Do Female Mandrills Prefer Brightly Colored Males?

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ABSTRACT

Although secondary sexual adornments are widespread in male primates, few studies have examined female choice for these characters. The mandrill (*Mandrillus sphinx*) presents an extreme example of sexual dimorphism, with males exhibiting an array of striking adornments. The most dominant adult male in a group exhibits the brightest and most extensive red coloration, while other males are less brightly colored. I examined whether female mandrills show a preference for brightly colored males using data on peri-ovulatory sexual behavior during the 1996 mating season for all males aged 8+ yrs (n = 5) and all parous females (n = 9) living in a semi-free-ranging colony at CIRMF, Gabon. Results showed that brightness of male coloration was significantly positively correlated with time spent within 2m of females, female responsibility for proximity, number of sexual presentations received, % approaches accepted by females, and % inspections that females cooperated with. Females also groomed only the brightest male. Behaviors indicative of female preference did not correlate significantly with male dominance rank, and partial correlations confirmed that the influence of male color on female behavior was stronger than that of male rank. When the influence of male dominance rank was controlled, correlation coefficients between female behaviors and male mating success were high and positive. In further support of the hypothesis that females show mate choice for brightly colored males, independent of dominance rank, I report an unusual case where the alpha male fell in rank without loss of coloration. This male experienced no significant change in female responsibility for proximity, sexual presentations received, or female reaction to approaches or inspections, although he was no longer observed to mate. These preliminary observations suggest that female mandrills attend to differences in male secondary sexual characters, and show mate choice in favor of brightly colored males. As brightly colored males are also dominant, this reinforces the influence of male-male competition on male reproductive success, and may explain the very high reproductive skew in males of this species, and the extraordinary appearance of male mandrills.

KEYWORDS: sexual selection; female choice; proceptivity; receptivity; coloration

INTRODUCTION

The question of female preference for certain males is important in terms of the evolution of male secondary sexual adornments. Experimental evidence suggests that extravagant adornments such as the enlarged tail feathers of widow birds (Andersson, 1994) and the ocelli in the peacocks train (Petrie *et al.*, 1991) have evolved on the basis of female choice. However, although male ornaments are widespread in primates (Dixson, 1998), very little information is available concerning female sexual preference for such characters. Indeed, comparatively little is known about female choice for any male trait in primates (Paul, 2002; Setchell and Kappeler, 2003). This is likely due to primates being difficult research subjects, with long generation times and correspondingly small sample sizes, as well as the complex interactions between male and female reproductive strategies (Setchell and Kappeler, 2003; Soltis *et al.*, 2001; van Schaik *et al.*, 2004), that make it extremely difficult to separate the effects of male and female strategies on mating and reproductive success. However, female choice for multiple mates appears to be ubiquitous in primates (Hrdy, 2000; Hrdy and Whitten, 1987), presumably because this allows females to effectively reduce their unusually high risk of infanticide by confusing paternity (van Schaik, 2000). In terms of choice for individual males, studies have shown that female orang-utans (*Pongo pygmaeus*) are more likely to show proceptive behavior to fully developed ("flanged") adult males than they are to "unflanged" males (Galdikas, 1985; Mitani, 1985; Schürmann, 1982; van Schaik and van Hooff, 1996), while female squirrel monkeys (*Saimiri oesterdii*) choose to mate with the largest males (Boinski, 1987). Female choice for behavioral or demographic, rather than morphological, male traits includes choice for dominant males in brown capuchins (*Cebus apella*, Janson, 1984; Welker *et al.*, 1990) and vervet monkeys (*Cercopithecus aethiops*, Keddy, 1986). In contrast, both Japanese (*Macaca fuscata*) and rhesus macaques (*M. mulatta*) choose to mate with males of all ranks (Manson, 1992; Soltis *et al.*, 2001), reducing the influence of male dominance rank on male reproductive success. Further, females of some species appear to choose novel males rather than familiar males, perhaps as an inbreeding avoidance mechanism (e.g. baboons, *Papio cynocephalus anubis*, Bercovitch, 1991).

The mandrill (*Mandrillus sphinx*) presents an extreme example of sexual dimorphism, with males exhibiting an array of striking adornments that rival those of the most ornamented birds, including

bright red and blue coloration on the face, and red, violet and blue coloration on the rump and genitalia. Indeed, Darwin noted that "No other member in the whole class of mammals is colored in so extraordinary a manner as the male mandrill", and proposed that the male mandrill "appears to have acquired his deeply-furrowed and gaudily-colored face from having been thus rendered attractive to the female" (Darwin, 1871 p. 558, 560). However, more than 130 years later, we know very little more than Darwin about the influence of female choice on the evolution of these male characters.

Mandrill groups are made up of female matrilines (Setchell, 1999), while multiple males vary in group association from solitary to spending all their time with the social group (Abernethy *et al.*, 2002; Setchell and Dixson, 2001a; Wickings and Dixson, 1992). The extent of development of male secondary sexual characters varies extensively between males and is related to dominance rank (Setchell and Dixson, 2001a, b; Wickings and Dixson, 1992). The alpha male has the most developed secondary sexual characters and is the most group associated male (Setchell and Dixson, 2001a). Alpha males mate-guard receptive females, and sire 80-100 % of the offspring born in any one mating season (Wickings, 1995; Wickings *et al.*, 1993). However, other high-ranking males occasionally mate-guard, while lower ranking males mate sneakily, and may sire offspring (Wickings *et al.*, 1993, Setchell et al. submitted).

Mate choice is defined as "any pattern of behavior, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than others" (Halliday, 1983). This is distinct from mate preference, which describes the underlying propensity to select certain partners, and can be measured only under experimentally controlled conditions (Heisler *et al.*, 1987). For example, females may prefer to mate with subordinate males, but be unable to exercise this preference due to sexual coercion by dominant males (Smuts and Smuts, 1993). Snowdon (2004) lists five criteria that must be met in order to demonstrate the influence of inter-sexual selection (mate choice) on communication: (1) signals must be sexually dimorphic; (2) variation in the signal must occur between same sex individuals; (3) discrimination and preference (or avoidance) by opposite sex individuals must occur; (4) this expression of preference (or avoidance) must occur in the context of reproduction; and (5) the outcomes of differential preferences based on signals must relate to

reproductive success. Red coloration (and secondary sexual development in general) in male mandrills fulfils the first two criteria. Here, I investigate the three remaining criteria, using observational data concerning male mating success, male-female proximity, grooming, female proceptivity, and female receptivity for a semi-free-ranging colony of mandrills. I also present a case study concerning the alpha male during the study, who was seriously wounded at the end of the mating season, and was out-ranked by four other males by the time of the next mating season. However, he remained brightly colored. This exceptional case (males that lose rank generally also decrease in color, Setchell and Dixson, 2001b) provided an interesting case study to separate the influence of a substantial decrease in rank, but no change in color, on male mating success and female sexual behavior, albeit for only one male.

METHODS

Study population and subjects

This study was carried out on Enclosure 1 of the mandrill colony at the Centre International de Recherches Médicales in Franceville, Gabon (CIRMF). This semi-free-ranging colony was established in 1983/4, when 14 animals (6 males, 8 females, originating from the wild) were released into a 6.5 ha naturally rain-forested enclosure. All further additions to the group, subsequent to 1984, are due to reproduction of the founder animals; some animals have been removed. During the 1996 mating season there were 36 animals living in Enclosure 1. The animals foraged in the enclosure, and received daily provisions of monkey chow, fruits and vegetables. Water was always available from a stream.

Subjects were all males aged older than eight years (aged 8.2 - 15.0 years, n = 5), and all parous females that showed sexual swellings during the 1996 mating season (aged 6.3 - 18 years, n = 9). Younger males were excluded from analysis, although male mandrills are likely to be reproductively competent from about 4 yr (Setchell and Dixson, 2002), because they were very rarely observed to interact with peri-ovulatory females. Males older than 8 yr have been observed to mate-guard females (Setchell *et al.*, submitted), and are able to dominate older adult males (whereas younger

males are not, Setchell, 2003), and can thus be considered socially adult (see also Alberts and Altmann, 1995).

Data collection

Daily behavioral observations were made during the 1996 mating period (May-September) from a tower overlooking the enclosures. The dense nature of the forested enclosures allowed a good view of the animals for only a few hours each day, and lengthy follows of individual focal animals were not possible. Instead, proximity data were collected every 2 minutes using scan sampling to note the identity of all neighbors within 2m of each male, and all occurrence recording (Martin and Bateson, 1994) was used for the following behaviors for all male-female dyads: approach to within 2m; avoid an approaching individual; flee; groom; sexual presentation; inspect perineum; mount attempt; ejaculatory mount. Descriptions of behaviors used in this paper are in Table 1. A total of approximately 150 hours of observation were made during the mating season.

Analyses of mating behavior were restricted to periods when females were peri-ovulatory. Female mandrills show sexual swellings that increase in size during the follicular phase, reaching maximum size around the time of ovulation. Daily records of female sexual swelling morphology were used to determine when females were peri-ovulatory. Ovulation was presumed to occur during the last few days of maximal swelling, as found in baboons (Hendrickx and Kraemer, 1969; Shaikh *et al.*, 1982; Wildt *et al.*, 1977), and the peri-ovulatory period was defined as the six days preceding the day of sexual skin detumescence ("break-down").

Male dominance rank was calculated using a dyadic interaction matrix, including all interactions where one male avoided or fled when another male approached. During the period when the females concerned were peri-ovulatory (May-July) only one relationship was ambiguous, with one male avoiding the other twice, and the other avoiding once. Reversing these two males in analyses did not change the significance of correlation coefficients with dominance rank. All other dominance relationships were clear, with one male avoiding the other on 3-18 occasions. Dominance rank is expressed as the number of males dominated (the alpha male ranked 4, and the lowest 0).

Measures of female mate selection

Behaviors potentially indicative of female preference investigated included responsibility for proximity, grooming, proceptivity and receptivity. Male-female proximity was examined as the amount of time that a male was observed within 2 m of a female. A score of female "responsibility for proximity" with males was calculated as the % of approaches between any female and each male that were made by the female. I used this rather than the more detailed Hinde's proximity index (Hinde and Atkinson, 1970), because it proved impossible to score all "leaves". Female proceptivity was also measured using sexual presentations. Receptivity was measured as female reaction to male approach to within 2m, inspection of her perineum: noted as negative (avoid, flee, or sit down in the case of an inspection) or positive (remain and cooperate with the male). Data concerning female acceptance of male mount attempts were too limited to be informative, due to the low number of mount attempts observed.

Male coloration

The brightness of the red/pink coloration on the face was used as an indicator of secondary sexual development for each male. Previous analyses have shown that this measure is closely linked to the general secondary sexual development of a male (Setchell and Dixson, 2002). Color was quantified for non-anaesthetized males by direct visual comparison with graduated color charts (published by the Royal Horticultural Society, London). Colors in this chart correspond to known co–ordinates of the C.I.E. (Commission Internationale de L'Eclairage) color system, each color chip being described in terms of hue, brightness and saturation. Of these, the brightness score (the total amount of light reflected by the color, or how the color is perceived by the normal eye on the scale of light to dark) was chosen as the best indicator of differences in mandrill skin coloration, and subtracted from 100 to give a figure that increased with color intensity. Measurements were made twice per month for each male, under natural light conditions, when animals entered the feeding pen and were thus close to the observer (generally within 2m). (Note that color measurements were made by the same person (the author) as behavioral observations, raising the possibility of unconscious bias in measures). For analyses presented here the mean of all measurements made during the mating period was used for each individual.

Data analysis

Insufficient data were available to allow dyadic analysis of mate choice. Data for individual females were therefore combined when comparing males, resulting in one value per male for each behavior examined. Of the 45 potential male-female dyads available, five were mother-son dyads, and nine were maternal brother-sister dyads. All but one male had female kin (mother or sister, maximum three females) present in the group. The decision to include these dyads in analysis was based on preliminary analyses that demonstrated no significant influence of kinship on sexual behavior (Setchell, 1999), and the difficultly of correcting for the number of female partners available when comparing males if these dyads were removed.

Mounts and sexual presentations are presented as number of events observed for each male. Male mandrills vary greatly in the extent to which they associate with the social group (Setchell and Dixson, 2001a; Wickings *et al.*, 1993), and some males were rarely observed with females, limiting the possibilities for interaction. However, results using mounts made and presentations received per hour the male was observed with females (and had the opportunity to interact with them) were not different from those using the number of events.

Nonparametric Kendall's tau-b correlations were used to compare behavioral measures with facial red coloration, male dominance rank and male mating success. Male color was positively, but not significantly, correlated with dominance rank ($\tau = 0.600$, $p = 0.142$, n=5), and was not significantly correlated with male age ($\tau = -0.200$, $p = 0.624$, n = 5). To examine the relative strength of relationships between behavioral measures and (i) coloration and (ii) dominance rank, I compared partial Kendall's tau-b correlation coefficients, holding first coloration and then dominance rank constant. Partial correlations were also used to examine the relationship between female behaviors and male mating success, controlling for male dominance rank.

RESULTS

Male sexual behavior and mating success

Although some males were rarely observed with females, all male subjects inspected the perineum of peri-ovulatory females and attempted to mount peri-ovulatory females. All copulations were initiated by males, who approached and followed the female, grinning, head-shaking, and often lip-smacking (behavioral descriptions are in Table 1). Males followed sexually attractive females persistently, but were not observed to act aggressively towards them (threaten, chase, hit or grab them). Threats were directed to other males, but not to the female. Fourteen of 19 mount attempts with peri-ovulatory females resulted in ejaculation (74%).

The number of ejaculatory mounts observed for each male is shown in Fig 1. The most brightly colored, alpha male was responsible for nine of 19 of all observed mounts (47%), and 8 of 14 observed ejaculations (64%). Male mating success was not significantly correlated with brightness of coloration or with dominance rank (Table 2). However, the partial correlation between mating success and coloration, holding dominance rank constant, was significant, while the partial correlation between mating success and dominance rank, holding coloration constant was non-significant (Table 2).

Female behavior, male coloration and dominance rank

Figures 2-5 show the relationships between time males spent within 2m of females, female proceptivity (responsibility for proximity, sexual presentations) and female receptivity (reaction to approaches and inspections from males) and male coloration. The most brightly colored, alpha male scored highest for all behaviors, and was also the only male to be groomed by peri-ovulatory females (7 occasions).

Correlations between potential behaviors indicative of female choice, male coloration, dominance rank and mating success are presented in Table 2. All behaviors examined were significantly positively related to male coloration, but were not significantly related to male dominance rank. Further, partial correlations between female behaviors and male coloration, holding male dominance rank constant, were significantly positive for time spent within 2m of females, and % of approaches made by the female, while results for female reactions to approach and inspection approached

significance. By contrast, partial correlation coefficients between female behaviors and dominance rank, holding coloration constant, were all small, and the relationships were non-significant (Table 2). Indeed, in three of seven cases, the partial correlation between female behaviors and dominance rank, holding coloration constant, could not be calculated, because the correlation coefficient between the behavior (time spent within 2m, female responsibility and reaction to approach by a male) and male coloration was 1.000.

Principle components analysis reduced the two scores of female proceptivity (responsibility for proximity, number of sexual presentations) and two scores of receptivity (reactions to approach and inspection) to a single variable: "attractiveness to females", which accounted for 93% of the variance (factor loadings: responsibility for proximity 0.886, presentations 0.878, reaction to approach 0.979, reaction to inspection 0.980). "Attractiveness to females" correlated perfectly with male coloration (Table 2), while it was positively, but not significantly, correlated with male dominance rank and male mating success (Table 2). The partial correlation between attractiveness to females and male coloration, holding male dominance rank constant, was high, positive and significant, while that between attractiveness to females and male dominance rank, holding coloration constant was close to zero (Table 2).

Female behavior and male mating success

None of the female behaviors examined were significantly correlated with male mating success (Table 2). However, when male dominance rank was controlled, correlation coefficients between female behaviors and male mating success were high, positive, and significant in all cases (Table 2).

The case of male 18

Male 18 was alpha male during the 1996 mating season, but was out-ranked by four other males during the next mating season (July 1997). However, unusually for an ex-apha male, his color brightness did not change. The influence of his decrease in dominance rank on mating success was clear: in 1996, when he was alpha male, male 18 was responsible for eight of 18 ejaculatory mounts observed (44%); in 1997, when he ranked 5, he did not make any of the 26 ejaculatory mounts observed (Fisher's exact p<0.001).

If female choice is based on dominance rank, then female proceptivity and receptivity towards male 18 should decrease from 1996 to 1997. However, if female behavior is based on coloration, then we should see no change between the two years, as his coloration did not change. Female responsibility for proximity to male 18 in 1996 was 50% (85 of 170 approaches). In 1997 this increased to 67% (28 of 42 approaches), an increase that approached significance ($\chi^2_1 = 3.759$, p = 0.053). In 1996, male 18 received 48% (21 of 43) of all sexual presentations observed, and this percentage did not change significantly in 1997, when he received 27% (5 of 18) of observed sexual presentations ($\chi^2_1 = 2.301$, p = 0.129).

Male 18 made far fewer approaches to peri-ovulatory females during 1997 (14 approaches) than during 1996 (170 approaches). However, female reaction to his approaches did not differ significantly between the two years (1996: 39 of 140 approaches avoided (28%, 1997: 1 of 14 approaches avoided (7%), Fisher's exact p = 0.309). Similarly, although male 18 made far fewer inspections during 1997, the percentage of positive reactions from females did not change (1996: 32 positive reactions to 51 inspections (63%), 1997: 6 positive reactions to 6 inspections (100%), Fisher's exact p = 0.164). Male 18 made no observed mount attempts in 1997, meaning that it was impossible to compare female acceptance of mount attempts between the two years.

DISCUSSION

This study shows that peri-ovulatory female mandrills spent more time close to brighter colored males than paler males, were more responsible for proximity to brighter males, groomed only the brightest male, solicited sexual attention more from brighter males, avoided fewer approaches from brighter males, and avoided less often when brighter males inspected their perineum. These findings are potentially confounded by the fact that coloration is related to male dominance rank, with the brightest male also being the alpha male (although rank and correlation were not significantly correlated in this sample of males). However, correlation coefficients between female behaviors and male coloration were consistently stronger than those between female behaviors and male dominance rank, and partial correlations between female behavior and male color were consistently stronger than between

female behavior and male rank, implying that male coloration had an influence separate to, and more important than, that of dominance rank. Further, in an unusual case when the alpha male fell in rank but did not decrease in color, he stopped mating, but female proceptivity and receptivity towards this male did not change significantly. Although there may be alternative explanations for these findings (e.g. female preference for an experienced, formerly alpha male, rather than a young, newly alpha male), they are in agreement with female preference for bright color, but are the reverse of predictions based on dominance rank.

These preliminary data imply that female mandrills do attend to differences in secondary sexual characters between males. When the influence of male dominance rank was controlled, male attractiveness to females was strongly related to male mating success. Bright color in males thus fulfils all five of Snowdon's (2004) criteria that must be met in order to demonstrate the influence of mate choice on communication: (1) bright color is sexually dimorphic; (2) variation in color occurs between males; (3) females discriminate between males and show preference for brighter colored males; (4) preference occurs in the context of reproduction; and (5) the outcome of preference for bright color influences male reproductive success (estimated using mating success). Despite a high degree of sexual dimorphism, and a correspondingly high potential for sexual coercion (Smuts and Smuts, 1993), female mandrills are clearly able to influence which males they mate with, and when. Females can out-run pursuing males, and easily climb smaller branches. Mate-guarding males were often observed guarding the bottom of a tree from other males while the female jumped to the next tree, effectively escaping.

Long-term data for the CIRMF colony show that alpha males account for 94% of peri-ovulatory mate-guarding (Setchell et al. submitted) and 76% of paternity (Charpentier et al., submitted). The results presented here suggest that the effect of male-male competition on male reproductive success is reinforced by female mate choice, increasing the mating advantage of more colorful (dominant) males over paler (subordinate) males, and may help to explain the very high reproductive skew among male mandrills (Cox and le Boeuf, 1977). This contrasts with findings for some other primate species, where female choice for males of various dominance ranks reduces the influence of male rank on male reproductive success (e.g. rhesus macaques, Manson, 1992; Japanese macaques, Soltis *et al.*,

1997; 2001), and the resulting strength of sexual selection in male mandrills may help to explain their extraordinary appearance.

Limitations of the study

The data presented here are limited in several ways by the nature of the colony. First, enclosure conditions limit the possibility for detailed behavioral observations severely, meaning that it was necessary to combine data for all females into a single value for each male for each behavior. This assumption that females show uniform mating preferences is unlikely to be upheld (e.g. Soltis *et al.*, 2001). In particular, if females choose males for genetic compatibility (e.g. Sauermann *et al.*, 2001), rather than for particular "good genes" (Brown, 1997; Penn and Potts, 1999; Trivers, 1972; Zeh and Zeh, 1997) then this will lead to individual variation in mate preferences between females, depending on their own genetic make-up.

Second, the results presented here examine the behavior of peri-ovulatory females. However, the peri-ovulatory period was estimated from female sexual swellings, and the exact date of ovulation was unknown. Female mate choice may be expected to change with the probability of ovulation and fertilization. For example, females may mate with many males across a receptive period, confusing paternity, and reducing the risk of subsequent infanticide, but choose to mate with dominant males when they are most likely to be fertile, biasing paternity towards dominant (high quality) males (Nunn, 1999).

A third limitation of this study is the closed nature of colony. With the exception of the eldest male in this study, who was one of the founder males, all the males were natal to the study group, and were also relatively young. Females thus did not have the opportunity to express a preference for unfamiliar or novel males, as observed in other primate species (e.g. Bercovitch, 1997; Pereira and Weiss, 1991; Small, 1989). However, in a detailed study of mate preference in rhesus macaques, Manson (1995) concluded that his data provided "at most, weak support for the hypothesis that female primates in multi-male groups exercise mate choice for novel males" (p. 285). Nor did the female mandrills in this study have a choice between several older adult males.

Future directions

Observational studies such as this one can provide evidence for mate choice, but detailed experiments will be necessary to fully control for the confounding influences of male dominance rank and reproductive strategies on female behavior, and to determine on which aspects of male appearance females base their mating decisions. For example, a recent experimental study found evidence that female rhesus macaques spent significantly more time looking at images of males with red faces rather than pale faces (Waitt *et al.*, 2003). Similarly, female *Eulemur fulvus* prefer to view photographs of more colorful males (Cooper & Hosey, 2003). Further experiments will allow examination of female decision rules, such as whether females choose the first male that exceeds a preset level of "quality" (threshold rule), or whether they choose the best of all males available (best of n rule) (Luttbeg, 2003).

Further questions relate to why female mandrills prefer brightly colored males. Models of female choice propose that female choice for male ornaments may be adaptive, increasing the females' own reproductive success via direct (resources) or indirect (genetic) benefits, or non-adaptive, with no associated fitness benefits (Andersson, 1994). Possible direct benefits accruing to female mandrills that mate with brightly colored males may include protection from harassment and sexual coercion by other males (e.g. Fox, 2002), or access to preferred resources (e.g. Janson, 1984), although the latter seems unlikely.

Indirect models of female choice propose that females mating with showy males will themselves produce attractive offspring (Fisher, 1930), or obtain "good genes" if male adornments demonstrate ability to avoid predation and acquire resources, survival to maturity, and superior competitive ability. Bright color may also convey information concerning ability to overcome a costly handicap (Zahavi, 1975), and/or pathogen resistance (Hamilton and Zuk, 1982). Bright color is associated with high levels of circulating testosterone in mandrills (Dixson *et al.*, 1993; Setchell and Dixson, 2001a, b; Wickings, 1993), and may therefore advertise the ability of a male to cope with the possible immunosuppressive effects of high testosterone levels (Folstad and Karter, 1992; Verhulst *et al.*, 1999; but see Hews and Moore, 1997; Owens and Wilson, 1999; Siva-Jothy, 1995). Finally, bright facial color in male mandrills is part of a suite of male signals, including a brightly colored rump and

genitalia, a sternal olfactory gland, and male vocalizations. Multiple ornaments in birds have been shown to communicate different aspects of male quality (e.g. Andersson *et al.*, 2002; Calkins and Burley, 2003; Jawor and Breitwisch, 2004), and the possibility exists that the different secondary sexual traits of male mandrills may convey different information to females, and/or to other males. Such signals of male "quality" may be particularly important in mandrills, which live in dense forest environments where individuals do not come across one another on a daily basis, and where males appear to move in and out of groups of 600 individuals (Abernethy *et al.*, 2002). Under such conditions of anonymity, where females lack prior information concerning male status and quality, status dependent secondary sexual characters may become very important in female mate choice.

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Table 1. Descriptions of mandrill behaviors mentioned in the text

Behavior	Description
Approach	Moved to within 2 m of another animal
Avoid	Moved away at least 1 m in reaction to an approach or sexual inspection
Flee	Ran away from another animal
Groom	Female parted a male's hair with one or both hands, picking at the skin and transferring particles to her mouth
Sexual presentation	Female moved to stand facing away from a male, with her perineal region directed towards him
Follow	Male walked after a female at a short distance, often looking at her perineum
Grin	Mouth retracted horizontally and vertically at the corners, but remained closed centrally, resulting in a '∞' shape
Head-shake	Shook head one or more times sideways in a '∞' motion
Lip-smack	Smacked lips together audibly, and moved tongue back and forward
Inspect perineum	Male looked closely at a female's perineum. He may also touch the female's vagina and lick or sniff his hands, or sniff the female's genitalia
Mount attempt	Male attempted to mount a female
Ejaculatory mount	Mount attempt with ejaculation, evidenced by convulsions and spasms of the male's upper torso, and appearance of semen in the female's vagina, and on the penis of the male

Table 2. Simple and partial Kendalls Tau-b correlation coefficients among male coloration, dominance rank, male mating success and putative indicators of female choice. N=5 males over the age of 8 years.

		Number of mounts	Scans within 2m of females	% approaches by female	Number of presents	Reaction to approach
Coloration	τ	0.527	1.000*	1.000*	0.800*	0.949*
Dominance rank	τ	-0.105	-0.600	-0.600	-0.400	-0.527
Coloration, controlling for dominance rank	τ	0.722*	0.686*	0.686*	0.524	0.638
Dominance rank, controlling for coloration[1]	τ	0.311	--	--	0.167	0.168
Male mating success	τ	--	0.527	0.527	0.738	0.667
Male mating success, controlling for dominance rank	τ	--	0.742*	0.742*	0.856**	0.855**

[1] Partial correlation coefficients could not be calculated where the correlation with colour was 1.000. However, adjusting the correlation with colour to 0.999 showed that the correlations were very small (-0.017).

*p<0.05; **p<0.01

FIGURE LEGENDS

Fig. 1.   Number of ejaculatory mounts with peri-ovulatory females vs. male coloration rank
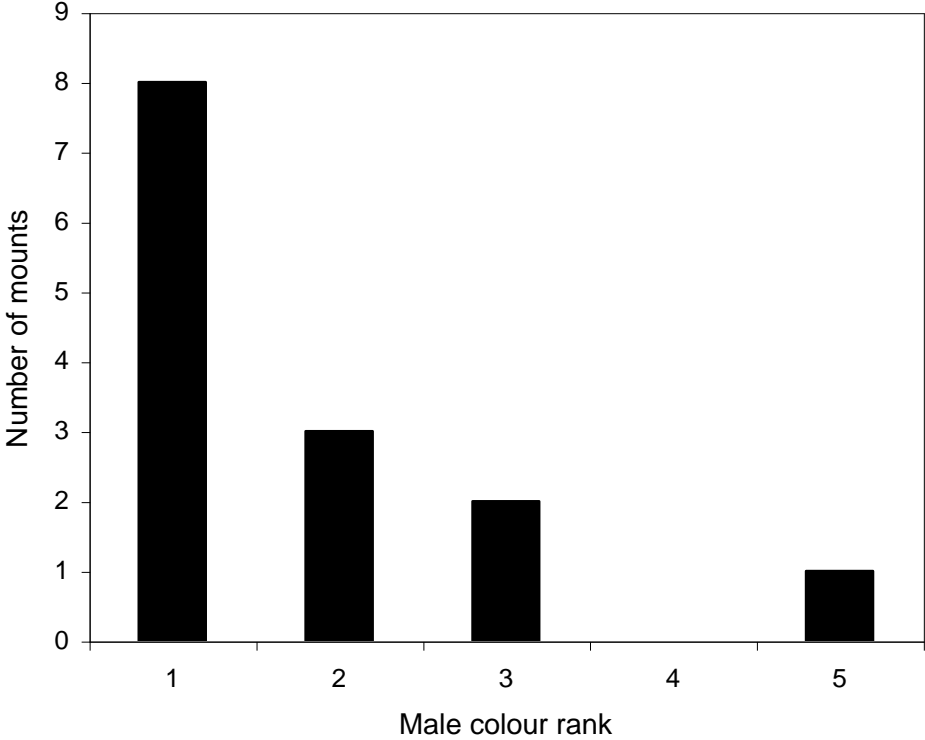
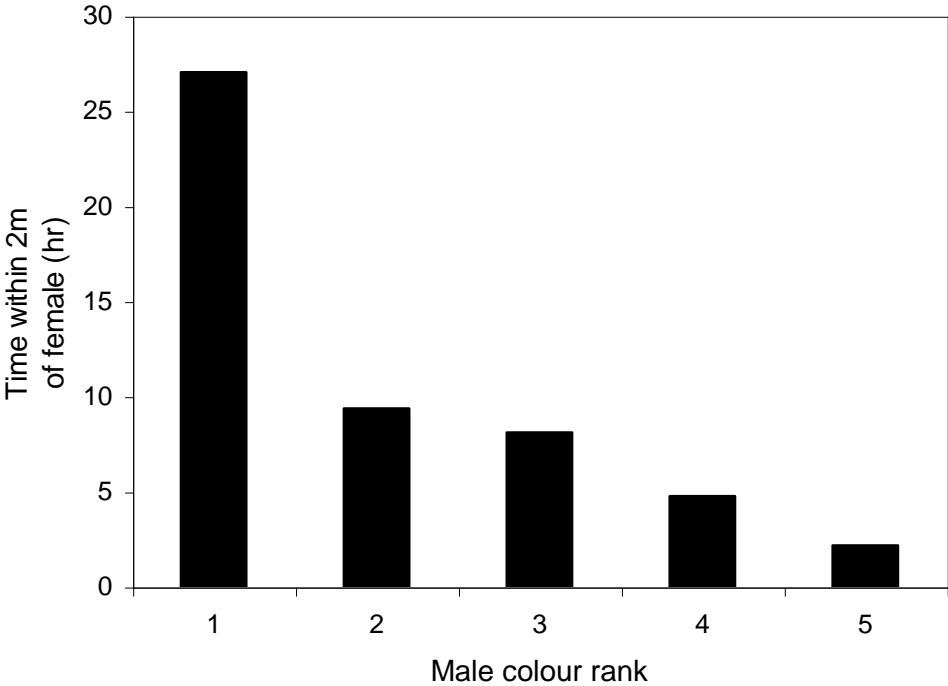Fig. 2. Time spent within 2m of peri-ovulatory females vs. male coloration rank

Fig. 3. Female responsibility for proximity, calculated as the number of approaches made by peri-

ovulatory females divided by the total number of approaches between males and peri-
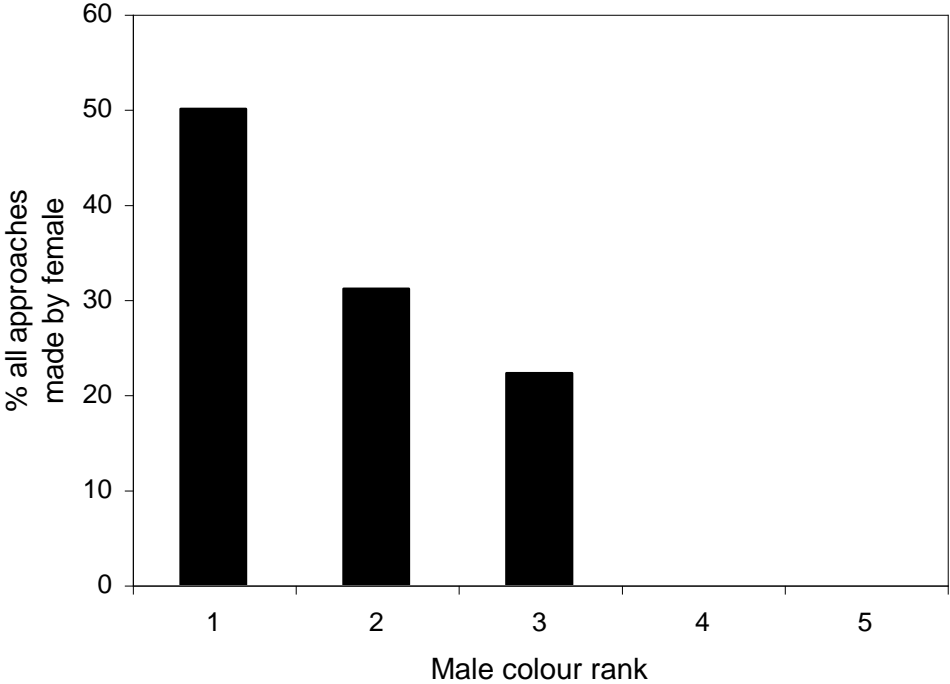
ovulatory females, vs. male coloration rank

Fig. 4. Percentage of positive reaction (female did not avoid) of peri-ovulatory females to an approach
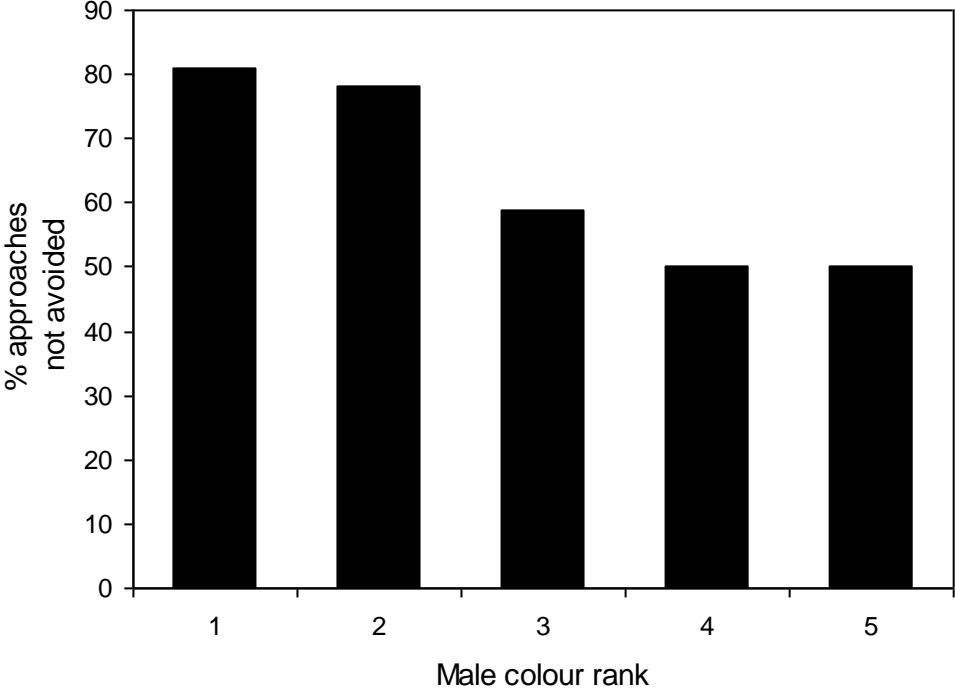
from a male vs. male coloration rank

Fig. 5. Percentage of positive reaction (female did not avoid) of peri-ovulatory females to an

inspection from a male vs. male coloration rank