RESEARCH PAPERS

Dominance, Status Signals and Coloration in Male Mandrills (*Mandrillus sphinx*)

Joanna M. Setchell & E. Jean Wickings

Centre International de Recherches Médicales, Franceville, Gabon

Abstract

Where individuals contest access to a resource, escalated physical fighting presents a risk to all involved. The requirement for mechanisms of conflict management has led to the evolution of a variety of decision rules and signals that act to reduce the frequency of aggression during competitive encounters. We examined strategies of conflict management in male mandrills (*Mandrillus sphinx*) living in two semi-free-ranging groups in Gabon. Adult male mandrills are large (31 kg), with long canines, making the costs of conflict potentially very high. We found that males formed dominance hierarchies, but that male–male relationships were characterized by avoidance, appeasement and ignoring. Fights were rare, but could result in death. Examination of the relationship between dominance and signaling showed that males use facial and gestural signals to communicate dominance and subordinance, avoiding escalated conflict. Male mandrills also possess rank-dependent red coloration on the face, rump and genitalia, and we examined the hypothesis that this coloration acts as a 'badge of status', communicating male fighting ability to other males. If this is the case, then similarity in color should lead to higher dyadic rates of aggression, while males that differ markedly should resolve encounters quickly, with the paler individual retreating. Indeed, appeasement (the 'grin' display), threats, fights and tense 'stand-off' encounters were significantly more frequent between similarly colored males, while clear submission was more frequent where color differences were large. We conclude that male mandrills employ both formal behavioral indicators of dominance and of subordination, and may also use relative brightness of red coloration to facilitate the assessment of individual differences in fighting ability, thereby regulating the degree of costly, escalated conflict between well-armed males.

Correspondence: Joanna M. Setchell, Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge, CB2 3DZ, UK. E-mail: mandrills@yahoo.co.uk

Introduction

Where individuals contest access to a resource, escalated physical fighting presents a risk to all involved (Maynard-Smith 1982). The requirement for mechanisms of conflict management has led to the evolution of a variety of decision rules and signals that act to reduce the frequency of aggression during competitive encounters (Lee 1994, Preuschoft & van Schaik 2000). These rules and signals form a continuum from encounters between unfamiliar animals to those with individualized social relationships (Preuschoft & van Schaik 2000).

When unfamiliar individuals meet, they must assess one another's fighting ability in relation to their own and determine the appropriate reaction (Preuschoft & van Schaik 2000). The outcome of an encounter will depend primarily on a comparison between the attributes (e.g. age, size, condition) of the two individuals concerned. Assessment of opponents can be costly (in terms of time lost from other activities), and signals can be advantageous in the recognition of power asymmetry (Preuschoft & van Schaik 2000). Morphological traits ('badges of status') or ritualized behavioral displays that reliably signal competitive ability can allow the settlement of potentially costly disputes without direct contest (e.g. bib and crown color in Harris' sparrows, *Zontrichia querela*: Rohwer 1975, 1977; Rohwer & Rohwer 1978, bib size in house sparrows, *Passer domesticus*: Møller 1987, color in midas cichlids, *Cichlosoma citrinellum*: Barlow 1973; Barlow & Wallach 1976, throat color in tree lizards, *Urosaurus ornatus*: Thompson & Moore 1991). Higher quality individuals benefit from a reduced number and intensity of aggressive interactions, and therefore from reduced risk of injury; inferior animals gain from a reduced rate of agonistic interactions with competitively superior individuals that they are likely to lose.

Game theoretical models, based on the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990), predict that rivals should employ stepwise escalation of aggression to acquire information concerning their opponent's strength relative to their own at the lowest possible cost to themselves. If, at any stage, an individual finds that its strength (or motivation) is not equal to that of the opponent, it will retreat, whereas if opponents are evenly matched, both will escalate the encounter. Thus the duration and the escalation of an encounter should be inversely proportional to the difference in fighting ability between opponents, as signaled by similarity in trait expression (Parker 1974; Enquist 1990), because more costly behavior is required to accurately assess relative fighting ability (e.g. Enquist & Leimar 1983; Leimar & Enquist 1984).

Badges of status tend to occur where rivals are unfamiliar with one another (Preuschoft & van Schaik 2000). Where individuals repeatedly encounter the same rival, individualized dominance relationships arise, based on knowledge of the outcome of previous encounters (Preuschoft & van Schaik 2000). In group-living animals a network of dominance relationships gives rise to a dominance hierarchy. Stable associations and familiarity with opponents leads to the use of transient, behavioral signals that reliably reflect motivation and fighting ability and serve to minimize the costs of competition by resolving interactions without

recourse to severe aggression. Here, formal indicators of submission may evolve, such as the bared teeth display in macaques (*Macaca mulatta*: de Waal & Lutrell 1985, *Macaca fascicularis*: Preuschoft et al. 1995) and bowing and pant-grunting in chimpanzees (*Pan troglodytes*: de Waal 1982). These signals are performed unidirectionally by the subordinate of a dyad (de Waal 1986), and allow both dominant and subordinate individuals to avoid the risks of escalated combat. Similarly, indicators of dominance, such as mock bites in stump-tail macaques (*Macaca arctoides*, Demaria & Thierry 1990) are performed only by the dominant individual in a dyad (Preuschoft & van Schaik 2000).

Finally, in purely dyadic relationships, power asymmetries depend on factors intrinsic to the individuals concerned (condition, weaponry, experience, etc.). However, in a social situation, individuals may also possess extrinsic power, through agonistic support received from third parties (Preuschoft & van Schaik 2000). Alliances are particularly important in female rank acquisition in matrilineal societies (Chapais 1992; Preuschoft & van Schaik 2000), but may also occur among males. For example, middle- and low-ranking savanna baboon males (*Papio* spp.) form coalitions to challenge high-ranking males for mating opportunities (e.g. Packer 1977; Noë & Sluijter 1990) and Barbary macaque (*Macaca sylvanus*) males often intervene in other male–male conflicts, supporting the inferior male, and thus balancing power asymmetries (Kuester and Paul, unpubl. data, cited in Preuschoft & van Schaik 2000).

Adult male mandrills (*Mandrillus sphinx*) are large (31 kg; Setchell et al. 2001), and possess upper canines measuring 44 mm (Setchell & Dixson 2002). The social organization of mandrills in the wild, where groups number from 15 to hundreds (e.g. Harrison 1988; Rogers et al. 1996; Abernethy et al. 2002), is unknown, although groups are known to include more than one adult male. Studies of a semi-free-ranging colony indicate that females are philopatric, organized in matrilines, while males peripheralize during adolescence (Setchell 1999). The alpha male is the only adult male to be 100% associated with the social group, while other adult males may spend the majority of their days with the group, live on the periphery of the social group, or be solitary (Setchell 1999; Setchell & Dixson 2001a). Solitary males are also found in the wild (e.g. Rogers et al. 1996). Under semi-captive conditions, male–male competition for access to sexually attractive females is intense, and reproductive skew is high (Wickings 1995; Charpentier et al. in press). It seems likely that male–male competition is also intense in the wild, as all adult males captured for a radio-tracking study of wild mandrills showed multiple scars from healed wounds (K. A. Abernethy, pers. comm.). We therefore hypothesized that males employ conflict management strategies to ameliorate the potentially high costs of male–male conflict associated with the presence of multiple, well-armed males. Furthermore, male mandrills also possess remarkable secondary sexual ornamentation, including bright red and violet coloration on the face, rump and genitalia. The expression of this coloration is related to dominance rank in adult males, with alpha males showing the brightest and most extensive red coloration and it has been suggested that male color acts as a badge of status in this species (Setchell & Dixson 2001a, b).

In this paper, we examine interactions between male mandrills living in two semi-free-ranging groups in Gabon. We begin by presenting a dominance hierarchy derived from avoidance behavior, and examining the incidence of male–male aggression and wounds. We show that males spend little time together, show little affiliative behavior, and exhibit signs of tension when they are in close proximity. We then address two main issues relating to status signals and conflict management in male mandrills. First, we evaluate the relationship between dominance and signaling, examining the difference in behavioral signals between dominant and subordinate animals and the relationship between signaling and encounter outcome. Here we predict that males should employ formal indicators of dominance and submission, to avoid the risks of escalated combat. Secondly, we examine the relationship between male relationships and secondary sexual coloration. Red coloration is closely related to male rank, and it was not possible to statistically separate the influences of coloration and rank on behavior in this semi-natural context. However, if red coloration does function as a badge of status, then we predicted that where color asymmetry is high, less colored males should spontaneously avoid escalation by showing submission, while aggression should occur more often between males that are similar in color, and thus unable to determine encounter outcome on the basis of simple rules.

As this is the first detailed examination of social dynamics in male mandrills, we also examined the question of whether male mandrills employ coalitions to temporarily or permanently reverse existing rank relationships, as described for related species (savanna baboons; Noë & Sluijter 1990). According to a model developed recently by Pandit & van Schaik (2003) coalitions are feasible only where contest among males is not too strong, and where costs of coalition formation are moderate. We therefore predicted that male contest is simply too strong in male mandrills for coalitions to be profitable, and that they should not occur.

Methods

Study Population

The mandrill colony at the Centre International de Recherches Médicales in Franceville, Gabon (CIRMF), was established in 1983–84, when 14 animals (six males, eight females, originating from the wild) were released into a 6.5-ha naturally rain-forested enclosure (group 1). All further additions to the group, subsequent to 1984, are due to reproduction of the founder animals; some animals have been removed. A second semi-free-ranging group was established in 1994 (group 2, in enclosure 2, 3.5 ha) by transferring 17 mandrills (including four adult males and six adult females) from the first enclosure. The animals eat a natural diet, supplemented by daily provision of monkey chow and seasonal fruits. Water is always available from a stream, which runs through both enclosures. At the beginning of 1996 there were 36 animals living in group 1 (including 13 reproductive females), and 24 in group 2 (including seven reproductive females).

Group size and composition thus corresponds to the smaller groups observed in the wild (fewer than 50 individuals; Rogers et al. 1996).

Behavioral Observations

Daily behavioral observations were made over 20 mo (March 1996 to November 1997) on all the 19 post-pubertal males (aged 4 to approx. 18 yr; Table 1) living in the two enclosures. Observations were made from a tower overlooking a grassy area of the enclosure. The otherwise dense nature of the forested enclosures allowed a good view of the animals for only a few hours each day, and males varied greatly in observability and group association (Table 1). In order to maximize collection of behavioral data under these conditions, all

Table 1: Males studied, with age, time observed, brightness of red coloration and group association

ID	Age at beginning of study[a]	Time observed with other animals[b]	Brightness of facial red coloration[c]	Rank	% days spent group associated[d]	% days spent solitary[d]
Group 1						
18	Approx. 15 yr	167 h 46 min	81.6	2	100	0
5C	9 yr 2 mo	70 h 50 min	78.3	5	9	52
12A1	9 yr 1 mo	53 h 40 min	72.6	4	7	68
2E	8 yr 0 mo	89 h 38 min	80.2	1	45	30
12E	7 yr 11 mo	135 h 04 min	79.4	3	30	17
5E	7 yr 0 mo	60 h 58 min	70.2	7	28	34
2C1	6 yr 10 mo	59 h 00 min	70.0	6	19	52
2F	6 yr 9 mo	125 h 52 min	52.3	9	61	6
2G	6 yr 1 mo	112 h 10 min	52.9	8	63	10
12C1	5 yr 2 mo	90 h 58 min	47.6	11	84	16
5D1	4 yr 1 mo	92 h 01 min	47.6	10	93	0
Group 2						
9	Approx. 18 yr	53 h 52 min	80.2	1	97	1
13	Approx. 17 yr	77 h 22 min	73.8	3	54	17
14	Approx. 17 yr	75 h 24 min	77.4	4	57	19
15	Approx. 16 yr	2 h 28 min	78.8	5	9	86
16B	8 yr 0 mo	84 h 36 min	78.6	2	70	14
10D	7 yr 0 mo	55 h 28 min	67.6	8	15	56
12F	6 yr 11 mo	35 h 52 min	69.1	6	35	45
17C	6 yr 1 mo	29 h 26 min	50.3	7	34	27

[a]Age of founder males estimated using dental records.
[b]As not all animals were 'in view' at all times, overall rates of behavior for individual males are expressed per hour the male was observed with other animals (and therefore had the opportunity to interact with other individuals; see Methods).
[c]Coloration is the mean score for facial coloration over the study.
[d]Male group association was scored as 'group associated', 'peripheral' or 'solitary. Thus % days group associated and solitary do not necessarily total 100%.

occurrences of the behaviors detailed in Table 2 were recorded for each male when he was in view (all-event recording; Martin & Bateson 1994).

As not all animals were 'in view' at all times, overall rates of behavior for individual males are expressed per hour the male was observed with other animals (rates per total time observed were unsatisfactory, because observation was biased towards periods when more than one animal was in view). Dyadic rates of behaviors are expressed per hour that two males were simultaneously in the observation area, and therefore had the opportunity to interact with one another. Simultaneous presence was measured using the number of instantaneous scans, made every 2 min, that both males were present, and multiplying the total number of scans by 2 min to obtain the total time males were observed together (mean 10 h 20 min, range 1 h 50 min to 20 h 50 min).

The context of a behavior was recorded in terms of immediately preceding and accompanying behaviors, and the response received. The reaction to an approach or a display (head-bob, stare, threat grunt and ground-slap; Table 2) was classed as 'no reaction', 'avoid' or 'aggressive' (see Table 2), and expressed as a percentage of the total number of approaches and threats (defined in Table 2).

Under the conditions of this study, it was not possible to determine the actual percentage of time that individual males spent near other group members. The group affiliation of each male was therefore scored each day as 'group associated': traveling, feeding, and interacting as part of the social group; 'peripheral': often more than 100 m from all other group members, traveling and feeding on the edge of the group; or 'solitary': traveling and feeding alone (Wickings & Dixson 1992). Peripheral males appeared to track group movements in the enclosures, while solitary males appeared to actively avoid contact with the group. Both classes of male avoided other males. Observations suggest that peripheral and solitary males also sleep alone (Joanna M. Setchell, unpubl. data). The measurement of days spent 'peripheral' meant that % days solitary was not equal to 100 minus % days group associated, but was the % days spent neither group associated, nor peripheral to the group.

Daily notes were also made of any evidence of combat between males [wounds and patches of hair missing from a male's coat (hair-pulls)] and of the reproductive status of females. Female mandrills develop prominent and conspicuous swellings of the perineal skin during the follicular phase of their cycle that reach maximum size around the time of ovulation (Dixson 1998). Records of these sexual swellings were used to examine the temporal distribution of agonistic interactions among males with respect to the presence of sexually attractive females.

Coloration Measurement

The brightness of the red/pink skin on the nose was quantified for non-anesthetized males by direct visual comparison of the male with graduated color charts (published by the Royal Horticultural Society, London). Colors in this chart correspond to known co-ordinates of the Commision Internationale de

Table 2: Behaviors recorded for male–male dyads

Behavior	Description
Facial and gestural threats	
Stare	Male stared at another male
Head-bob	Male stared at another male and jerked his head down and forwards rapidly. Could be repeated
Ground-slap	Male slapped one or both hands on the ground in a fast movement, while staring at another male
Threat grunt	A short, bark directed towards another male
Lunge	Male lunged towards another male, but did not follow-up with a chase
Chases and contact aggression	
Chase	Male ran rapidly after another male
Hit or grab	Male hit or grabbed another male
Fight	Males grappled with one another face-to-face
Submission	
Avoid (retreat)	Male moved away at least 1 m in reaction to an approach or threat by another male
Flee	Male ran away from another male
Presentation	Male approached another male and turned to orient his rump in the other's line of vision. Could be accompanied by a crouch
Scream	Sharp, sometimes repeated scream, with wide-open mouth and retracted lips
Social behavior	
Groom	Male parted the recipient's hair with one or both hands, picking at the skin and transferring particles to his mouth
Play	Two or more males engaged in vigorous wrestling and tumbling, or chased, showing a 'play face' (mouth wide open, but teeth covered)
Self-directed behavior	
Scratch	Male scratched himself vigorously with hand or foot
Body-shake	Male shook his entire body once or several times
Auto-groom	As for groom, but self-directed
Other	
Approach	Male moved to within 2 m of another male, passing him, or standing near him
Grin	Male's mouth was retracted horizontally and vertically at the corners, but remained closed centrally, resulting in a '∞' shape
Head-shake	Male shook his head one or more times sideways in a '∞' motion
Lip-smack	Male smacked his lips together audibly, and moved his tongue back and forward
Crest-raise	The crest of hair on the nape of the neck and top of the skull was vertically erected
Stand-off	See Results for details
Roar	One syllable, energetic, low, groaning sound emitted once or a few times
Two-phase grunt	Two syllable energetic, low, groaning sound. Continuous and regular

L'Eclairage (C.I.E.) 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 under natural light conditions, twice per month for each male, when animals entered the feeding pen, and were thus close to the observer (generally within 2 m). For analyses presented here, the mean of all measurements made during the study period was used for each individual.

Behavior and Dominance

To determine the dominance hierarchy between males, a dyadic interaction matrix was constructed for each group, including all interactions where one male clearly submitted to another by avoiding or fleeing.

To evaluate different behavioral signals as indicators of a dominance relationship actor–receiver matrices were also constructed for approaches, facial and gestural threats (head-bobs, stares, threat grunts and ground-slaps; Table 2), lunges, chases and fights. To qualify as a display of dominance or submission, a behavior should be expressed in most dyads in a predominantly unidirectional manner; and should be expressed in most of the relationships in the group (van Hooff & Wensing 1987). For each matrix, 'coverage' was examined in terms of the number and percentage of dyads in which events occurred; unknown relationships were dyads in which no act occurred; one-way relationships were those in which only one male in the dyad performed the action; two-way relationships were those in which both males performed the action, irrespective of frequency of interaction; and tied relationships were those where both males performed the action the same number of times. The directional consistency index (DCI) of a matrix was calculated as the total number of times that a behavior was performed in the direction of higher frequency within each dyad (H) minus the total number of times the behavior occurred in the direction of the lower frequency within each dyad (L), divided by the total number of times the behavior was performed by all individuals: $DCI = (H - L)/(H + L)$. This score varies from 0 (completely equal exchange) to 1 (complete unidirectionality) (van Hooff & Wensing 1987).

Linearity of the hierarchy is not a necessary prerequisite for the demonstration of dominance relationships, as every dyad can have a decided relationship while at the same time the overall hierarchy is non-linear (e.g. A dominates B, B dominates C and C dominates A). The linearity of the hierarchy constructed for each behavior was therefore examined using de Vries' (1995) improved version of Landau's index of linearity (Appleby 1983), which corrects for unknown relationships (h'). A value of $h' \geq 0.80$ was taken to indicate a strongly linear hierarchy. The statistical significance of h' was tested by means of a two-step randomization test with 10 000 randomizations (de Vries 1995) using MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands).

Coloration and Behavior

A coloration difference matrix was constructed to test the hypothesis that males interacted aggressively more with other males that were closer in red color than they did with dissimilar males. Matrix correlations (Mantel's Z-statistic) were computed between this matrix and dyadic interaction frequencies, and their significance tested using 10 000 randomizations, using Matman 1.1 (see de Vries et al. 1993). A significant negative association with color distance implies that males interacted more with other males that were similar in appearance than with dissimilar males, while a significant positive association with color distance implies that males interacted more with dissimilar males than with similar males.

Results

Dominance Hierarchy

Dominance hierarchies for groups 1 and 2, constructed using avoids and flees as signs of submission, are shown in Tables 3 and 4. Of 55 dyadic male–male relationships in group 1, 25 were strictly asymmetrical, with all avoids and flees made by the same male, and in a further 18 dyads one male made 90% or more of avoids and flees recorded. In group 2, 18 of 28 dyads were strictly asymmetrical, and in a further 3 dyads one male made 90% or more of avoids and flees recorded. Avoids and flees were highly directionally consistent in both groups, and both hierarchies were strongly and significantly linear (Table 5). The most ambiguous relationships occurred between males aged over 8 yr at the beginning of the study. Examination of interactions over time revealed that in group 1 these relationships were unstable, with frequent changes in relative status, with the exception of one

Table 3: Avoids and flees made by males in group 1. Males listed down the table avoided or fled from males listed across the table

Actor	Recipient										
	2E	18	12E	12A1	5C	2C1	5E	2G	2F	5D1	12C1
2E	*	9	0	0	2	2	1	0	0	0	0
18	85	*	34	0	3	1	2	2	1	0	1
12E	67	49	*	7	8	2	0	1	2	0	0
12A1	11	12	10	*	7	0	0	1	0	1	0
5C	29	22	18	7	*	0	0	1	0	0	3
2C1	16	41	10	8	7	*	0	1	1	0	0
5E	31	35	29	4	15	20	*	5	0	0	0
2G	47	51	34	18	19	42	22	*	7	1	1
2F	42	52	47	12	23	30	34	25	*	1	0
5D1	20	12	38	3	23	13	23	37	40	*	7
12C1	15	17	14	1	2	10	3	14	27	37	*

Male 2E was the most dominant and male 12C1 the most subordinate male.

Table 4: Avoids and flees made by males in group 2. Males listed down the table avoided
or fled from males listed across the table

Actor	Recipient							
	9	16B	13	14	15	12F	17C	10D
9	*	10	0	0	0	0	1	0
16B	39	*	33	11	0	1	0	0
13	23	95	*	0	0	0	0	0
14	27	57	70	*	0	5	5	0
15	4	9	1	1	*	0	0	4
12F	30	29	37	29	2	*	6	2
17C	43	87	53	53	2	50	*	0
10D	24	31	28	25	7	21	27	*

Male 9 was the most dominant and male 10D the most subordinate male.

dyad where a permanent rank reversal occurred (male 18 was defeated as alpha-male by male 2E). Similarly, in group 2 most events going against the dominance hierarchy involved male 16B, who gained top rank during the study period. Despite these changes in rank, which might be expected to co-occur with changes in behavior, data are pooled over the entire study period for the purposes of these analyses. Partition of the data set into periods before and after changes in alpha male considerably reduced the information available, and did not substantially alter the results.

In general, older males out-ranked younger males, and rank was significantly, but not perfectly, correlated with age in males of both groups (group 1: $r_s = 0.673$, $p = 0.004$, $n = 11$; group 2: $r_s = 0.976$, $p < 0.001$, $n = 8$). The imperfect linearity was partly, but not entirely, due to prime-aged males out-ranking both younger and older males (Table 1).

Incidence of Aggression and the Costs of Fighting

Overall, 1818 instances of male–male agonism were observed in group 1, and 614 in group 2. Of these, 67% (1216) incidents in group 1 were vocal or gestural only (377, 61% in group 2), while only 10% (188) involved physical contact between the two males (33, 5% in group 2). On the majority of occasions where contact aggression occurred, males grappled with one another in brief exchanges (< 5 s). These fights ended with one partner fleeing on 28 occasions (23%), but all other fights were unresolved. One-sided contact aggression, when one male hit or grabbed another but no fight ensued, occurred on only 17 occasions.

Higher-ranking males fought significantly more often than lower-ranking males in both groups (Table 6). Although no damaging fights were witnessed, a total of six separate wound events were observed in four adult males over the 20-mo study period. Wounds occurred on the face (one minor), hands (three minor), shoulder (one serious), and back (lethal). Hair-pulls were more common,

Table 5: Number, frequency, coverage, directionality and linearity of different behaviors in male–male dyads in two groups of mandrills

Action	Group	Number	No. per hour [mean (range)]	Coverage (number and % of relationships)				DCI	h′
				Unknown (%)	One-way (%)	Two-way (%)	Tied (%)		
Avoid or flee	1	1487	1.22 (0.00–5.23)	1 (2)	25 (45)	29 (53)	1 (2)	**0.85**	**0.88***
	2	982	4.72 (0.00–27.19)	0 (0)	18 (64)	10 (36)	0 (0)	**0.84**	**1.00***
Grin	1	814	0.40 (0.00–2.38)	6 (11)	15 (27)	34 (62)	5 (9)	0.51	**0.86***
	2	495	2.87 (0.00–29.52)	6 (21)	5 (18)	17 (61)	0 (0)	0.37	0.63
Present	1	186	0.16 (0.00–1.47)	15 (27)	38 (69)	2 (4)	1 (2)	**0.98**	0.63*
	2	31	0.15 (0.00–1.42)	15 (50)	12 (43)	2 (7)	1 (4)	**0.87**	0.58
Scream	1	47	0.03 (0.00–1.12)	48 (87)	7 (13)	0 (0)	0 (0)	**1.00**	0.30
	2	15	0.09 (0.00–2.99)	25 (89)	3 (11)	0 (0)	0 (0)	**1.00**	0.37
Approach	1	4669	2.6 (0.5–6.6)	0 (0)	0 (0)	55 (100)	0 (0)	0.24	0.31
	2	881	3.6 (0.0–21.0)	0 (0)	3 (11)	25 (89)	0 (0)	0.35	0.58*
Head-bob	1	677	0.90 (0.00–6.43)	1 (2)	14 (25)	40 (73)	6 (11)	0.43	**0.82***
	2	97	0.61 (0.00–5.00)	6 (21)	7 (25)	15 (54)	4 (14)	0.57	0.55
Stare	1	197	0.24 (0.00–1.32)	10 (18)	25 (450)	20 (36)	6 (11)	0.55	0.48
	2	106	0.18 (0.00–1.76)	8 (29)	10 (36)	10 (36)	2 (7)	0.58	0.68
Ground-slap	1	197	0.21 (0.00–1.40)	11 (20)	29 (53)	15 (27)	4 (7)	0.70	0.72*
	2	29	0.17 (0.00–6.00)	13 (46)	13 (46)	2 (7)	1 (4)	0.79	0.50
Threat-grunt	1	145	0.12 (0.00–2.25)	29 (53)	22 (40)	4 (7)	0 (0)	**0.90**	0.56*
	2	145	0.48 (0.08–1.76)	9 (32)	13 (46)	6 (21)	0 (0)	0.68	0.67
Lunge	1	143	0.13 (0.00–0.92)	8 (15)	46 (86)	1 (2)	0 (0)	**0.96**	**0.84***
	2	62	0.23 (0.00–5.00)	8 (29)	19 (68)	1 (4)	1 (4)	**0.94**	**0.74***
Chase	1	271	0.25 (0.00–2.32)	15 (27)	35 (64)	5 (9)	0 (0)	**0.88**	0.74*
	2	142	0.18 (0.00–1.33)	10 (36)	13 (46)	5 (18)	0 (0)	**0.85**	0.62
Hit/grab	1	188	0.22 (0.00–2.43)	28 (51)	4 (7)	23 (42)	20 (36)	0.04	0.18
	2	33	0.16 (0.00–3.00)	14 (50)	8 (29)	6 (21)	3 (11)	0.58	0.42

Values in bold indicate a high degree (≥0.8) of directionality or linearity.
Coverage: % unknown (dyads in which no act occurred), one-way (only one male in the dyad performed the action), and two-way (both males performed the action) relationships sum to 100%. Tied relationships are those in which both males performed the action the same number of times.
DCI, directional consistency index.
h′, linearity index.
*h′ is statistically significant (p < 0.05).

occurring 21 times in eight males. Several males also had broken canine teeth, possibly resulting from fights.

Given that access to receptive females is the prime ultimate function of male agonistic interactions, we examined variation in agonistic behavior with respect to the presence of cycling females. Although our data were limited, the monthly incidence of male–male aggression (using the mean across males) was not significantly related to the number of maximally swollen females present in group 1 ($r_s = -0.150$, p = 0.516, n = 21, data were too few for group 2). Indeed, incidence of male–male aggression peaked during periods when no females were

Table 6: Results of Spearman rank correlations between frequency of behaviors observed and male rank

Group	% days Group associated	Solitary	Play	Grins Made	Grins Received	Presentations Made	Presentations Received	Threat Made	Threat Received	Lunge Made	Lunge Received	Chase Made	Chase Received	Fight	Stand-off
1 (n = 11)															
r_s	0.300	-0.409	0.842	-0.182	-0.645	0.936	-0.700	-0.700	-0.009	-0.936	0.788	-0.936	0.764	-0.882	-0.936
p	0.370	0.211	0.001	0.593	0.032	<0.001	0.016	0.016	0.979	<0.001	0.004	<0.001	0.006	<0.001	<0.001
2 (n = 8)															
r_s	-0.922	0.970	–	0.132	-0.395	0.898	-0.611	-0.850	0.731	-0.988	0.707	-0.826	0.563	-0.810	-0.850
p	<0.001	<0.001	–	0.756	0.333	0.002	0.108	0.007	0.040	<0.001	0.050	0.011	0.146	0.015	0.007

The highest ranking male in a group ranks number 1, the second highest-ranking ranks number 2 etc. Thus a positive correlation indicates that the behavior is observed more often in low-ranking (subordinate) males than in high-ranking (dominant) males.

available. The first peak in aggression (November 1996) coincided with the change in alpha male (see above), but the second, higher peak (March 1997) was not associated with any particular events in the group.

Proximity Patterns, Affiliation and the 'Stand-off'

Males spent a median of only 0.9% of the time they were observed within 2 m of another male (range 0.1–3.6%). Peripheral or solitary males ranged alone rather than forming all-male bands. Neither the percentage of days that males were group associated, nor the percentage of days spent solitary correlated significantly with rank in group 1 (Table 6), because mid-ranking males were the least group-associated, while top-ranking males and younger, low-ranking males spent the most time group associated. However, in group 2, higher-ranking males were significantly more group associated, and significantly less solitary than lower-ranking males (Table 6).

Affiliative behavior was extremely rare between males. Grooming was recorded on only 11 occasions between males (all brief), and play was also relatively rare, occurring only among younger males, who also played with juveniles. The oldest male observed to play was aged 8 yr, and frequency of play was positively correlated with male rank in group 1 (Table 6, insufficient data were available for group 2 to test the relationship between play and rank).

A notable behavior when two males did find themselves in close proximity was the 'stand-off', which occurred when one male failed to avoid as another approached. On these occasions the two males stood side by side or at right angles to one another (so that each saw the other in profile), generally within reach of one another, for several minutes. Males avoided one another's gaze, shifted position frequently, and occasionally defecated. They also exhibited self-directed behavior, including scratching, body-shaking, auto-grooming and grooming the ground (likely a displacement behavior), which has been shown to be an indicator of stress and anxiety in non-human primates (Maestripieri et al. 1992). Males showed other signs of extreme arousal, including raised nuchal crests and, while mandrills normally carry their short tails approximately at right angles to the spine, during stand-offs it was directed forwards and laid flat along the spine. Males also yawned, showing their canines, but yawns were directed away from the other male. Males threatened one another with stares, head-bobs or ground-slaps, and threatened surrounding individuals, or at no obvious target. Stand-offs could also be associated with reciprocal contact aggression (wrestling), which occurred prior to, during or following the stand-off.

Stand-off encounters ended in one of three ways. Most encounters (228 of 312, 73%) ended unresolved, with both males walking away. Otherwise, one male might walk away, while the other male remained, or followed the other in an aggressive manner, resolving the encounter in favor of the non-retreating male. Finally, one male might hit the other, leading to brief bout of wrestling, after which one male might flee (resolved encounter), the males might re-enter a stand-off, or both might walk away (unresolved).

All males engaged in stand-offs, which occurred in 26 of the 55 possible male–male dyads in group 1, and 25 of 28 dyads in group 2. Involvement in stand-offs increased significantly with higher rank (Table 6), although stand-offs occurred more amongst the three peripheral or solitary adult males in group 1 than between the alpha male and other males.

Absence of Male–Male Coalitions

Male–male coalitions were not observed during the study. Lower-ranking males occasionally joined in when a high-ranking male chased a third male, but this was not solicited by the chasing male, and appeared to be opportunistic on the part of the lower-ranking male.

Dominance and Signaling

Submission

In addition to avoiding or fleeing, males showed submission to other males by presenting their hindquarters to them ('presentation'), although this was a much rarer behavior (Table 5). Forty-five percent (86) of presentations occurred in the absence of any obvious eliciting behavior. Otherwise presentations occurred in reaction to approaches by the other male (65, 35%), threats (35, 18%), a grin, a chase, a grab, and a wrestle (one each). Presentations were accompanied by a walking (64, 24%) or running (18, 9%) approach to the recipient male in 82 (43%) of cases, after which the presenting male moved away. Otherwise presentations were accompanied by no other behavior (33, 17%), avoidance (44, 23%), a grin (15), a scream (four), a threat (one) or a hit (one) from the presenting male.

The recipient male did not react to 79% (151) of presentations. Otherwise, males responded with a threat in 19 (10%) cases, by inspecting the presenting male's perineum or touching his rump (seven cases), by escalating aggression (four), grinning (three), approaching the other male (two), playing (one), or grooming the other male briefly (one).

Presentations were highly directionally consistent, occurring unidirectionally (from subordinate to dominant) in the majority of dyads in which they occurred. They were thus a good signal of subordinance, although the linearity of the hierarchy was low, due to the high number of unknown relationships (Table 5). Lower-ranking males presented more often than did higher-ranking males (Table 6), and higher-ranking males also received more presentations than lower-ranking males in group 1, although this was not the case in group 2 (Table 6).

A further submissive signal was screaming (Table 5). Screams were rare, directed at top-ranking males, and appeared to be a sign of absolute terror. The screaming male often remained in close proximity (within 2 m) to the recipient male, rather than fleeing, and often defecated. The recipient generally ignored the

screaming male. Only older adult males (males 18, 9, 13 and 14), and the youngest adolescent males (males 12C1 and 5D1) screamed, and coverage was very low (Table 5). Screams were perfectly directionally consistent in both groups, with all screams made by the subordinate male of a dyad (Table 5), indicating that screams were an excellent measure of relative rank in the dyads in which they occurred. As with presentations, h′ was low because of the number of blank relationships.

The grin

All males both grinned and received grins, and the only dyads for which no grinning display was observed involved males that were rarely observed together. Forty-three percent (334) of grins occurred in the context of distance reduction between two males, and grins occurred during 9% of all observed approaches by one male to another. Both the approaching and the approached male grinned, but the approached male grinned significantly more often than the approaching male (315 vs. 218 times; $\chi_1^2 = 17.65$, p < 0.001). Close approaches evoked a grin response more often than more distant approaches: 247 (16%) of 1571 approaches to 1 m or less elicited a grin from the approached male, whereas only 89 (4%) of 1986 approaches to more than 1 m elicited a grin in response ($\chi^2 = 132.7$, p < 0.001).

Grins also occurred in response to a threat from another male (113 occasions, 14% of grins). Of all threats, 9% provoked a grin in the threatened male. A male's failure to respond to a previous action or display could also provoke a grin from the displaying male (n = 94, 12% of grins). Grins could also be spontaneous (no obvious eliciting behavior by the recipient, n = 111, 14%), in reply to a grin by the receiving male (52 grins, 7%), or in response to an avoid (44 grins, 6%), a chase (31 grins, 4%), or when two males wrestled (18 grins, 2%). Males usually showed no response to a grin (72%). Otherwise, males responded by grinning back (12%), avoiding (8%), or threatening (6%).

Grins made by one male to another male were accompanied by head-shaking on 207 (26%) occasions, and lip-smacking on five (< 1%) occasions. With the exception of these behaviors, which can be regarded as a part of the display, 57% (444) of grins occurred in the absence of any other action, 25% (197) of grins occurred as the grinning male avoided the other male (11% of the 1796 avoids that occurred), 12% (97) of grins accompanied an approach (only 3% of the 3557 approaches recorded), and 4% (29) of grins accompanied a threat (only 2% of 1315 threats that occurred).

Grins were not a unidirectional signal of either dominance or subordinance in male mandrills: both the dominant and subordinate male of a dyad grinned in more than 60% of dyads in both groups, and the directional consistency index was low, although the linearity of the hierarchy was high in both groups, and significant in group 1 (Table 5). The frequency at which males grinned was not significantly correlated with rank. However, higher-ranking males received significantly more grins than lower-ranking males in group 1, although this was not the case in group 2 (Table 6).

Approaches and threats

Approaches to within 2 m, with no accompanying aggressive behavior, occurred in all dyads in both groups. Males showed no reaction to the majority of approaches (Fig. 1). All males in group 1 approached all other males, while in group 2 approaches were bi-directional in all but three dyads, and approaches showed very low directional consistency, and a low degree of linearity (Table 5).

By far the most common threat used by males was the head-bob. Stares, threat grunts and ground-slaps were much less frequent (Table 5). Males often made no response to head-bobs, stares, ground-slaps and threat-grunts, and aggressive responses to threats were relatively uncommon (14% of all threats) (Fig. 1). All males both made and received head-bobs, which occurred bi-directionally in the majority of dyads, and the directional consistency was therefore low (Table 5). All males also made and received stares and ground-slaps, and these threats also had low directional consistency (Table 5). Threat-grunts were more directional, and 80% were made by the two top-ranking males. With the exception of head-bobs in group 1, none of these gestural threats gave a strongly linear hierarchy (Table 5), and none qualified as a formal indicator of dominance in mandrills. As the directionality of threats increased, males became more likely to avoid the threatening male [% avoidance vs. directionality of display: group 1: $r_s = 1.000$, $p < 0.001$; group 2 $r_s = 0.943$, $p = 0.005$, $n = 6$ displays (approach, head-bob, stare, ground-slap, threat-grunt, lunge)].
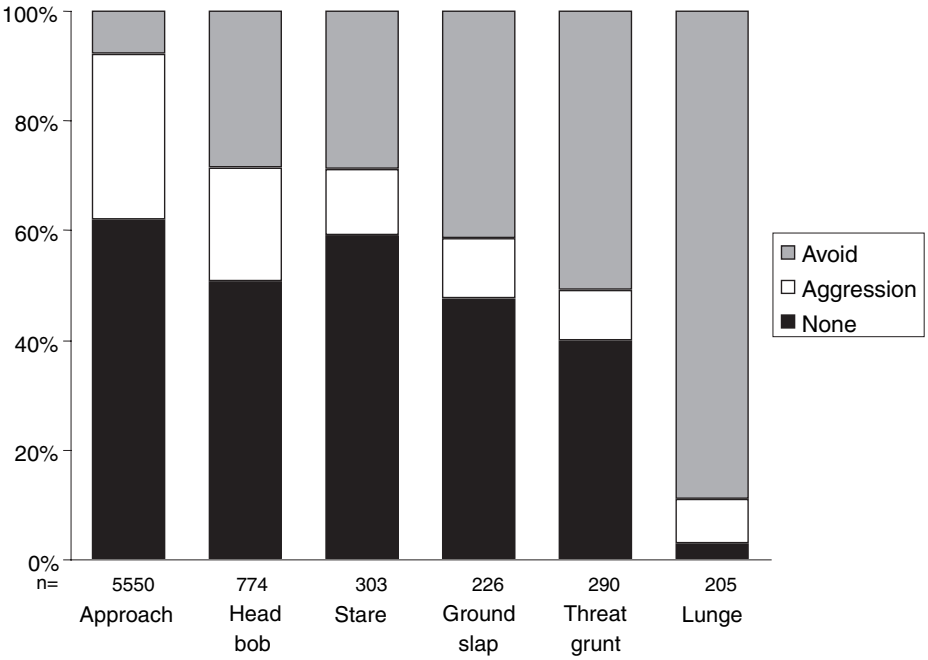
Fig. 1: Male reactions to approaches and threats from another male

Higher-ranking males threatened other males significantly more often than lower-ranking males (Table 6). However, the top-ranking male did not necessarily threaten the most often. In group 1, the most aggressive males were ranked 3 and 5, and these males threatened other males twice as often as other males. In group 2, the most aggressive males were the males ranked 2, 3 and 4, and included the male that gained alpha rank during the study. Lower-ranking males received significantly more threats than higher-ranking males in group 2, although this was not the case in group 1 (Table 6).

Lunges and chases

Unlike gestural threats, lunges were a good indication of the dominance hierarchy. They occurred in the majority of dyads (good coverage), and were very highly directionally consistent, with strong and significant linearity in both groups (Table 5). Accordingly, males usually avoided or fled when lunged at (Fig. 1). Chases were also highly directional, and a good dominance indicator (Table 5). By definition, males always fled when chased, although the fleeing male occasionally subsequently stopped, turned and threatened the chasing male. Higher-ranking males lunged and chased other males significantly more often than lower-ranking males (Table 6). Receipt of lunges and chases was significantly positively correlated with dominance rank in group 1, although this was not the case for chases in group 2 (Table 6).

Other behaviors

Only alpha males two-phase grunted more than occasionally, making this vocalization a signal of high rank. During 1996, the alpha male in group 1 (male 18) made this vocalization almost continuously, and no other male was heard to two-phase grunt. When male 2E took over as alpha male both he and the ex-alpha male 18 two-phase grunted occasionally. During both 1996 and 1997, the alpha male in group 2 (male 9 in 1996, male 16B in 1997) two-phase grunted occasionally, while no other males did.

Males were observed to roar 33 times; although this loud vocalization was heard far more often from males that were out of sight. Roars often co-occurred with branch-shaking, followed chases involving other males, were usually produced by males that were not involved in the chase, and were not directed specifically at other animals. Roars from one male provoked roars from males in other parts of the enclosure, and in the neighboring enclosure. All males over the age of 7 yr roared, and although our data are too limited to determine the function of the 'roar', the context and energetic appearance of the display suggest that it may be similar to the 'contest wahoo' described in baboons, which appears to function as a vocal display of stamina and competitive ability (Kitchen et al. 2003).

Finally, all males yawned. Although yawns usually revealed the canine teeth, they appeared not to be a threatening display, and 91% of yawns were not

directed at other animals or occurred whilst males were alone. Adolescent males also made half-yawns, yawning while keeping their canine teeth covered with the lips.

Secondary Sexual Coloration, Dominance and Male Interactions

Red facial coloration was positively related with both age (group 1: $r_s = 0.916$, $p < 0.001$, $n = 11$; group 2: $r_s = 0.762$, $p = 0.028$, $n = 8$), and dominance rank (group 1: $r_s = 0.970$, $p < 0.001$, $n = 11$; group 2: $r_s = 0.833$, $p = 0.010$, $n = 8$). The matrix constructed to examine correlations between color difference and dyadic frequencies of behavior in the larger group (group 1) was thus very similar to a rank difference matrix (with three similarly colored male dyads reversed), and correlations between behaviors and rank difference matrix were consistent with those presented for coloration.

Interaction frequency between male dyads was significantly related to color difference. Males made submissive presentations more often to males that were dissimilar than to similarly colored males (presentation matrix vs. color difference matrix: $Z = 75$, $r = 0.188$, $p = 0.023$; Fig. 2), but grinned significantly more often at similarly colored males than at dissimilar males ($Z = 258$, $r = -0.273$, $p = 0.008$; Fig. 2). Males also interacted aggressively more often with other similar males than they did with dissimilar males. Threats were significantly more common between similar males than between dissimilar males (threat matrix vs. color difference matrix: $Z = 334$, $r = -0.397$, $p < 0.001$; Fig. 2), and similarly colored males fought one another more often than dissimilar males (fight matrix vs. color difference matrix: $Z = 62$, $r = -0.376$, $p < 0.001$; Fig. 2), although the dyadic frequency of lunges and chases was not significantly correlated with color difference (lunges and chases matrix vs. color difference matrix: $Z = 166$, $r = 0.043$, $p > 0.050$). Finally, stand-offs were significantly more frequent between males that were similar in color than between those that were dissimilar (stand-off matrix vs. color difference matrix: $Z = 55$, $r = -0.307$, $p = 0.004$; illustrated in Fig. 2).

Discussion

Our analysis of male mandrill behavior suggests that, as expected, males were unwilling to engage in overt confrontation with one another. Escalated fights were rare, but could occasion substantial costs to both combatants, including serious injury and death. The primary conflict avoidance strategy employed by males was avoidance and spacing. Males were very rarely found in close proximity to one another, and showed very little affiliative and no coalitionary behavior. Peripheral males did not form all male groups, but ranged alone. When fights occurred, the majority were unresolved, and a notable behavior was the apparently highly stressful 'stand-off', that occurred when males found themselves at close quarters.

Males could be organized into linear dominance hierarchies, using avoidance behavior. However, dominance relationships could be ambiguous between
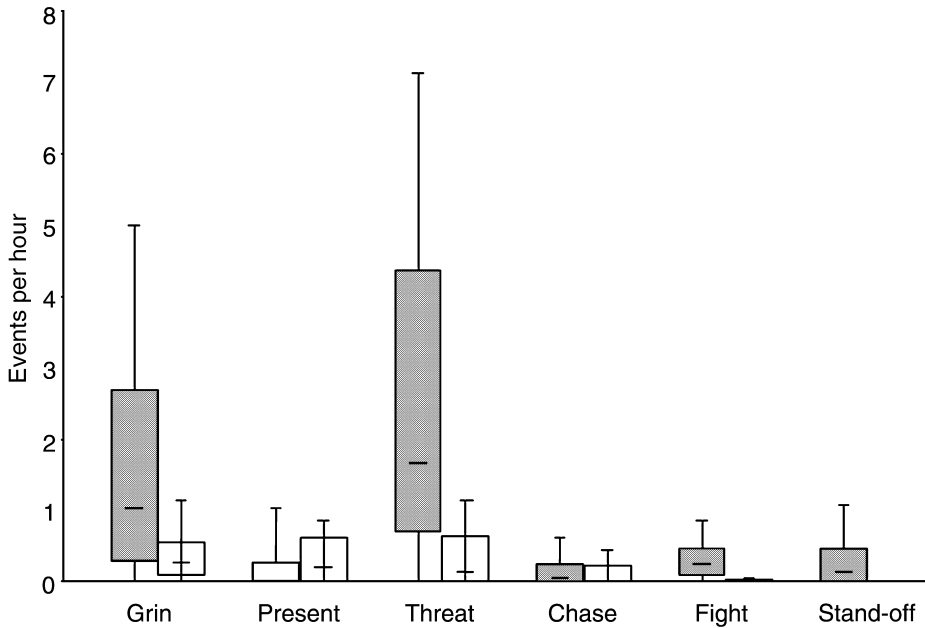
Fig. 2: Frequency per hour of behaviors made by similarly and differently colored males in group 1. Events are per hour male–male dyads were observed simultaneously. Shaded boxes: similarly colored male–male dyads with color rank difference 1 or 2 (n = 19). Open boxes: differently colored dyads with color rank difference ≥7 (n = 10). Plot shows median (bars), inter-quartile range (boxes) and extreme values (whiskers). No stand-offs occurred between dyads of differently colored males

close-ranking males, and this was particularly so amongst adult males. Higher-ranking males were more aggressive than lower-ranking males, but alpha males were not the most aggressive males, implying that alpha males do not need to constantly reinforce their top position with aggression. Although data are not presented here on the initiation of conflict, as this was often ambiguous, threats were often directed to dominant males by subordinates, and adolescent males were observed to harass dominant males, by repeated directing mild threats at them, behaviors that might be interpreted as 'testing' the fighting ability of the dominant (as opposed to 'policing', or conflicts initiated by the dominant male, Cant & Johnstone 2000). Finally, male agonism was not more frequent when more sexually attractive females were available. This contradicts findings for other seasonally reproducing primate species (e.g. rhesus macaques, *M. mulatta*: Wilson & Boelkins 1970, toque macaques, *Macaca sinica*: Dittus 1977), and non-seasonal species, in which males are more aggressive when sexually receptive females are present (baboons: Packer 1979), and may be partly explained by events that occurred between the two mating periods in this study. The first peak in male–male agonism coincided with the replacement of the alpha male; however, the second, higher peak in agonism was not associated with any obvious events in the group.

Dominance and Signaling

Dominant and subordinate males consistently employed different behavioral signals in dyadic interactions. Submission was evidenced by spatial yielding (avoidance or fleeing), but also by ritualized presentation of the rump and screaming. Aggression between males was predominantly gestural and rarely involved physical contact. Males used four distinct stereotyped threat displays (stares, head-bobs, ground-slaps and threat-grunts), as well as more energetic lunges and chases. This list of displays shows a general increase in energy, and as reported for other species (female iguanas; Rand & Rand 1976), the success of a threat, in terms of submission elicited, increased with energy expended. About half of approaches and mild threats from other males were ignored. Individuals of all ranks directed mild threats at one another, and these signals were directionally inconsistent and could not be used as formal indicators of the dominance relationship between males. Threat grunt vocalizations were more directionally consistent, but had low coverage, and were employed mostly by high-ranking males. By contrast to milder threats, lunges and chases were very highly directionally consistent, elicited submission, and were good indicators of dominance relationships between males. These results are in accordance with Hinde's (1981, 1985) proposal that threat signals of graded intensity function to express readiness to escalate aggression. Thus the receiver need not necessarily yield in response to a mild signal, as it indicates only a mild tendency to attack, but should yield in response to a more intense signal of willingness to attack.

Males also employed a stereotyped 'grin', that was much rarer in severe agonistic encounters than in approach or mild threat encounters. Although higher-ranking males received more grins in the larger of the two groups studied, grins did not qualify as a signal of submission (both the dominant and subordinate male grinned in the majority of encounters, and grins showed only low directional consistency). These data thus clarify this display as signalling non-agonistic motivation, in agreement with van Hooff's (1967) interpretation of the grin as affiliative or appeasing, rather than aggressive (as suggested by Jouventin 1975). The mandrill's grin appears to function in a similar way to 'greetings' in male baboons, which also occur in conflict-provoking situations, such as when males meet or in the presence of attractive resources, and are also often reciprocal (e.g. Colmenares 1990, 1991). Interestingly, since this study ended, a behaviour similar to the 'diddling' of the penis and/or scrotum reported for baboons (Colmenares 1990) has been observed twice between adult males in the CIRMF colony, accompanied by grin displays.

Red Coloration and Interactions between Males

Patterns of interactions between male mandrills followed predictions arising from game theoretical models of animal combat. Unidirectional submission occurred more often where color differences between males were clear, while mild

threats and escalated aggression occurred more often between closely matched males, where the outcome of an encounter was less clear-cut. Similar results, with fights occurring most frequently between similar individuals, have been found for many species (reviewed in Andersson 1994). Interestingly, however, the occurrence of unidirectional dominance signals (lunges and chases) was not related to color difference in male mandrills.

Where males are closely matched in color (and thus dominance rank), combatants may be unwilling to retreat, or unable to resolve small differences between themselves and their opponent. Direct assessment, via fighting, is therefore required. However, an alternative explanation for more frequent aggression between similarly colored males than between dissimilar males may be a greater need to 'clarify' dominance relations among close-ranking individuals (Clutton-Brock & Harvey 1976). de Waal (1991) has suggested that this might explain why ritualized status signals are exchanged most frequently between stump-tailed macaques (*M. arctoides*) of similar rank (Demaria & Thierry 1990), and why juvenile baboons (*Papio anubis*) frequently supplant close-ranking age peers from food sources (Johnson 1989).

A further possible explanation for the occurrence of more escalated fights involving higher-ranking (more brightly colored) males may be that such males present a greater potential threat to the reproductive success of rivals, while subordinate (paler) rivals are tolerated because they are less attractive to females. A badge of status that honestly signals male 'quality', and success in male–male competition, is also of interest from the female perspective (Berglund et al. 1996). Females that choose to mate with males possessing conspicuous, honest signals of 'quality' are selecting mates that indicate successful in male–male competition. Such success implies general fitness that (if it is heritable) will be passed on to the female's offspring (Zahavi 1975; Berglund et al. 1996). Indeed, preliminary evidence suggests that female mandrills may base their mating choices on male coloration, preferring to mate with brightly colored males (Setchell 1999, 2002). However, experiments will be required to disentangle the influence of male dominance and coloration on female choice, and to determine whether females do indeed prefer to mate with more highly colored males.

Where opponents are closely matched, and well-armed, the risks of escalation are high for both individuals, and may result in a stalemate (Packer & Pusey 1985; Sigg & Falett 1985). Under such circumstances, Preuschoft & Paul (2000) predict that unidirectional status signals should not occur, but that relationships should be characterized by 'sporadic outbursts of severe aggression complemented by powerful de-escalation mechanisms', such as ignoring (p. 207). Preuschoft & Paul (2000) describe 'ignore duels' in Barbary macaques, during which males ignore closely matched rivals, and avoid their gaze. The stand-off encounters that we observed between male mandrills also occurred more often in high-ranking males than in low-ranking males, and more often between closely-matched males than between dissimilar males. As high-ranking males also tend to be the largest males, with the longest canine teeth, stand-offs may be similar stalemate situations to ignore duels.

Stand-offs may also function as a non-contact assessment behavior, employed by closely matched males to acquire accurate information concerning comparative body and weapon size, as well as competitive motivation (cf. parallel walks in red deer, *Cervus elephas*: Clutton-Brock et al. 1979). Under such conditions, no information concerning withdrawal intentions should be shown in advance of withdrawal, as the opponent may still retreat first (Maynard-Smith 1974). Indeed, withdrawal from a stand-off was not predictable (at least to the human observer). However, actions occurring within stand-offs were not mirrored by rivals, nor did they show an escalating pattern of intensity. Rather, outbursts of wrestling were sudden. The position of males relative to one another also casts doubt on the interpretation of the stand-off as a means of acquiring information about a rival's physical characteristics, as males often seemed to avoid looking at one another. However, stand-offs may function as a 'war of attrition' (Bishop & Cannings 1978), or a 'war of nerves' (Clutton-Brock et al. 1979) whereby closely-matched rivals assess one another's competitive motivation, and relative willingness to spend time in a high risk position (i.e. at close quarters to another large male and his canine teeth).

Red Coloration as a Badge of Status in Mandrills

Dyadic dominance–subordinance relationships in male mandrills are known to be closely related to relative size, weaponry and coloration, although the alpha male at any one time is not necessarily the absolutely largest individual (Setchell & Dixson 2001a, b). As in baboons, this is likely to be because dominance ranks are more transient than body size (Kitchen et al. 2003). Red coloration, by contrast, is always brightest and most extensive in the top-dominant male (Setchell & Dixson 2001a, b; J. M. Setchell unpubl. data). This study shows that the male dominance hierarchy was closely, although not perfectly related to brightness of red coloration.

Observational data, such as that presented here, do not allow us to factor out the separate influences of behavior, age, mass, red coloration, and other morphology on male interactions, as these variables are highly interrelated. Introduction experiments (e.g. Gerald 2001), or manipulative studies will be useful to determine whether male mandrills use relative coloration to determine whether or not to initiate or escalate an agonistic encounter, when other variables are controlled. Alternatively, if brightness does function as a badge of status, then two males should behave differently if their relative coloration changes over time. Examination of color and behavior before vs. after a rank reversal could function as a 'natural experiment' to disentangle the relative influence of various factors on male interactions. Unfortunately, the data available during the present study were insufficient to allow such temporal analyses.

Animal combat theory has traditionally focussed on encounters between unfamiliar rivals, and badges of status are most commonly found in species where strangers meet. However, honest indicators of competitive ability may also occur in species where individuals have a long history of prior interactions. For example, a recent study of contest wahoos in male baboons (*Papio cynocephalus*)

showed that acoustic features of these loud calls were correlated with male dominance rank and age. High-ranking males were more likely to participate in wahoo bouts than mid- or low-ranking males, wahoo bouts occurred more often between closely ranked males, and these bouts were longer, with more calls (Kitchen et al. 2003). Like the baboons in Kitchen et al.'s study, the male mandrills in our semi-free-ranging study groups knew each other from repeated interactions, and showed differentiated dominant–subordinate relationships. Whether wild males are similarly familiar with one another remains unknown. Reports of hordes of mandrills numbering more than 600 individuals, with varying male group membership (Abernethy et al. 2002) suggest that most males under these conditions may be relative strangers to one other. Under such conditions of anonymity, status dependent red coloration may be of extreme importance in the avoidance of costly conflict between large, well-armed strangers. Moreover, as male status can change drastically over short periods of time, males that interact only occasionally may use red coloration to assess the current status of a rival, rather than basing decisions on prior information that may no longer be relevant.

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