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RESEARCH ARTICLE

Changes in Social Interactions During Adolescence in Male Mandrills (*Mandrillus sphinx*)

MARIE CHARPENTIER[1*], PATRICIA PEIGNOT[2], MARTINE HOSSAERT-MCKEY[1], AND E. JEAN WICKINGS[2]
[1]*CEFE-CNRS, Montpellier, France*
[2]*UGENET, CIRMF, Franceville, Gabon*

The adolescent period in male mandrills extends from the time the testicles descend (at the age of 3–4 years) to the time adult characteristics develop (at the age of 10 years), and is thus one of the longest adolescent periods in cercopithecines. In this short cross-sectional study of 11 male mandrills (4.7–9.1 years old), we analyzed social behavioral patterns to investigate partner preference and changes in types of interactions throughout puberty. The mandrills were separated into two clusters on the basis of all of the social interactions scored, as well as the age and sex of the protagonist. During early to mid puberty, immature individuals interacted preferentially with other male adolescents and juveniles. Playing was an important activity, and some affiliative interactions with juveniles were observed. Older adolescents interacted more with adult males and females. These older adolescents were predominantly aggressive toward other adolescents, females, and juveniles, and showed little or no affiliative or playful behaviors. These results indicate a shift in social partners: older males interacted more frequently with adult males, and their behavior involved more aggression and less submission compared to younger adolescents, which showed predominantly submissive and playful behavior. These changes are consistent with preparation for dispersal and future intermale competition. Am. J. Primatol. 63:63–73, 2004.

Key words: ***Mandrillus sphinx*; adolescence; social behavior; aggression; submission; play**

INTRODUCTION

Selection in both human and nonhuman primates for large brain size delays physical and sexual maturation [Harvey et al., 1987; Walters, 1987] because the

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*Correspondence to: Marie Charpentier, CEFE-CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France. E-mail: mariecharp@yahoo.fr

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energy costs of maintaining brain function are balanced against slower somatic growth [Tanner, 2001]. Thus, there is often an extended period of development between weaning and adulthood [Ross & Jones, 1999], corresponding to puberty, from the first changes in hormonal activity until the time social and physical reproductive competence is acquired [Pereira & Altmann, 1985]. Adulthood, which marks the acquisition of the social and physical capacity to reproduce, occurs later in sexually dimorphic, larger-bodied male primates. Physical changes during adolescence are necessarily accompanied by changes in behavior, as animals mature and learn by experience and apprenticeship [Fairbanks, 1993]. Much of this social experience is gained through play, first with siblings and then with peers [Dolhinow, 1999; Ehardt & Bernstein, 1987; Fagen, 1993; Walters, 1987; Watts & Pusey, 1993].

Where sexual dimorphism exists, the rate of maturation is slower in the larger males than in the females (i.e., the males have an extended juvenile phase and delayed puberty, and/or longer pubertal development). The mandrill (*Mandrillus sphinx*, Papionini; Cercopithecoidea) exhibits the most pronounced degree of sexual dimorphism known in primates, in terms of both size (males are over three times as large as females [Setchell et al., 2001; Wickings & Dixson, 1992a]) and spectacular secondary sexual adornments [Jouventin, 1975; Setchell & Dixson, 2001a, b]. Hence, male mandrills, which are the heaviest and one of the most sexually dimorphic of all cercopithecines, also have the longest adolescent development phase (6 years), from the time of pubertal testicular descent at 3–4 years to adulthood at 9–10 years. By contrast, female mandrills have a very ill-defined period of adolescence, since conception frequently occurs during the first external sexual tumescence that marks pubertal hormonal changes and ovarian maturation, from the age of 3.5 years onward [Setchell & Wickings, in press a]. On average, sexual maturity is reached at 4.7 years, and adult size is gained at 7 years [Setchell et al., 2002; Wickings & Dixson, 1992b] (these data all refer to mandrills maintained in the semi-free-ranging colony at the Centre International de Recherches Médicales de Franceville, CIRMF, Gabon). As in other primate societies, male mandrills apparently leave their natal group before they reach adulthood [Abernethy et al., 2002]. This phenomenon is maintained in the semi-free-ranging colony, where peripheralization of males, within the margins of the enclosure, replaces migration [Setchell & Dixson, 2002].

Very few studies have targeted behavioral changes during the adolescent period [Pereira & Altmann, 1985; Setchell, 2003; Strum, 1987; Walters, 1987]. Such studies are hampered in the wild, where age and family kinship are not always known, and field conditions may preclude repeated sightings of known individuals over long periods. The semi-free-ranging colony of mandrills at CIRMF lends itself to the study of social behavior because birth and breeding records are available and the animals are accessible for prolonged periods of observation. However, the very extended nature of puberty in male mandrills, which makes them a good model for the study of adolescence, makes it difficult to follow the same individuals closely from the time of testicular descent to adulthood. The longest study to date was conducted over a period of <2 years [Setchell, 2003]. As an alternative approach, we undertook a short cross-sectional study of the social interactions of 11 mid- to late-adolescent males with all members of the colony. We suggest that the physical maturation during puberty that prompts resource and social competition also leads to changes in social behavior and group affiliation.

MATERIALS AND METHODS

Animals and Husbandry

The semi-free-ranging colony at the CIRMF, Gabon, was established in 1983–1984 when 15 animals (seven males and eight females of different origins, and hence unrelated [Wickings, 1995]) were released into a 6-ha, naturally rain-forested valley enclosed by an electric fence. Any further increases in the group have been due to natural reproduction of these founder animals, which were countered by deaths and some removals for experimental purposes. At the time of this study (February–May 2000), the group consisted of 69 individuals (Table I). All mandrills in the colony were tattooed shortly after birth, and individuals >3 years old were given numbered and colored ear tags for ease of recognition. This study focused on 11 adolescent male mandrills (Table II).

The naturally rain-forested enclosure had a small fenced pen (to facilitate feeding and capture of the animals) overlooking an open grassy area. The mandrills were fed twice a day with seasonal fruits, vegetables, and monkey pellets to supplement their foraging. Water was available ad libitum. The mandrills were visible before and after the meal, and remained at the edge of the forest for approximately 2–3 hr during each feeding period.

TABLE I. Age and Sex Classes of the 69 Mandrills of the CIRMF Colony in February 2000, at the Beginning of the Study

	Adults	Adolescents	Juveniles	Infants
No. of individuals				
Males	9	11	5	9
Females	17	-	13	5
Age (years)				
Males	10–19	4.7–9.1	2.9–4.1	0.75–1.2
Females	4.8–22	-	1.8–2.5	1.0–1.2

TABLE II. Information on the 11 Adolescent Male Mandrills Included in this Study, Data as of February 2000

Individuals	Date of birth	Age on entry into study (months)	No. min observed	No. interactions scored	Social integration (% group presence)
12C1	14/01/91	109	425	598	100
5D1	31/01/92	97	545	987	85.7
12J	14/02/93	84	545	694	100
10H	10/03/93	83	545	668	100
12A6	12/03/93	83	545	659	100
2D3	07/01/94	73	545	914	100
2C5	03/01/95	61	545	1167	71.4
10E1	07/01/95	61	545	717	100
12L	24/02/95	60	545	564	100
5D2	06/04/95	58	545	589	85.7
10J	18/06/95	56	545	632	100

Ethical Considerations

The observations carried out during this study required no change in the animals' normal daily routine. Approval was given by the local primate ethics committee before this study was conducted.

Behavioral Observations

A total of 8,188 interactions across six social behavioral categories (Table III) were scored between the 11 adolescent males, and between these adolescents and all other members of the mandrill colony during 126 hr of observations, which were carried out during 10 weeks of the nonbreeding season. We conducted the observations before feeding, between 0900–1100 and 1500–1700, to avoid any effects of feeding competition on behavior. We collected data using the focal method, by randomly sampling the 11 adolescent males [Lehner, 1996; Martin & Bateson, 1986]. The sequence in which the animals were observed was also randomized. During a 5-min period, all social behaviors (bouts) initiated and received by the focal animal were noted, along with the identity of the partners. The duration of each bout was not recorded, but the end of the bout corresponded to the cessation of the considered activity. To standardize the behavioral observations, we observed the 11 adolescents for the same overall length of time, except for one individual (12C1; Table II). The social integration of the adolescent mandrills was scored on each occasion according to the presence or absence of an individual from the group during the overall observation period. A percentage score of presence was calculated for each month with the use of long-term records of the colony and data collected prior to, during, and after the study. For inclusion in this study, an adolescent male was required to be predominantly socially integrated ($>70\%$ of time spent within the group; Table II).

The social variables studied here have been applied to this colony of mandrills for 10 years [Wickings & Dixson, 1992a]. For the purposes of this study, aggressive, submissive, affiliative, playful, appeasing, and sociosexual behaviors between adolescents and all other age classes were scored. Details of the individual activities scored are shown in Table III.

Statistical Analyses

To investigate whether any substructuring occurred within the adolescent mandrill cohort (in terms of how the six social behaviors were initiated and

TABLE III. Details of Interactions Comprising the Six Social Behavior Categories Scored During the Study

Aggression		Submission	Affiliative	Socio-sexual	Play	Appeasement
Noncontact	Contact					
Head-bob Ground slap Lunge Chase	Hit or grab Bite	Flee Squeal Avoidance Displacement Presentation	Grooming Mouth-to-mouth	Mount	Play face Chasing play Rough and tumble	Grimace Head shake

received vis-à-vis all other categories of members of the colony), we performed a hierarchical ascendant clustering analysis (StatBox 6.0). We performed this analysis on quantitative data without posing any constraints on the data set, using dissimilarity coefficients. We generated dendrograms to identify different clusters, using different types of classification. The most parsimonious tree was then chosen for analysis.

We then performed statistical analyses to test for significant behavioral differences between the clusters obtained (Mann-Whitney rank sum tests). All tests were two-tailed.

RESULTS

For all of the cluster analyses, which employed different types of dissimilarity coefficients (Pearson, Kendall, χ^2, and Euclidian distance), the topologies of the dendrogram were similar, with the deepest branching pattern separating the adolescents into two groups. The first cluster consisted of three adolescents that were separated from the remaining eight. For further description of our data, we used the Kendall dissimilarity index (Fig. 1). Hence, for the purposes of this study, we considered the most parsimonious result of two clusters: cluster 1 (C1: individuals 5D1, 12C1, and 12J; average age 96.7 months) and cluster 2 (C2: individuals 10H, 2D3, 12A6, 5D2, B, 10J, T, and 12L; average age 66.9 months). Each adolescent was then removed from the cluster analysis so that potential outliers could be examined. The dendrogram showed similar topologies for each combination.

All social behavioral interactions initiated or received by adolescent male mandrills in each cluster were examined with respect to the different age and sex

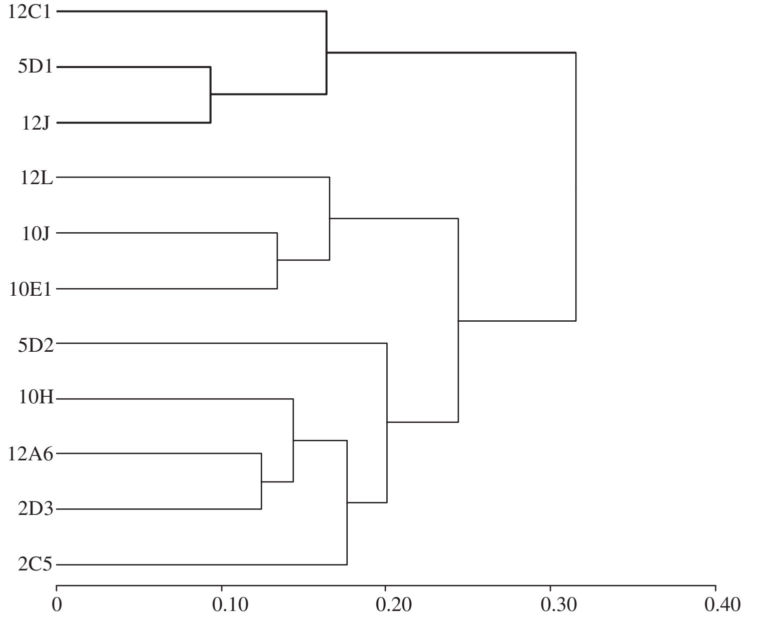

Fig. 1. Tree generated by cluster analysis of 11 adolescent mandrills. The analysis examined different behavior categories for each individual mandrill toward all other members of the colony, and took into account both the age class and sex of the protagonist (StatBox 6.0).

classes of the protagonists. The three mandrills of C1 initiated more interactions with adult males and significantly fewer toward other adolescents compared to the mandrills in C2 (Fig. 2). Interactions initiated by individuals of C1 tended ($U = 3$, $n_1 = 3$; $n_2 = 8$; $P = 0.06$) to be more frequently directed toward adult females compared to individuals of C2, but no differences were observed between the two clusters in the frequency of interactions initiated toward juveniles/infants. As regards received interactions, there was no difference between the two clusters in the frequencies of interactions received from either adolescents or adult males. Individuals of C1 received significantly more interactions from adult females compared to C2 individuals; and C2 individuals tended ($U = 21$, $n_1 = 3$; $n_2 = 8$; $P = 0.06$) to receive more interactions from juveniles than the C1 individuals.

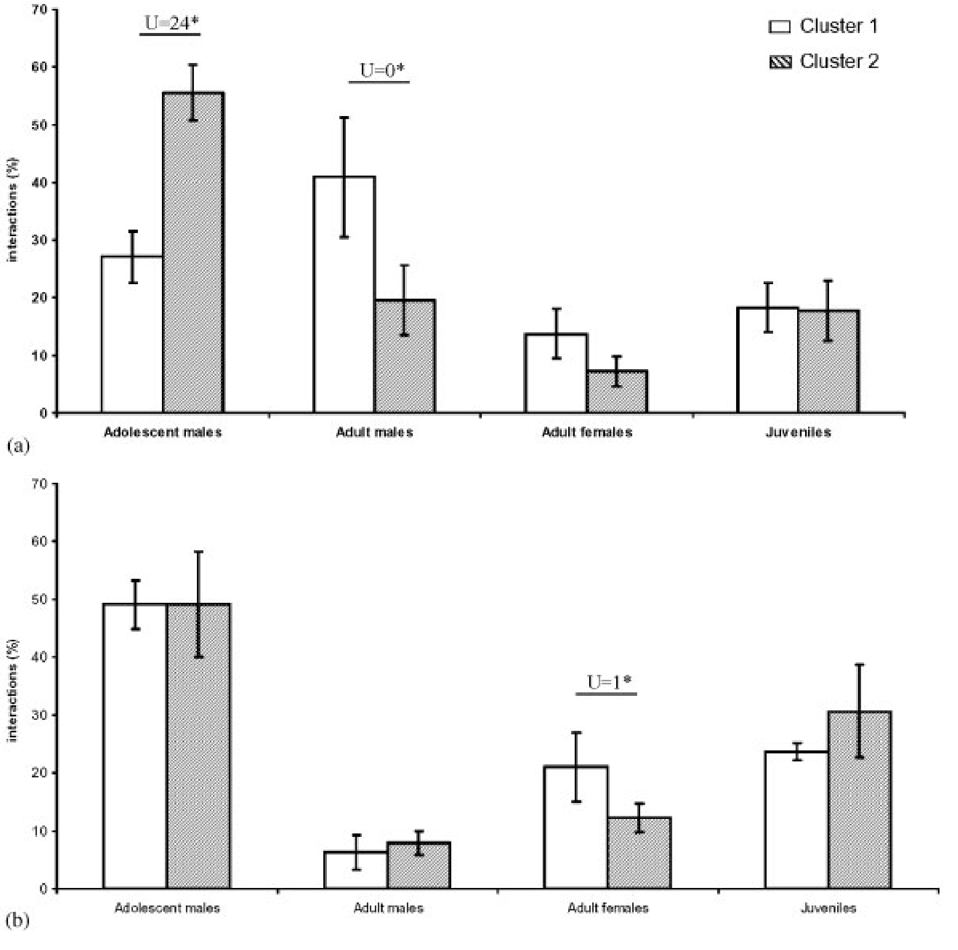

Fig. 2. Percentages of initiated (a) and received (b) interactions of the two clusters differentiated according to the age class and sex class of the protagonist, with no distinction made among the six behavioral categories (Mann-Whitney tests, * $P < 0.05$; C1: $n = 3$, C2: $n = 8$). Number of bouts initiated toward adolescents, adult males, adult females, and juveniles/infants, respectively, by C1 (251, 382, 128, and 229) and C2 (1742, 618, 176, and 585) individuals. Number of bouts received from adolescents, adult males, adult females, and juveniles/infants, respectively, by C1 (669, 85, 268, and 320) and C2 (1321, 222, 335, and 857) individuals.

Taking into account all social partners, C1 individuals initiated significantly more aggression ($U = 0$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$), less submission ($U = 23$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$), less play ($U = 24$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$), and less affiliation ($U = 22$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$) than the C2 adolescents. No differences were seen between the clusters for appeasement or sociosexual behavior (Table IV). C1 individuals received less aggression ($U = 23$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$), more submission ($U = 0$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$), and less play ($U = 24$, $n_1 = 3$; $n_2 = 8$; $P < 0.05$) than the C2 individuals. No significant differences were seen in affiliation, appeasement, or sociosexual behaviors received.

When relations across each age and sex class were examined, mandrills in C1 differed from those in C2 in initiating significantly more aggressive behavior toward all age and sex classes (Fig. 3a). C1 mandrills were less submissive than C2 adolescents. This measure was significantly different between C1 individuals and all adolescents, and between C1 individuals and adult females. C2 males initiated significantly more play behavior with adolescents and juveniles. All other behaviors were seen too infrequently to yield significant results, except for a tendency toward an increased level of affiliation between C2 individuals and juveniles compared to that between C1 mandrills and juveniles ($U = 21$, $n_1 = 3$; $n_2 = 8$; $P = 0.06$). Adolescents in C1 received more submission from adolescents, females, and juveniles compared to those of C2 (Fig. 3b). No submission by adult males was directed toward adolescents of either cluster. For both clusters, almost all behavior received from adult males was in the form of aggression. The mandrills of C2 received significantly more play bouts from adolescents and juveniles than those of C1, and more aggression from adolescent males.

Adult male mandrill behavior is characterized by an elaborate avoidance of direct contact aggression, since it may escalate into violent combat with potentially lethal injuries. However, the adolescents were frequently involved in aggressive bouts (Table IV). We therefore examined whether there was any difference in the levels of contact and noncontact aggression between the individuals of the two clusters and other colony members. Adolescents initiated no contact aggression with adult males, and although C1 mandrills showed more aggression toward other adolescents and juveniles compared to C2 individuals, it was in the form of noncontact aggression ($U = 0$ and 1, respectively, $n_1 = 3$; $n_2 = 8$; $P < 0.05$). In contrast, C2 individuals initiated more contact aggression toward adolescents and juveniles compared to C1 individuals ($U = 24$ and 23, respectively, $n_1 = 3$; $n_2 = 8$; $P < 0.05$). There was no difference in the levels of contact and noncontact

TABLE IV. Numbers of Social Interactions Between Adolescents of C1 and C2 and All Colony Members, Divided Into the Six Behavioral Categories

	Bouts initiated	C1 (n = 3)	C2 (n = 8)	Bouts received	C1 (n = 3)	C2 (n = 8)
Aggression	720	466	254	600	110	490
Contact	113	31	82	89	14	75
Noncontact	607	435	172	511	96	415
Submission	2,069	317	1,752	2,517	1,145	1,372
Play	903	24	879	714	19	695
Affiliative	64	1	63	11	4	7
Appeasement	266	103	163	149	64	85
Socio-sexual	89	25	64	86	0	86
Total	4,111	936	3,175	4,077	1,342	2,735

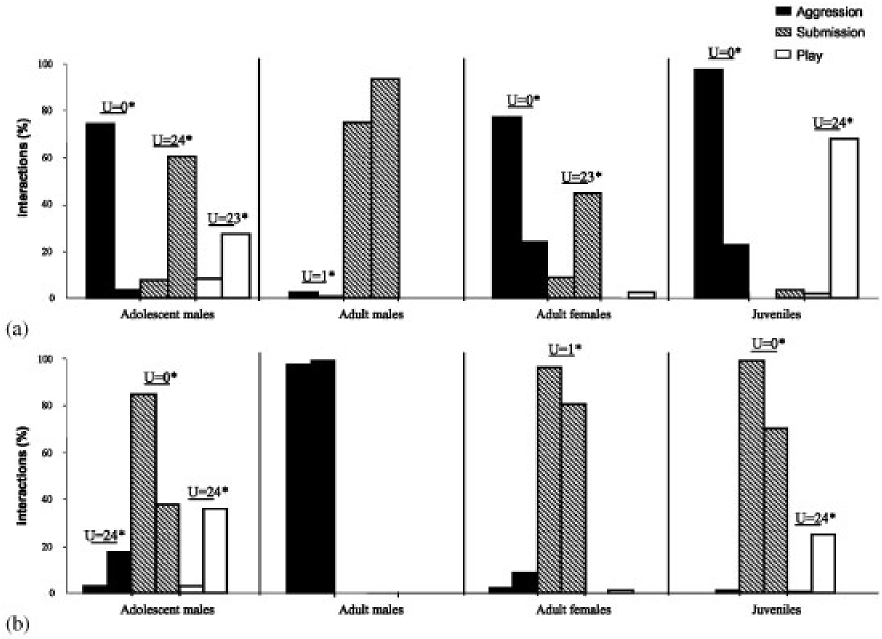

Fig. 3. Behavioral patterns of adolescent male mandrills in each cluster according to the age class and sex of the protagonist. a: Interactions initiated by individuals in C1 (first bar) and C2 (second bar). b: Interactions received by individuals in C1 (first bar) and C2 (second bar). (Mann-Whitney tests, * $P < 0.05$; C1: $n = 3$, C2: $n = 8$).

aggression received by individuals of the two clusters from other group members, except in the case of adult females: C1 individuals received more contact aggression from females compared to C2 mandrills ($U = 3$, $n_1 = 3$; $n_2 = 8$; $P = 0.05$).

DISCUSSION

Adolescence constitutes an important period of development in primates, occurring between the onset of puberty and adulthood [Walters, 1987]. The longer this period lasts, the more important it is deemed to be for the acquisition of adult physical characteristics, and the socioecological experience necessary for group life in a complex environment [Alberts & Altmann, 1995]. It is during this period that male mandrills undergo a massive growth spurt, increasing from approximately 10 kg at 5 years to an adult weight of 30–35 kg [Setchell & Dixson, 2002; Wickings & Dixson, 1992b]. A rapidly maturing male may be perceived as a threat to other members of the group, and hence we would expect to see a continual adjustment in social interactions between adolescents and other group members as the adolescents grow older.

In this cross-sectional study of 11 adolescent mandrills of various ages, cluster analysis revealed two groups whose behavior could be characterized separately. Younger individuals (4.7–6.9 years old) formed one cohort (C2) corresponding to early/mid-puberty. This cohort of mandrills was a closely-knit group, similar to that described for rhesus monkeys [Ehardt & Bernstein, 1987]. Other members of the adolescent cohort were their preferred partners, and playing was one of their preferred social activities. In the majority of studies on primates in which developmental behavioral patterns were studied, playing was observed from a very early age. It increased in frequency during the juvenile period, and then declined again in adolescence [Fagen, 1993; Pereira & Altmann, 1985; Thompson, 1998; Walters, 1987]. Young C2 adolescents showed little interaction with the adult females of the colony, indicating that they no longer formed part of the closely-knit matrilineal network, as is the case for several primate species (see Watts and Pusey [1993] for review). The affiliative and playful behavior with conspecifics and younger animals that was demonstrated in early adolescence was replaced by predominantly agonistic interactions with all of the mandrills (except adult males) in late adolescence, as has been observed in several primate species [Pereira, 1995; Pereira & Altmann, 1985; Rostal & Eaton, 1983; Setchell, 2003]. Interestingly, all members of the group except adult males reacted submissively toward adolescents–even C2 individuals, which showed little aggression in general and for whom submission was the most frequently initiated behavioral category scored. In contrast, all of the adolescents were almost wholly submissive toward the adult males. The submissive and avoidance gestures that are characteristic of mandrill society [Setchell & Wickings, in press b] alleviate tension in potentially dangerous situations, but they also render the subordinate individual vulnerable and expose it to the risk of injury. In addition, they create stress for the submissive individual [Sapolsky, 1993], and while play may be one way in which younger adolescents relieve this stress, older individuals tend to move toward the periphery of the group [Biben, 1998].

Older, more aggressive adolescents showed reduced levels of contact aggression (e.g., grabbing and biting) compared to younger adolescents. However, contact aggression in the latter group never led to injuries, since these younger males did not possess the serious weaponry that develops in older adolescents. This transition in the type of aggression displayed may mark the acquisition of the social competence necessary for adulthood, which can only be achieved within the social framework of the group before males peripheralize. Adherence to the female-bonded social organization of the group had already broken down, and the contact aggression targeted toward older adolescents by adult females may be an additional factor influencing male peripheralization. This spatial marginalization was observed in the oldest male of C1 (12C1) during the period of the study, and continuing observations of the colony have documented this phenomenon in both of the young males (8–9 years old) of C1 (Wickings, unpublished observations).

In conclusion, a behavioral distinction between adolescent males in early to mid puberty and late adolescence has been documented. Whereas younger adolescents interacted primarily with their own age cohort and younger juveniles in a playful or submissive manner, older adolescents incited submission from all protagonists (except adult males) and submitted only to adult males. The changes in social behavior documented here are consistent with preparation for dispersal (a strategy adopted to avoid feeding competition), and the potential for social conflict as the males mature and acquire adult status and appearance.

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