produced was greater in males than in females at all ages once males began to reproduce (Fig. 3b). Sexually mature males produced 3.5±1.1 offspring, with a maximum output of 41 (Table 3). Of 53 males that reached sexual maturity, 36 (68%) produced no offspring, while the 17 successful males sired 10.4±2.7 offspring each. Variance in male reproductive output was 140.7 for breeding males. Inclusion of non-breeders reduced the overall variance in reproductive output for sexually mature males to 68.6, of which

Table 3 Reproductive output, length of the breeding period and reproductive rate in male and female mandrills

	n	Mean	SEM	Median	Range	Variance
Reproductive output						
Sexually mature females	51	4.7	0.6	2.0	1–17	19.8
Founder females	6	13.0	1.1	12.5	10–17	7.6
Sexually mature males	53	3.5	1.1	0.0	0–41	68.2
Sires	17	10.3	2.7	5.0	1–41	140.7
Alpha males	9	17.9	4.4	15.0	4–41	171.1
Dead sires	9	14.1	5.0	5.0	1–41	228.1
Length of the breeding period, L (year)						
Sexually mature females	51	6.1	0.9	3.4	0.3–20.0	34.8
Sexually mature males	53	5.6	0.7	3.1	0.2–16.2	24.5
Sires	17	11.3	0.7	11.0	5.7–16.2	9.2
Alpha males	9	12.0	0.9	11.0	7.8–15.2	7.7
Dead sires	9	13.3	1.1	15.5	8.1–16.5	10.5
Reproductive rate, F						
Sexually mature females	46	0.8	0.0	0.8	0.4–1.0	0.0
Males aged >4.9 year	46	0.3	0.1	0.0	0.0–2.8	0.5
Sires	17	0.8	0.2	0.6	0.1–2.6	0.7
Alpha males	9	1.4	0.3	1.3	0.3–2.6	0.8
Dead sires	9	1.0	0.3	0.6	0.1–2.6	1.0

Length of the breeding period = age at death/removal/end of the study period less the age at first reproduction (females) or 3.5 year (males); reproductive rate = number of offspring produced per year of breeding period; alpha males = males that became alpha at some stage during their career; dead males = males that died naturally during the study, for whom LRS was known; sample sizes vary between variables, as not all information was available for all individuals

34.3% was attributed to non-breeders, and 65.7% to males that bred. The great majority of variation in male output was accounted for by joint variation between L and F (91.7%), due to the strong positive relationship between male output and age. L (5.7–16.2 year, Table 3) accounted for only 0.5% of variance in total reproductive output in breeding males, while F (0.0–2.6 offspring per year, Table 3) accounted for 7.8%.

Of the 25 males that died naturally during the study, and for whom lifetime reproductive output was therefore known, five died without reaching sexual maturity (20%), 11 reached sexual maturity but died without siring offspring (44%), and nine bred (36%). The nine breeding males sired 14.1±5.0 offspring, with a variance of 228.1 (Table 3). Inclusion of the 16 non-breeders reduced this variance to 85.4, of which 3.8% was due to non-breeders, and 96.2% was due to variance among breeders. L (8.1–16.5 year, Table 3) accounted for 0.3% of this variance, F (0.1–2.6 offspring per year, Table 3) for 6.8%, while joint variation between L and F accounted for 92.8% due to the increased probability of becoming a sire with age.

Social rank and male reproductive output

Nine males attained top (alpha) rank during the study period. Males gained alpha-status between the ages of 9 and 14 year, with the exception of a 4-year old who had no competing adult male. Males that survived longer were thus significantly more likely to become alpha (logistic regression: alpha vs. non-alpha, $B=0.38$, standard error=0.12, Wald statistic=10.66, df=1, $p=0.001$, Exp(B)=1.46). However, of the 22 males that reached adulthood and could potentially attain alpha status, only nine (41%) did so, while only four of ten males (40%) that reached 15 years (older than the oldest male that became alpha) became alpha during their career. Tenure as dominant male varied between 1 month and 6 year (mean 34±9 months, median 24 months).

Attaining alpha rank had a clear influence on reproductive output (Fig. 5), and alpha males sired 85% of offspring (163 of 193 resolved paternities). Alpha males sired up to 13 infants in any one year, versus a maximum of four infants for non-alpha males.

Maternal rank was not related to age at first sirehood ($n=11$, $r_s=-0.267$, $p=0.467$), and did not significantly influence the probability that a male sired, controlling for male age (Table 4). Nor did maternal rank predict the probability that a male became alpha male, controlling for male age (Table 4).

Discussion

This study provides the first long-term data concerning sex differences in the reproductive careers of mandrills, one of the most sexually dimorphic mammalian species. The results follow the patterns predicted by sexual selection theory (Bateman 1948; Trivers 1972). As predicted for species with a polygynous mating system (Ralls et al. 1980; Dunbar 1988; Promislow 1992), mortality was higher in males, and male lifespan was one third shorter than that of females. Males began to reproduce significantly later than females, with the pre-reproductive period representing a much greater proportion of the entire lifespan in males than in females. Males were thus far more likely to die without reproducing than females were. Variance in male reproductive output was high and markedly greater than among females. Whereas the great majority of females produced at least one infant, two-thirds of sexually mature
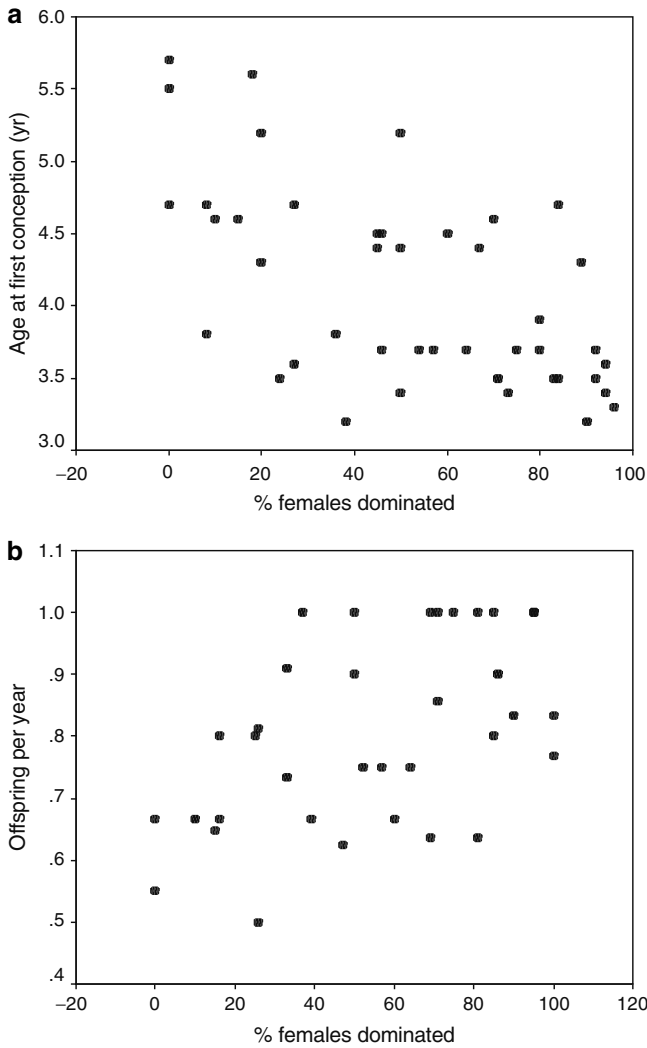
a

b

Fig. 4 Influence of social rank on age at first conception (**a**) and reproductive rate (**b**) in female mandrills

males did not sire offspring during the study period. Conversely, the maximum reproductive output per male in this study was far higher than that possible for females.

Female reproductive careers

The relationship between female age and reproductive rate matched the predicted inverted U-shape, and was similar
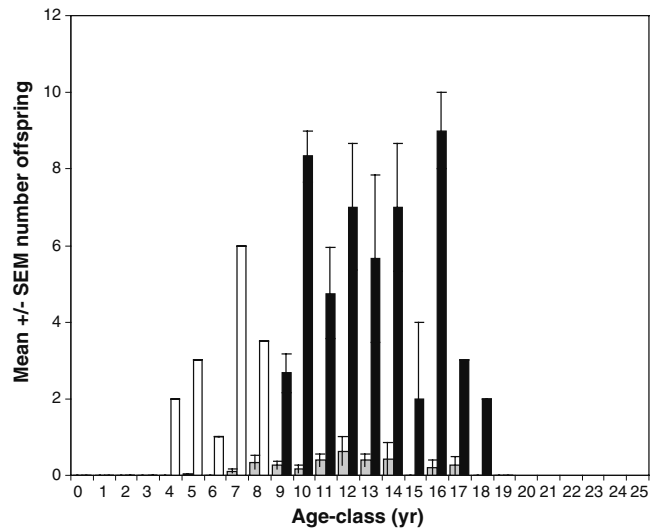

Fig. 5 Age-specific reproductive output in alpha (*black bars*) and non-alpha (*grey bars*) male mandrills. White bars represent infants sired by the alpha male during the first few years of the colony, when there were no older males present in the group. Sample sizes for each age-class can be found in Table 1 (individuals contribute to several age-classes)

to that reported for various species of macaque (Fig. 12 in van Noordwijk and van Schaik 1999), baboons (Alberts and Altmann 2003) and vervets (Cheney et al. 1988). Reproductive rate was markedly greater in these provisioned mandrills than in wild baboons (Alberts and Altmann 2003), but very similar to that in provisioned Barbary macaques (Paul and Kuester 1996). Whether mandrills experience a post-reproductive period of any substantial length, as in some other primate species (e.g. Paul et al. 1993; Pavelka and Fedigan 1999) remains to be established.

As in other primate species (Fedigan et al. 1986; Altmann et al. 1988; Bercovitch and Berard 1993; Kuester et al. 1995; van Noordwijk and van Schaik 1999; Rhine et al. 2000), variance in the length of the breeding period was a more important influence on female reproductive output than variance in the number of offspring produced per year, although joint variation between the two was the most important factor influencing female output, due to low rates of reproduction in younger females. Rank also significantly influenced female reproductive output, both in terms of age at first birth and reproductive rate. The nepotistic system of matrilineal rank inheritance in

Table 4 Results of logistic regressions testing for the influence of maternal rank on the dichotomous variables "sire versus non-sire" and "alpha versus non-alpha" controlling for male age

	B	SE	Wald	df	p	Exp (B)
Sire versus non-sire						
Male age	1.40	0.62	5.12	1	0.02	4.07
Maternal rank	−0.01	0.02	0.28	1	0.60	0.99
Constant	−9.33	4.34	4.63	1	0.03	0.00
Alpha versus non-alpha						
Male age	0.54	0.22	5.97	1	0.015	1.72
Maternal rank	−0.01	0.02	0.07	1	0.796	0.99
Constant	−5.87	2.52	5.45	1	0.020	0.00

female mandrills thus appears to result in a distinct reproductive advantage to high-ranking females, as also shown for wild long-tail macaques (van Noordwijk and van Schaik 1999).

Limitations of the study: females

Several aspects of this study limit the potential for extrapolation of our results to mandrills under more natural conditions. Among females, access to unlimited, high-quality food is likely to reduce the age at first reproduction and increase reproductive rate in all individuals (Asquith 1989; Lee and Bowman 1995). Provisioned resources may also artificially equalise variance in female reproductive rate by reducing intra-group competition by comparison with the wild (Fedigan et al. 1986; Hrdy 1987). However, food distribution, rather than abundance, is likely to be the most important factor influencing the nature of intra-group competition (Harcourt 1987; Isbell and Young 2002; Sterck et al. 1997; van Schaik 1989). Provisioning in the mandrill colony is provided as a clustered resource, promoting contest competition, and food is (if anything) less likely to be evenly distributed between individuals than in the wild.

Our estimate of variance in female reproductive success is also likely to underestimate variance among wild females because rates of survival are likely to be far lower in the wild than in this captive situation, and females that die early will leave fewer offspring. Increased mortality may also increase the influence of rank on female reproductive output, as low-ranking female primates tend to occupy peripheral positions in the social group, leading to higher predation risk (e.g. toque macaques, *Macaca sinica*, Dittus 1977; long-tail macaques, van Noordwijk and van Schaik 1987; baboons, Ron et al. 1996), and shorter breeding life spans (e.g. long-tailed macaques, van Noordwijk and van Schaik 1999; but not vervets, Cheney et al. 1988). Finally, offspring survival has an important influence on individual reproductive success (Harcourt 1987; Cheney et al. 1988; Bercovitch and Goy 1990; but see Paul and Kuester 1996), and may also be influenced by female rank in wild mandrills (as in long-tail macaques, van Noordwijk and van Schaik 1999).

Male reproductive careers

Lifespan in male mandrills was similar to that of wild baboons, which all die by 21 year (Alberts and Altmann 2003). Mortality patterns suggest that males are subject to strong selection once they reach sexual maturity, unlike females. Growth patterns also diverge at this age: while female growth rates decline, males begin their adolescent growth spurt (Setchell et al. 2001). Similar patterns of higher survival rates in females than in males have been found for several species of polygynous mammals (Clutton-Brock et al. 1982; Owen-Smith 1993; Fedigan and Zohar 1997; Loison et al. 1999), although not for all polygynous species studied (review in Loison et al. 1999), and are

likely due to the high costs of preparation for reproduction (growth) and male-male competition (Promislow 1992).

Male mandrills become reproductively competent at a similar age to females (Setchell and Dixson 2002), and the youngest sire was only a few months older than the mean age at first reproduction in females. Similar findings have been reported for Barbary (Paul and Kuester 1996) and rhesus macaques (Bercovitch and Nürnberg 1996). However, age at first reproduction was far more variable in males than in females, and reproductive output was very low in adolescent males. Male reproductive rate improved with age, and the majority of male reproduction was compressed into the few years during which males are in their prime. Large male size and competitive ability thus appear to be strongly favoured by sexual selection. Nonetheless, adolescent males did contribute to the gene pool. Low reproductive success in adolescent males may be due to males delaying their entry into the competitive arena, reducing mortality risks associated with male-male competition, while increasing rapidly in body size and developing elaborate secondary sexual traits, to increase their chances of reproduction as an adult (Clinton and le Boeuf 1993; Kokko 1997). However, simple competitive exclusion by larger, stronger males may also explain the delayed onset of reproduction following sexual maturity (e.g. fallow deer, Komers et al. 1997; McElligott et al. 1998).

Attaining alpha rank during adulthood strongly influenced male reproductive output, confirming previous findings of dominance-based priority of access in this highly sexually dimorphic species, at least in this captive situation (Wickings et al. 1993; Wickings 1995). Many males died without attaining alpha rank: a quarter of males died before reaching adulthood, while fewer than half the males that did reach their prime became alpha male. Acquisition of top-rank, with its large reproductive pay-offs, may trade off against future reproduction and survival (Partridge and Harvey 1985), because high-ranking males risk injury in male-male competition (Drews 1996), show decreased foraging time due to mate-guarding activity (Bercovitch 1983; Alberts et al. 1996), and have increased energy expenditure (Bobek et al. 1990). This raises the possibility that non-alpha males may survive longer, sneaking fertilisations over a period of years, while alpha males sire many offspring during a short period. Our data were insufficient to test whether alpha males were more likely to die than non-alpha males of the same age. However, several studies of other mammal species have found that mating males are more, rather than less, likely to survive (Clutton-Brock 1984; Clinton and le Boeuf 1993), perhaps because such males are of higher quality, and therefore better able to afford (or avoid) the costs associated with reproduction (McNamara and Houston 1992; Promislow 1992).

High-ranking adolescent male rhesus macaques are more likely to sire offspring than low-ranking males in captivity (Bercovitch and Goy 1990; Bercovitch and Nürnberg 1996). As in rhesus macaques (Bercovitch 1993; Dixson and Nevison 1997), high-ranking adolescent male mandrills mature faster than lower-ranking age-mates in this colony (Setchell and Dixson 2002), and thus might be

expected to sire more offspring than low-ranking males. Unfortunately, relative rank data were unavailable for the majority of adolescent males in this study, meaning that we could not test whether high-ranking adolescent males were more likely to reproduce.

Maternal rank may also be expected to influence male reproductive success, with high-born sons beginning their reproductive careers earlier (e.g. Barbary macaques, Paul et al. 1992), and/or being more likely to attain alpha status (e.g. long-tail macaques: van Noordwijk and van Schaik 1999). However although adolescent sons of high-ranking female mandrills are larger for their age than are sons of mid- or low-ranking mothers (Setchell and Dixson 2002), maternal rank influenced neither age at first sirehood nor attainment of alpha status. It seems likely that the potential advantages of high-maternal rank are outweighed by the many other factors involved in male reproductive competition in mandrills, as in male baboons (Alberts and Altmann 1995).

Limitations of the study: males

Whereas our estimate of variance in female reproductive success is likely to be artificially low, colony conditions may increase variance in male reproductive success. In particular, dominant males may be better able to monopolise fertile females than under natural conditions, increasing variance in male reproductive success. As in other primate species living in multi-male, multi-female groups, subordinate male mandrills sneak copulations (Setchell and Kappeler 2003), and they may be better able to do so in the wild. However, this effect may be counteracted to some extent by the higher predation risk faced by low-ranking males in the wild, as in the CIRMF colony low-ranking males are more likely to be solitary than dominant males are (Setchell and Dixson 2001).

The absence of immigrant, non-natal males may artificially increase the tenure of dominant males, and also act to increase variance in male reproductive success in this closed colony. With the exception of the founder animals, all males in the colony were natal to the group in which they reproduced. Whether this resembles the situation in the wild is unknown. Male mandrills in the colony peripheralise from their natal group during adolescence (Setchell and Dixson 2002; Setchell 2003), and preliminary data suggest that a similar phenomenon occurs in the wild (Abernethy et al. 2002). Mandrill groups appear to be sufficiently large in the wild (mean group size of 620 animals, Abernethy et al. 2002) for the risk of inbreeding to be minimal for returning natal males. However, whether wild males return to their natal group to breed when adult (as in this colony), or whether they disperse and join other groups remains unknown.

Hrdy and Williams (1983) have proposed that, over a life-time, variance in female lifetime reproductive success may equal that in males. However, this did not appear to be the case for these mandrills. When the entire sample was considered, males showed 1.7 times more variance in reproductive output than females, while males that had died (and therefore finished their reproductive career) showed 12.9 times more variance than the founder females, that were likely to be nearing the end of their careers. Although colony conditions may exaggerate these sex differences in variance in reproductive success, studies of other provisioned populations of multi-male, multi-female primate species where males have frequent transfer opportunities and/or groups are extremely large, reducing the ability of the highest ranking males to monopolise females, have also found greater variance in male output than in females, with male:female ratios of 3–4:1 in Barbary macaques (reproductive success, Kuester et al. 1995), 2.5:1 in Japanese macaques (mating success, Fedigan et al. 1986), and 3:1 in rhesus macaques (mating success, Meikle et al. 1984).

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