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The Establishment and Reproduction of a Group of Semifree-Ranging Mandrills

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Mandrills, *Mandrillus sphinx,* colorful terrestrial primates from the tropical forests of West Central Africa, are poorly known in the wild. The formation at the International Medical Research Center of Franceville, Gabon, of a semifree-ranging, cohesive, reproducing group of mandrills in a highly naturalistic setting provided a unique resource for the study of this threatened species. The acquisition and release of 15 mandrills into a 1.4 ha and then a 5.3 ha enclosure of natural gallery forest is described. Thirty-three births in the group resulted in 23 surviving offspring over a period of six years. Apparent early reproduction in females was indicated by small size at conception, presence of several deciduous teeth at the time of first parturition, continued weight gain through subsequent births, and decreasing inter-birth intervals. © 1992 Wiley-Liss, Inc.

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INTRODUCTION

Mandrills, *Mandrillus sphinx,* are the most sexually dimorphic [Popp, 1983; Feistner, 1989] and certainly the most colorful of all baboons. They inhabit equatorial tropical forest in western Cameroon, south of the Sanaga River, throughout Equatorial Guinea, in Gabon, west of the Ivindo and Ogooué Rivers, and in the southern Congo [Sabater Pi, 1972; Grubb, 1973; Harrison, 1988; Blom et al., in press]. Together with drills, *M. leucophaeus,* they are also the least known in nature of any of the baboons. Reports from early zoological expeditions [Malbrant and MacLatchy, 1949] and from 1970s field studies [Sabater Pi, 1972; Jouventin, 1975] provided some elementary information on mandrill distribution and ecology. More recent field studies in Cameroon [Hoshino et al., 1984; Hoshino, 1985] and in Gabon [Lahm, 1986; Harrison, 1988] have added to this knowledge. However, to date, habituation

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and sustained observation of wild mandrills has not been accomplished, and hence much about life in nature of these elusive, largely terrestrial forest-dwellers remains obscure.

Gabon may contain the largest portion of the world's remaining mandrill population [Wolfheim, 1983]. The establishment in their native country of a semifree-ranging, cohesive, reproducing group of mandrills in a highly naturalistic setting represented a unique resource for the study of this threatened species. This report describes the founding and growth of a mandrill group at the International Medical Research Center of Franceville (CIRMF).

METHODS

Acquisition and Quarantine

Between mid-1979 and mid-1981, the Primatology Center at CIRMF acquired by donation a total of 12 mandrills (6 males and 6 females), mostly infants or juveniles, originally orphaned by hunters as infants or, in several instances, trapped in snares as juveniles. With the exception of one young adult female about 5 years old, they ranged from approximately 6 to 24 months of age upon receipt at CIRMF and were most commonly about 1 year old. Age estimations were based primarily on dentition, [Lawrence et al., 1982; Swindler, 1985], but also on body weight and dimensions [Cooper and Feistner, unpublished observations] and, in a few cases, previous history in captivity.

All mandrills were quarantined and each passed three negative intradermal tuberculin tests and a similar number of fecal cultures negative for enteric bacterial pathogens. All infestations with potentially pathogenic protozoa and helminths of the gastrointestinal tract were treated until fecal exams were repeatedly negative. Following quarantine, each mandrill was placed in one of two 7.50 × 6.50 × 2.50 m outdoor cages in which they were segregated according to size—the oldest and largest mandrills in one, the smallest and youngest individuals in the other.

Enclosures

A narrow gallery forest lines much of the bank of the M'passa River, where it forms the northern boundary of the hilly 40 ha CIRMF campus. An extension of this relict forest exists southward along a small stream at CIRMF in terrain too steep near its double origins and along most of its 500 m course, and too swampy near its terminus, to have been cleared in the past for plantations. During the construction of CIRMF in the late 1970s, nearly 7 ha of this relict gallery forest were fenced and divided to provide two enclosures as naturalistic settings for the study of Gabonese primates. The area was surrounded and partitioned by a low cement block wall (0.60 m) which supported a chain link fence 1.86 m tall atop which five pairs of electrified and ground wires were angled inwards. On the perimeter and connected to both enclosures was a small service structure with an enclosed cage 5.95 × 2.90 × 1.80 m for animal introductions or treatment, and adjacent feeding yards measuring 11.85 × 5.50 m, in which animals could also be captured or held.

Immediately inside the perimeter fence, was a 2 m ring of bare or sparsely vegetated earth, thus maintained by occasional cutting. Between this peripheral clearing and the taller trees in the center of the enclosures was a variable band of grass,

fern, shrubs, and saplings. The most dominant tree species was *Musanga cecropiodes* [Norris, 1988].

Release

In August 1982, the six youngest mandrills (Nos. 6, 10, 12, 13, 14, 15) were released into the lower and smaller (1.4 ha) of the two enclosures, followed by the next three oldest animals (Nos. 2, 3, 5) in September, and the three oldest and largest (Nos. 1, 7, 9) in October of the same year. They were provided once daily, at a site near the service structure, with the diet to which they were already accustomed, namely bread and a variety of cultivated fruits and vegetables. Despite this provisioning, the mandrills spent most of their time foraging elsewhere in the enclosure [Norris, 1988]. Six months later extensive damage to the vegetation in the enclosure was evident, particularly in young *Musanga* trees at the enclosure's edge. This was caused by the mandrills feeding heavily on emerging leaves and the apical end of branches. In addition, the extensive undergrowth of vines and Marantaceae had been virtually cleared by mandrills feeding at ground level on leaves, stem pith, and roots. Because of this degradation of the enclosure, in May 1983 the group of 12 mandrills was moved into the larger (5.3 ha) and steeper enclosure, encompassing the middle portion of the stream and its two upper branches. Shortly thereafter a juvenile female (No. 17) was added to the group. Another juvenile female (No. 16) and a juvenile male (No. 18) joined the group in March and December 1984, respectively. All further additions to this population of 15 mandrills occurred only by birth.

The mandrills continued to be provisioned once daily in the large enclosure. In addition, automatic drinking valves were added at the feeding site and a dispenser for providing pelleted primate diet ad libitum [Extralabo Croquettes Singes, Pietrement, Provins, France] was installed. The mandrills continued to visit the feeding area at the elevated perimeter of the enclosure only briefly each day (about 30 min) and to spend the rest of their time in the forest below, foraging largely in the leaf litter and, to a lesser extent, in the dense emergent vegetation, and sleeping in the trees at night [Feistner, 1989].

Captures

The entire group was examined in October 1983, 1985, 1986, 1987, and in April 1988. The mandrills were trapped at the feeding site by closing the access door when all the group had entered. They were anesthetized with a mixture of ketamine hydrochloride at 100 mg/ml and acepromazine at 5 mg/ml on the bases of 8–10 mg ketamine per kilogram body weight. Adult females and ventral infants were given intramuscular injections using a hand-held syringe. Juveniles were caught in a net and then injected, and subadult and adult males were darted using a blow-pipe. The anesthetized mandrills were taken to the Primatology Center for health examinations.

The health examinations included the following assessments and measurements: weights (in kilograms to the nearest 10 g), dental record including measurements of all permanent canine teeth (length was measured from the tip of the tooth to the gingiva in millimeters using calipers), testicular measurements of all males (length and width of the left testis in millimeters using calipers), and digital rectal palpation for pregnancy of adolescent and adult females. The mandrills were then returned to the enclosure and placed in the shade to recover from the anesthesia. Large males were left at widely separated locations, infants were left with their mothers, and all

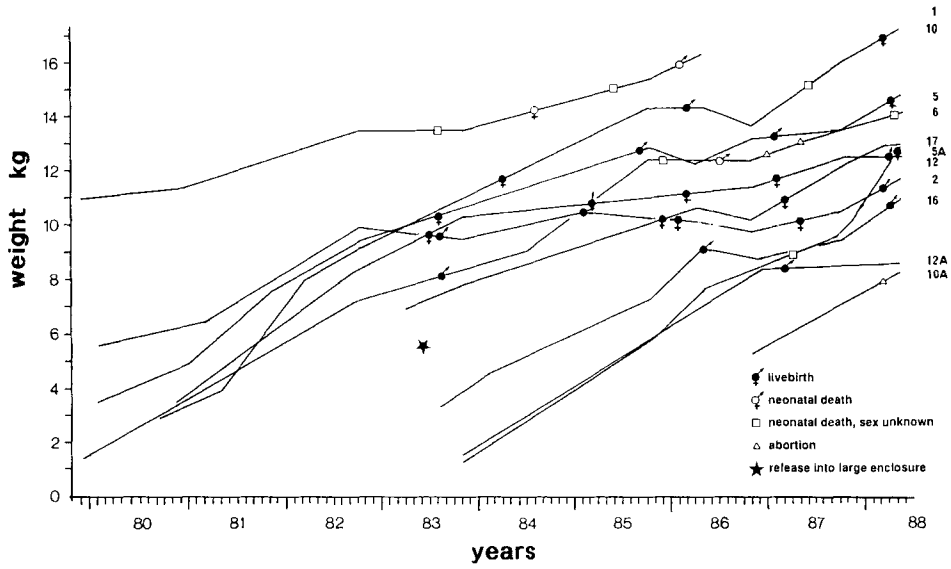

Fig. 1. Body weight and parturitional history in female mandrills.

individuals were monitored to recovery. In addition, females with infants were captured within a few months of giving birth, to mark the infant.

RESULTS

From June 1983 to March 1988, 33 infants were born. Nine (born to females Nos. 1, 5A, 6, 10) were stillborn or died within a few days of birth. Another died of unknown causes at 14 months of age. The dates of all births and concurrent maternal dental eruption status are presented in Table 1.

The body weight profiles and parturitional history for each of the eight introduced females and their reproducing daughters from their arrival at CIRMF up to April 1988 are shown in Figure 1. Weights are shown chronologically, since ages of individuals in this population were not precisely known.

The first five infants were born over a six-week period in June and July 1983, shortly after the transfer of the mandrills from the 1.4 ha into the 5.3 ha enclosure (indicated in the figure by a star). However, this particular restricted period of births probably reflects the achievement of reproductive competence in the oldest male some six months earlier.

The body weight profiles and testicular volumes for each of the seven introduced males from their arrival at CIRMF through April 1988 are presented in Figure 2.

At the approximate time of the first conceptions (shown by the arrow in Fig. 2), only male No. 7 was likely to have sired these infants. At the time he had the largest testicular volume of any of the males, was behaviorally dominant, and was the only male observed to copulate [J. Norris, personal communication]. He was estimated to be 5 years old at most, weighed 14 kg, had deciduous upper canines and lower first

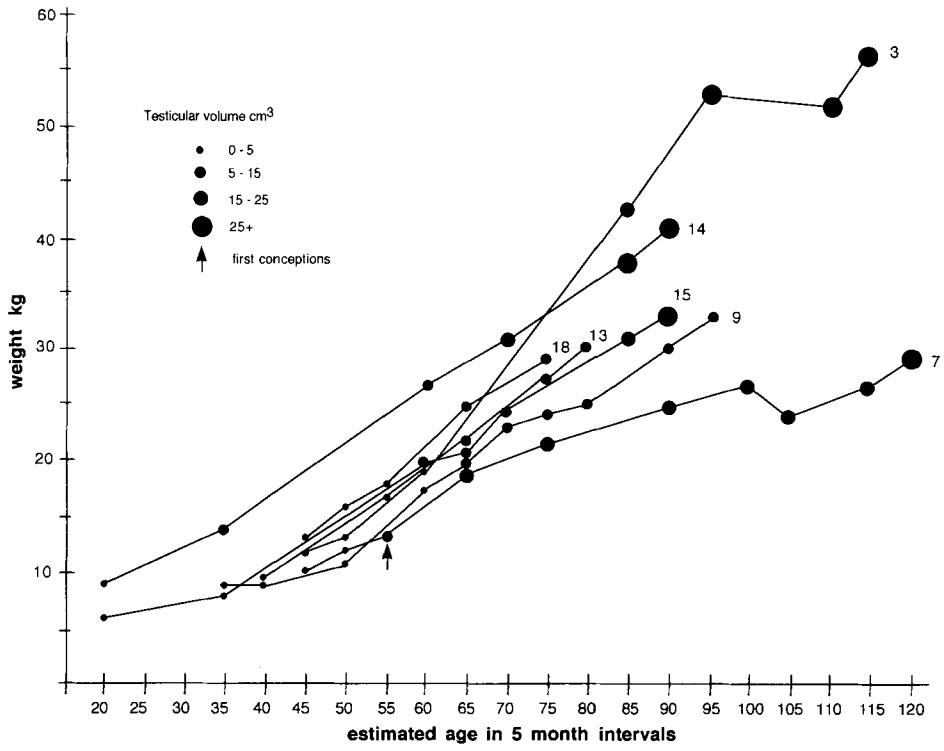

Fig. 2. Body weight and testicular volume increase in male mandrills.

premolars but no third molars (i.e., he was 8 teeth short of complete adult dentition). His testicular volume determined 2 months prior to these conceptions (6.0 cm^3) was only 30% of the adult volume, achieved sometime between 20 months (15.2 cm^3) and 36 months (20.9 cm^3) later.

Apparent early reproduction was also seen in female mandrills. Excluding a female received as an adult (No.1) and another (No. 2) who was also reproductively mature well before male No. 7, the mean estimated age at first known conception was approximately 47 months (range 41–54). At the birth of their first infant, these six females still possessed an average of four deciduous teeth (range 0 to 9) and lacked an average of 8.5 adult teeth (range 4–15).

A uniform decrease in the length of inter-birth interval subsequent to surviving infants was observed in all four qualifying females (Nos. 2, 5, 10, 12). When inter-birth intervals (in months) were plotted against the number of maternal unerupted permanent teeth (at the first of each qualifying pair of successive births) longer interbirth intervals were associated with less mature maternal dentition (r_s = 0.668, $P < 0.05$). This is illustrated in Figure 3.

The F1 generation of females born at CIRMF in 1983 and 1984 (Nos. 5A, 10A, 12A) began breeding at a young age. They began to have large sexual swellings and engage in copulation at a mean age of 38 months (range 37–42). These young females conceived by their second cycles and at 40 months of age (range 38–43), when their only fully erupted adult teeth were incisors and first molars.

TABLE 1. Reproduction in the mandrill group at CIRMF

Maternal				Offspring			
Identity	Estimated age at 4/88 (months)	Estimated age at first conception (months)	No. adult teeth at parturition	Identity	Date of birth	Sex	Inter-birth interval (months)
1[a]	161	98	32	101[b]	07/83	?	
			32	1[c]	12/83	?	5
			32	102[b]	07/83	F	7
			32	103[b]	05/85	?	10
			32	104[b]	01/86	M	8
2	130	67	28	2A	07/83	M	
			32	2B	01/85	M	18
			32	2C	01/86	F	12
			32	2D	04/87	F	15
			32	2E	02/88	M	10
5	117	54	28	5A	07/83	F	
			32	5B	09/85	M	25
			32	5C	01/87	M	16
			32	5D	03/88	F	14
5A	57	38	16	5A01[b]	03/87	?	
			25	5A1	03/88	F	12
6	106	43	22	6A	07/83	M	
			28	601[b]	11/85	?	28
			30	602[b]	06/86	M	7
				6[c]	12/86		6
				6[c]	04/87		4
				603[b]	02/88	?	10
10	104	49	28	10A	03/84	F	
			32	10B	02/86	M	23
			32	1001[b]	05/87	?	15
			32	10C	02/88	F	9
10A	49	43	22	10A[c]	02/88	?	
12	105	41	21	12A	06/83	F	
			28	12B[d]	02/85	M	20
			30	12C	02/86	F	12
			32	12D	01/87	F	11
			32	12E	03/88	M	12
12A	58	38	13	12A1	02/87	M	
16	71	41	16	16A	04/86	M	
			28	16B	03/88	M	23
17	86	51	28	17A	11/85	F	
			30	17B	02/87	F	15

[a]Removed from the group in 03/86.
[b]Stillborn or died within a few days of birth.
[c]Abortion.
[d]Died at age 14 months.

DISCUSSION

The establishment of this particular group of mandrills in Gabon from unrelated, predominantly immature individuals was clearly very successful. A cohesive group formed, which remained healthy and reproduced well, to easily become the largest colony of this threatened species in the world.

In the absence of data from the field, it is impossible to determine whether the rate of reproduction observed in this group is natural for mandrills. However, it is clear from the data that both male and female mandrills are capable of producing offspring before they have acquired full adult characteristics (weight and dental complement). A similar observation, that reproductive capability is reached much earlier than physical adulthood, has been noted in captive *Papio anubis* baboons [Coehlo, 1985].

While data on mandrills in nature are essential to confirm this apparent early age of first reproduction, data on other baboons strongly suggest that captivity can advance the rate at which baboons mature and reproduce. Altmann et al. [1981] have reported a 3:5 ratio for the ages at which captive versus wild *P. cynocephalus* baboons reached clearly distinguishable developmental markers including menarche and the period of rapid testicular enlargement.

Captive primates are presumed to benefit from a higher quality diet, frequently provided in excess of quantities consumed, together with a reduction or lack of gastrointestinal parasites. Acceleration in reproductive rates has been commonly attributed to the increase in body weight which results from a diet high in calories [e.g., Mori, 1979; Sugiyama and Ohsawa, 1982; Lee, 1987]. The ecology and behavior of primates with enhanced food intake have been described in a recent volume [Fa and Southwick, 1988]. In particular, the effects of supplementary feeding on maturation and fertility have been reviewed by Loy [1988]. While he considers that a broad trend exists for increased reproductive output with enhanced caloric intake, few firm conclusions can be drawn because of the lack of comparative data. However, more recently Strum [1991] has demonstrated for *P. anubis* baboons that improved food conditions can modify growth and development in naturally foraging as well as food-enhanced groups.

Considering all the available evidence, it seems reasonable to suggest that the young age at which the CIRMF mandrills reproduced was related to their capture as infants or young juveniles and their subsequent high caloric quality diet, provided in excess of amounts consumed, together with their lack of gastrointestinal parasites. However, there is also the possibility that the effect of nutrition on reproductive parameters in mandrills may be operating over an existing tendency to begin reproduction earlier in comparison to savanna baboons.

A cross-species comparison of age of onset of reproductive behavior reveals that CIRMF-born female mandrills (in 1983 and 1984, $n = 3$) began to show large sexual swellings and engage in copulations at a mean of 38 months of age, whereas *P. anubis* baboons at Gilgil, Kenya [Scott, 1984] did not show similar behavior until 53 months (range 48–57), and those at Gombe, Tanzania until 59 months (range 54–67) [Packer, 1979]. The relatively long period between onset of cycling and conception lasting 1–2 years in feral *P. cynocephalus* baboons [Altmann et al., 1977] and 8–11 months in feral *P. anubis* [Scott, 1984], and a delay in mating reported for captive *P. anubis* [Coehlo, 1985], was not observed in the CIRMF mandrills.

Popp [1983], arguing for ecological determinism of life history strategies in baboons, concluded that mandrills could be expected to have a more intense, earlier, and shortened reproductive life. Broadly speaking baboons are generalist herbivores and their food supply, in terms of plant species diversity and primary productivity, is positively correlated with mean annual rainfall. Any increase in utilizeable energy gained through feeding can be put into reproductive effort, and so populations of

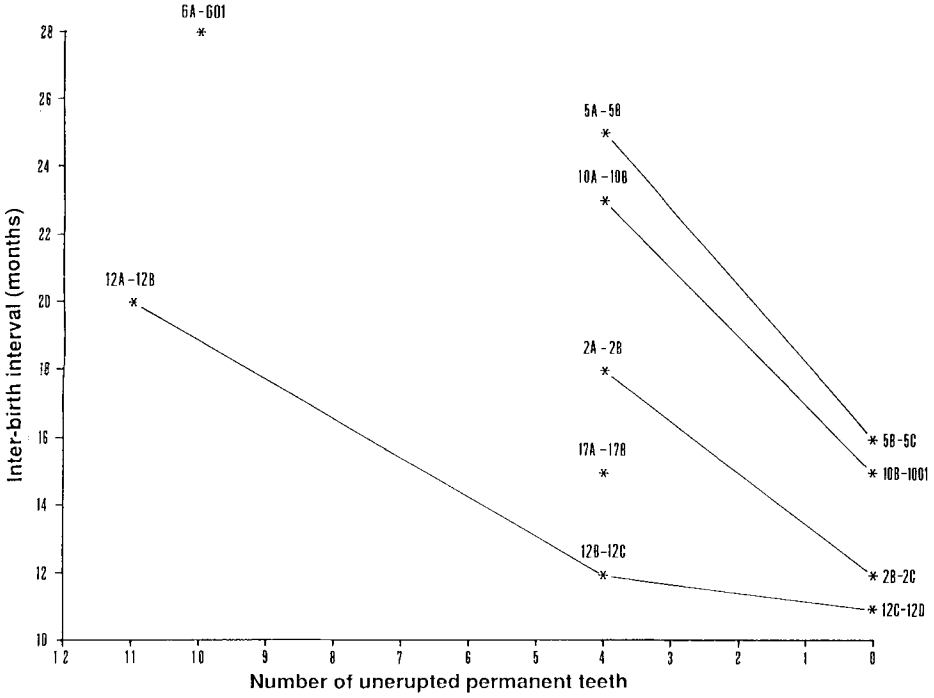

Fig. 3. Inter-birth interval relative to maternal dental status in mandrills. Numbers represent identities of dams, and letters the birth of successive infants.

relatively well-fed baboons in energy-rich environments might be expected to contain individuals who have high rates of reproduction. Mandrills inhabit areas of higher rainfall than other baboons, and the data presented here provide evidence for early reproduction, at least in captive females.

This group of mandrills showed evidence of reproductive seasonality; mating was observed in the months of July to October and births occurred approximately six months later [Feistner, 1990]. Inter-birth intervals in this group have been shown to be shorter than those of *P. anubis* and *P. cynocephalus* [Feistner, 1990]. Overall, the mean inter-birth interval was 17.3 months [Feistner, in press] but as the data presented here demonstrate, longer inter-birth intervals occurred between the first and second offspring than between subsequent offspring, and were clearly associated with less mature maternal dentition. Feral *P. anubis* have been shown to have an inter-birth interval which is age dependent; inter-birth intervals decreased sharply until mid-life and showed an increase with old age [Strum and Western, 1982].

The apparent early acquisition of reproductive capacity and high fecundity of mandrills at CIRMF augers well for the preservation in captivity of this threatened species, especially as the age at first birth has been shown to have the greatest influence on lifetime reproductive potential [Martin and Harvey, 1987]. However, this potential to reproduce at an apparently early age also suggests some obvious concerns for their captive management. Mandrills in the wild have the highest ratio of males to group members of any of the baboons [Feistner, 1989], suggesting a high

rate of male emigration from their natal groups. This is supported by field observations of mandrills of which an average of 15% (range 5–75%) of sightings were of solitary males: 75% of 4 sightings [Harrison, 1988]; 5% of 187 [Hoshino et al., 1984]; 26% of 39 [Jouventin, 1975]; 21% of 14 [Lahm, 1985]; 31% of 16 [Sabater Pi, 1972]; 45% of 31 [C. Tutin, personal communication]. The probable competition from these solitary males suggests that breeding males may not maintain this status long enough to have reproductive access to their own daughters. This was not the case in the CIRMF colony, where the dominant male (No. 7) performed 73% of the copulations of one of his daughters (No. 5A) and prevented other males from mating with her during her periods of estimated maximum fertility [Feistner, 1989]. In nature opportunities exist for the dominant male to be challenged by solitary males, and fights between males have been reported [Jouventin, 1975]. Also in the CIRMF group the dominant male was challenged (a fight was observed) by a previously group-living adult male (No. 3) who had become largely solitary by mid-1986 [Feistner, 1989]. Unfortunately, some time after this study ended, the solitary male was removed from the enclosure and the opportunity to determine whether he would eventually supplant the breeding male was lost.

The apparent early reproduction of mandrills in captivity has the potential to promote greater father-daughter inbreeding than would be expected in nature. To avoid the resultant high mortality rate of inbred young that has been documented for mandrills at the Bronx Zoo (78.3% in inbred infants vs. 0% in non-inbred infants [Ralls and Ballou, 1982]), we suggest that adult females and their daughters be maintained as a breeding nucleus and the breeding male be replaced approximately every three years, or before his daughters reach their first estrus. As there are at least 125 male mandrills currently in zoological institutions, cooperation between zoos should enable an outbred population to be successfully maintained in captivity. The existence of international and regional studbooks should aid in this effort.

The establishment of the CIRMF group of mandrills in Gabon was an effective means of integrating individuals which had been orphaned or caught in snares, and these results suggest that mandrills placed in similar conditions could flourish rapidly. This is particularly encouraging for the proposed project to set up an in-situ breeding centre in Nigeria for the highly endangered close relative of the mandrill, the drill (*Mandrillus leucophaeus*), using confiscated animals of a similar age and sex composition to the founders of the CIRMF mandrill groups [Gadsby et al., in press].

CONCLUSIONS

1. A healthy, cohesive, reproducing group of mandrills was established from unrelated, predominantly immature individuals.
2. Both sexes reproduced before attaining adult weight and dental complement.
3. Captive groups of mandrills must be managed, so as to prevent father-daughter inbreeding.

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