

Male Dominance and Genetically Determined
Reproductive Success in the Mandrill
(*Mandrillus sphinx*)

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ABSTRACT. DARWIN referred to the adult male mandrill (*Mandrillus sphinx*) as the most brightly coloured of all mammals, citing the brilliant red and blue pigmentation of the face, rump, and genitalia as extreme examples of evolution by sexual selection. Considerable controversy exists concerning possible effects of sexually selected phenotypes via intermale competition on reproductive success. Behavioural and genetic studies of a large, semi-free ranging mandrill colony in Gabon have now demonstrated that clear-cut relationships exist between male secondary sexual development, social dominance, copulatory behaviour, and reproductive success in this primate species. Two morphological variants of adult male were identified; "fatted" males, with maximum secondary sexual coloration, which occupied dominant positions in the social group, and "non-fatted" males, with muted secondary sexual adornments, smaller testes and lower plasma testosterone levels, which lived as peripheral/solitary individuals. DNA fingerprinting analyses on infants born over five successive years showed that only the two most dominant, fatted males in the group had fathered offspring. Throughout the annual mating season these males attempted to mate-guard and copulate with females during periods of maximal sexual skin tumescence. Male rank and mating success were strongly positively related and the alpha male sired 80–100% of the resulting offspring during three consecutive years. Non-fatted adult males and group associated subadult males engaged in infrequent, opportunistic matings and did not guard females. Loss of alpha status resulted in a fall in reproductive success, but the effect was gradual; the deposed alpha male continued to father 67% and 25% of infants born during the next two years. Thus, whilst claims that male dominance determines mating success and paternity in primates have caused considerable debate, these results on mandrills provide unequivocal evidence for the existence of such effects.

Key Words: Male dominance; Sexual behaviour; DNA fingerprinting; Reproductive success; Mandrill.

INTRODUCTION

Mating systems among primates are more complex than previously realized and may vary even within a single species (e.g. monogamy and polyandry in tamarins and marmosets: GOLDIZEN, 1987; SUSSMAN & GARBER, 1987; single male and multimale system in patas monkeys: CHISM & ROWELL, 1986). Claims that male dominance influences mating success and hence determines reproductive success in social groups of monkeys and apes have given rise to considerable debate (BERCOVITCH, 1986; BERNSTEIN, 1976; COLISHAW & DUNBAR, 1991; McMILLAN, 1989). Relationships between male rank and reproductive success are perhaps best understood in those mammals where there are clear indications for effects of sexual selection upon male secondary sexual characters and behaviour (e.g. in the elephant

seal: LE BOEUF, 1974; red deer: CLUTTON-BROCK & ALBON, 1979). Among primates, the mandrill (*Mandrillus sphinx*) may represent such an extreme example; indeed DARWIN (1871) commented that "no other member in the whole class of mammals is coloured in so extraordinary a manner as the adult male mandrill." The degree of sexual dimorphism evident in this species (adult males weigh 2–3 times as much as adult females) accentuates the magnificent secondary sexual adornments of the male. If such adornments develop as advertisements of an individual's prowess, both in intra- and inter-sexual encounters, then we may expect to see a dominance hierarchy amongst male mandrills, coupled with greater mating success amongst the highest ranking males. But the ultimate measurement of reproductive success can only be achieved by correlating mating activity with genotypic assignment of paternity, e.g. using the techniques of DNA fingerprinting developed for humans (JEFFREYS et al., 1985), and now being more widely applied to studies of avian and mammalian species (BURKE et al., 1991; MARTIN et al., 1992). During a behavioural and genetic study of a semi-free ranging mandrill colony in Gabon, paternity was determined in offspring born over a 5-year period and correlated with measurements of male dominance rank and sexual behaviour.

The mandrill's geographical range is restricted to the area of tropical rain forest south of the Sanaga River in Cameroon, extending through to Rio Muni, Gabon and Congo (HARRISON, 1988). Limited observations of wild mandrills have revealed little information on their social organization, except to identify both one-male groups of 10–15 individuals and multi-male hordes of up to 450 mandrills. Solitary adult males also occur (HARRISON, 1988; HOSHINO et al., 1984; JOUVENTIN, 1975; KUDO, 1987). Whether smaller groups form breeding units, several of which then coalesce for movements through the forest, or whether large multi-male troops are the focus group, which then break into smaller foraging groups remains to be elucidated. We have studied the semi-free ranging mandrill group (in 1991, numbering 57 individuals, with 6 adult males and 14 adult females) held at the Centre Internationale de Recherches Medicales de Franceville (CIRMF) in Gabon to investigate questions of social organization, mating system, and reproductive outcome.

ANIMALS AND BEHAVIOURAL OBSERVATIONS

The mandrill group was established in 1983/84 with 14 animals (6 males aged 2–4 yrs; 8 females aged 1–6 yrs) being released into a 6 ha rainforested enclosure. At the beginning of the study period (the 1986 mating season), there were 22 mandrills in the enclosure (6 males, 8 females, and 8 infants and juveniles). By the 1990 mating season, numbers had risen to 45 [17 males, 16 females, and 12 individuals (>2 yrs old) of undetermined sex]. Six adult males and 3 subadult males were present, as well as 14 females of reproductive age. Details of growth and sexual development in this mandrill colony have been reported elsewhere (WICKINGS & DIXSON, 1992). All group members aged 12 months or more were given numbered ear tags. Infants were identified according to their matriline, receiving a letter after the mother's identify number. Between May and November 1990 behavioural observations were made 5–7 days/week (300hr) from a tower overlooking the provisioning area. Male dominance rank was assigned on the basis of measurements of agonistic behaviour (frequency and direction of facial threats, lunges, chases, and attacks) as well as occurrence of displacement and avoidance between males. Details of sexual

behaviour in relation to the female's sexual skin swelling cycle were also recorded, as described pp. 530–531.

DNA FINGERPRINTS

The mandrills were captured annually for a veterinary check. During this procedure, blood samples were collected into ACD vacutainers, immediately diluted with an equal volume of 1 × SSC buffer (0.15M NaCl, 0.015M sodium citrate, pH 7.0), and stored at –60°C. Thawed blood samples were lysed, digested with proteinase K and extracted with salt-saturated phenol-chloroform to yield DNA pellets which were alcohol precipitated, washed, and then taken up in TE buffer (10–50 µg/50 µl buffer; 10mM Tris HCl, 1mM EDTA, pH 8.0). DNA (10µg) was digested with Alu 1 (2U/µg DNA) and the digest was run out on an agarose gel (0.75%) in TAE buffer (0.04M Tris-acetate, 1mM EDTA) until the 2kb molecular weight marker had migrated about 16 cm from the origin (about 40–45 h at 20–25V). Under a 40 mbar vacuum, the DNA was transferred and fixed under alkaline conditions to a Hybond N-Plus membrane before being hybridized. A 15-base, single-stranded synthetic oligonucleotide probe, (GTG)₅, was used for hybridization. The probe (30 ng) was 5'-end labelled using polynucleotide kinase (1 U) and γ-AT³²P (100 mCi), and was used without further purification. Hybridization was carried out for 5h at 48°C in 5 × SSC, 0.5 × Denhardt's soln, 0.1% SDS, 0.1% sodium pyrophosphate and membranes were washed at low stringency. Labelled blots were exposed to film with 2 intensifying screens for approximately 24h. Bands in the molecular weight range 3.5 to approximately

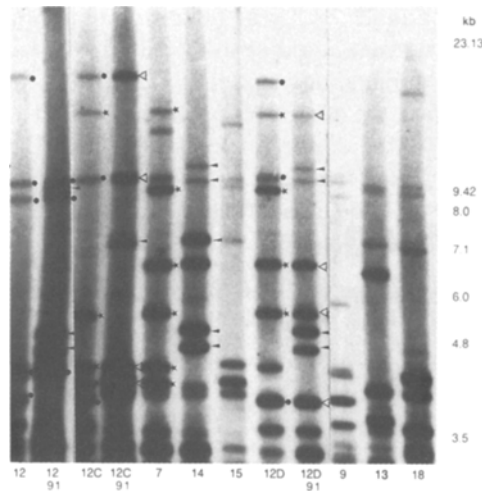


Fig. 1. Autoradiograph of Alu 1 DNA digests of 12 mandrills probed with (GTG)₅, showing fingerprints of all 6 adult males No. 7, 14, 15, 9, 13, and 18, and the matriarchial line of No. 12, her 2 daughters by male 7 (*I2C* and *I2D*) and their 3 offspring by male 14 born in 1991 (*I2/91*, *I2C/91*, and *I2D/91*). ●: Bands inherited from female 12; ◄: bands inherited from male 14; *: bands inherited from male 7; ◄: bands inherited by *I2C* or *I2D* from female 12 or male 7, and passed on to their respective offspring.

20 kb were used to generate band sharing indices between individuals. In each case mother-infant dyads and all six adult male mandrills were run on the same gel. A band sharing index (D)=0.5 indicated a first-degree relationship, whereas $D \ll 0.25$ was taken to identify non-related individuals. Over the 5-year study period 37 infants were born, of which 36 survived, and DNA fingerprinting analysis allowed paternity allocation in 33 of these (Fig. 1).

RESULTS

Two morphological and social variants of adult male mandrills were identifiable (Table 1). Those adult males which developed as heavy rumped, fatted individuals with brightly coloured red and blue "sexual skin" on the face, rump and genitalia had larger testes and higher plasma testosterone levels than their non-fatted counterparts, which were characterized by a slower and lesser development of secondary sexual adornments. Fatted males associated almost constantly with the social group of females, subadults, and juveniles, whereas non-fatted males were peripheral or solitary in behaviour. Age and body weight differences could not account for this somatic and social dichotomy. In addition, there was a clear dominance hierarchy between the three males in each social class.

Male 7 was the original dominant male in the group (FEISTNER, 1989), but was deposed by male 14 before the 1989 mating season, following severe fighting. Remarkably, only these two high ranking, fatted, social males fathered offspring throughout the 5-year study period (Fig. 2). Non-fatted, peripheral/solitary males or low ranking social males failed to father any of the offspring for which DNA fingerprints were available; the third fatted, social male (male 15) remained at rank No. 3 in the hierarchy and did not sire any offspring; nor did the three sub-adult males in the group (males 2B, 5B, and 6A, aged 5, 5, and 7 yrs, respectively, in 1990). During male 7's 3-year tenure as alpha male, 18 infants were born; of the 15 infants in which paternity could be assigned, male 7 had fathered all except one; male 14 was the father of the remaining infant (Fig. 2). In the first mating season when male 14 was the dominant male, the overall conception rate in the colony dropped to 54.5%, despite an increase of 22% in the number of females of reproductive age. This cannot be attributed to the increase in young females reaching sexual maturity; three of the five non-pregnant females were parous, and mandrills frequently conceive in their first season of

Table 1. Social affiliation, rank, and paternity in the six adult male mandrills of the colony during the 1990 mating season, differentiated according to fatted versus non-fatted appearance; also included are somatic parameters for these six males.

Male No.	Fatted males			Non-fatted males		
	14	7	15	13	18	9
Social status						
% time with group*	100	85	96	7	1	0
Rank	1	2	3	1	2.5	2.5
Paternity (%) ($n = 12$ infants)	9 (75)	3 (25)	0	0	0	0
Somatic data						
Age (yr)	10	11	9	10	9	11
Body weight (kg)	37.0	23.5	33.6	33.3	34.4	34.8
Vol. left testis* (ml)	31.4	26.2	46.2	19.3	12.7	24.4
Plasma testosterone* (ng/ml)	16.3	5.2	15.0	1.8	2.1	1.2

*Differences between means for fatted males ($n=3$) and non-fatted males ($n=3$) were significantly different (Mann Whitney test; $U=0$, $p < 0.05$).

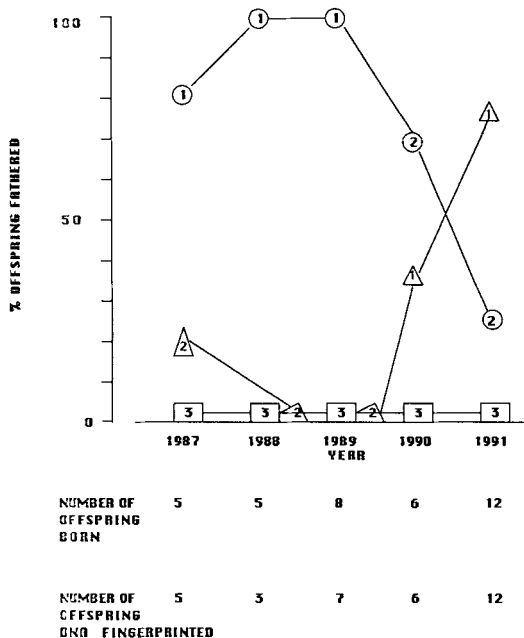


Fig. 2. Association between rank and paternity for the three fatted adult males (numbers 7, 14, and 15) showing effects of rank changes upon percentages of infants sired each year for the period 1987–1991. Each male is represented by a separate symbol (male 7: ○; male 14: △; male 15: □) and his rank (1, 2, or 3) is written inside the symbol. Note that male 15 remains at rank 3 and sires no offspring throughout the 5-year period. Male 7 commences at rank No. 1 and then falls to the No. 2 position; his fall in rank is associated with a gradual decrease in reproductive success during 1990 and 1991. The numbers of offspring born and numbers DNA fingerprinted are given for each year of the study.

ovarian cyclicality, without showing the post-menarchial infertility common in other primate species (WICKINGS & DIXSON, 1992). We speculate that it may rather reflect a degree of choice or stress in the colony in the presence of the newly dominant male, and in fact four of the six pregnant females conceived by the previously dominant male 7. This effect was less apparent in the second year following deposal of male 7, when the majority of the females conceived by male 14.

Male sexual activity during conception cycles of the 1990 mating season was correlated with the paternity of the 12 surviving offspring born the next year (January–March 1991). Male 14 succeeded in mate-guarding and copulating with 11 of these females during at least part of the 6-day period preceding sex skin breakdown and it was notable that guarding and ejaculatory mounts ceased abruptly at the first sign of sexual skin detumescence (Fig. 3). Male 14 accounted for 24 (i.e. 77%) of ejaculatory mounts observed with females during the presumptive fertile period of these 12 conception cycles. Male 7 mate-guarded three females, typically for shorter time periods than achieved by male 14 and accounted for 13% of ejaculatory mounts. Only two other males were observed to copulate with females during the presumptive peri-ovulatory period; a peripheral male (male 13: twice) and a subadult group male (male 5B: once). Paternity assignment for each offspring resulting from copulations during these cycles showed that male 14 had sired nine infants and male 7 accounted for the remaining three (Fig. 3). Interestingly, there are certain instances

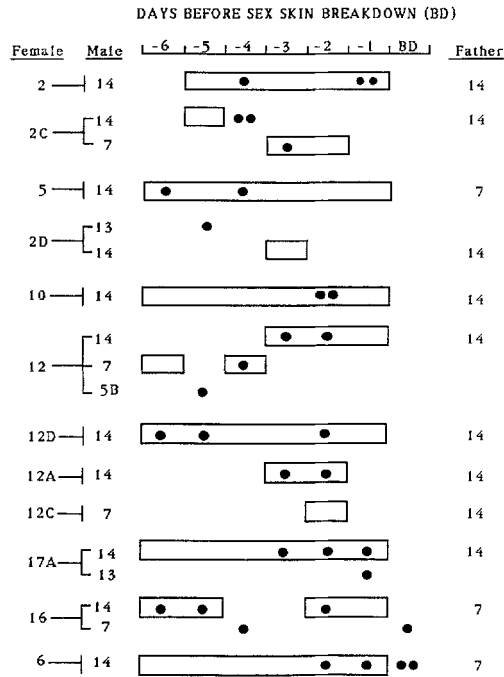


Fig. 3. Male mating behaviour during the 12 conception cycles of the 1990 mating season. Individual females are identified in the extreme left hand column and those males which engaged in sexual activity are identified in the adjacent column. Sexual behaviour was scored during the six days leading up to and including the day of sexual skin breakdown (BD), which includes the peri-ovulatory period (WILDT et al., 1977). Male mate-guarding activity (during which the male follows and closely associates with a specific female, usually at the height of sexual skin tumescence) is indicated by the open boxes, and the occurrence of ejaculatory mounts by closed circles. The male identified from DNA fingerprints as being the resulting infant's father is given in the right-hand column.

when male 14 guarded and copulated with females, yet failed to father the resulting offspring, and conversely where male 7 guarded a female exclusively, yet male 14 was her offspring's father. Nonetheless, there was a strong association between mating activity and paternity for male 14 during the 1990 mating season.

DISCUSSION

Since mandrill groups have enormous home ranges in dense rainforest (HOSHINO et al., 1984; JOUVENTIN, 1975) it has thus far proven impossible to follow groups and to study sexual behaviour in the wild. It is possible that solitary or peripheral male mandrills in the wild achieve greater reproductive success through opportunistic matings or pass on to the fatted stage of development more readily than animals in the rainforested enclosure used in our study. Our observations on captive mandrills show that a number of males are sexually active during the annual mating season, but that it is only the top ranking males which guard individual females during periods of sexual swelling. There are, however, instances of guarding not resulting in paternity, and vice versa, paternity with no observed mate-guarding behaviour.

“Herding” of females by high ranking males and formation of small one-male units occurs in geladas (CROOK, 1966; DUNBAR, 1979) and hamadryas baboons (KUMMER, 1968). Such behaviour was not observed in the semi-free ranging mandrill group during the present study, however. In the chacma baboon, some females form long-term affiliations with specific adult males, which appear to be independent of the male’s rank in the group (“Friendships”: SMUTS, 1985). It is unknown whether this occurs in the mandrill. Also problematic is the extent of the female’s active participation in mate-guarding relationships. Females are not necessarily passive in this respect, and we have observed females avoiding and fleeing from males which were attempting to guard them.

KUDO (1987) suggests that, on the basis of their vocalizations, the large multi-male groups of mandrills are more usual in the wild, but that these are different from the multi-levelled social organization of hamadryas and gelada baboons. Our more detailed behavioural studies on semi-free ranging mandrills indicate a multi-male organization, but that the strong male hierarchy restricts access to females to dominant males. It has frequently been suggested that male dominance rank determines mating success in social groups of primates and that male rank therefore correlates with reproductive success (ALTMANN, 1962; KEVERNE, 1979; KUMMER, 1968). However opinions are divided (BERCOVITCH, 1986; BERNSTEIN, 1976; COLISHAW & DUNBAR, 1991; McMILLAN, 1989) and combined studies of behaviour and genetic assignment of paternity, still few in number, have yielded conflicting answers (DE RUITER et al., 1992; MÉNARD et al., 1992). The results presented here show that, in the mandrill, there are clear-cut relationships between adult male dominance rank within the social group, degree of secondary sexual development, mating success, and reproductive outcome.

Acknowledgements. CIRMF is funded by the Gabonese Government(70%) and by Elf Gabon(30%). Our thanks to Prof. A. JEFFREYS(Leicester) and Prof. N. HASTIE(Edinburgh) for advice and assistance in setting up DNA typing procedures at CIRMF.

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— Received: January 17, 1993; Accepted: April 25, 1993

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