

**Females Move in Tight Crowds, Males Roam: Socioecology and
Movement Ecology of Mandrills**

Shun Hongo

The Center for African Area Studies, Kyoto University
46, Yoshida Shimoadachi-cho, Sakyo-ku, Kyoto, 606 8501, Japan
hongo.shun.8s@kyoto-u.ac.jp
Orcid: 0000-0001-8167-1348

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Abstract

Mandrills (*Mandrillus sphinx*) have a unique social system for primates, with huge groups of hundreds of individuals and males moving in and out of the group seasonally. Despite intensive field studies conducted at several sites in the Congo Basin rainforests, the mechanisms and adaptation of their social organization are still poorly understood. How do groups maintain their huge size while moving around in the forest with poor visibility? How do solitary males find groups in the vast forests? And what are the adaptive advantages of these behaviors? In this review, I summarize what we know surrounding these questions and compare mandrill ecology with that of Neotropical social mammals, offering potential explanations for these questions. Group crowdedness and frequent exchange of long-distance calls could be keys to the collective movement of large groups that engage in regular sub-grouping. The adaptive benefits of the large group size possibly lie in female tactics relating to infanticide avoidance and polyandrous mating. While very little is known about how solitary males find groups at the onset of the mating season, the adaptive function of their seasonal influxes can be relatively well explained as foraging and mating tactics. Since the major questions of mandrill social organization are strongly related to their movement ecology, intensive movement research using GPS telemetries and remote sensing is crucially needed to disentangle the social system of this intriguing monkey. Further, broader comparisons among the social movement of rainforest mammals will be essential to comprehensively understand their movement ecology.

Keywords

group crowdedness; group size; long-distance call; male influx; *Mandrillus sphinx*; social organization

1. Introduction

1.1. Mandrill: a fascinating primate

The mandrill (*Mandrillus sphinx*) is a diurnal, semi-terrestrial primate living exclusively in the rainforests near the coast of the Gulf of Guinea (Fig. 1). Distribution range of this cercopithecine monkey is dominated by lowland forests with canopy heights of about 30–40 m, covered by evergreen and semi-deciduous trees and dense undergrowth. Some areas, including the Lopé and Moukalaba-Doudou National Parks in Gabon, also have small-scale savannas surrounded by riverside forests, forming landscapes called the forest–savanna mosaic. Annual precipitation of the mandrill range falls between 1,200 and 2,200 mm, with one clear dry season lasting 3 to 4 months and one rainy season of 8 to 9 months. In some areas, there is another “small” dry season in the middle of the rainy season.

As Darwin (1871) noted, mandrills exhibit prominent sexual dimorphism (Fig. 2): Adult males weigh about 30 kg—more than three times as heavy as adult females (Setchell et al. 2001); males also have long canine teeth (Leigh et al. 2008) and display bright red-and-blue coloration on their faces, genitalia and buttocks (Setchell and Dixon 2001). These striking characteristics have been naturally regarded as a model of sexual selection. Consequently, their sexual behavior and physiology are now well understood, mainly as products of intensive research conducted on the semi-free ranging groups at the Centre International de Recherches Médical de Franceville (CIRMF), Gabon (Dixon 2015, Setchell 2016).

This interesting creature has also attracted researchers struggling with the deep forest. Since the 1970s, field ecologists have studied mandrills in rainforests of Cameroon, Equatorial Guinea and Gabon (Sabater Pi 1972, Jouventin 1975, Hoshino et al. 1984, Harrison 1988). Despite poor visibility and limited mobility in rainforests, they have persistently followed the movement of mandrill groups, gradually unraveling their ecology and society.

The pioneer field studies revealed, for example, that mandrills are highly omnivorous in their diet. They prefer the pulp of ripe fruits when available, but other

foods—seeds, monocotyledonous herbs, barks, roots and invertebrates (mainly ants and termites)—are also regularly consumed (Hoshino 1985, Lahm 1986). They also eat vertebrates occasionally: Hoshino (1985) and Lahm (1986) sometimes found vertebrate matter in mandrill feces; Kudo and Mitani (1985) observed an adult male killing a juvenile bay duiker (*Cephalophus dorsalis*) and eating its meat. More recent studies have clarified the flexibility of mandrill groups to respond to seasonal fruit production. During the long dry season (generally for 3–4 months), when fruit production becomes very low, group members spend more time foraging (Nsi Akoue et al. 2017) and increase dietary diversity by relying more on less preferred foods, particularly seeds and wooden tissues buried in the leaf litter (Hongo et al. 2018). However, this fruit-based omnivorous diet and its seasonal variation are observed in many African primates (Hemingway and Bynum 2005). The feeding ecology is thus not a point that fully illustrates the uniqueness of wild mandrills—the big mysteries lie in their social organization and movement ecology.

1.2. Mysteries of large groups and seasonal male influxes

First of all, their extremely large group size is a curiosity in itself. In the Lopé National Park, central Gabon, Abernethy et al. (2002) counted wild mandrill groups crossing the savannah between gallery forests 20 times by video recording. The observed group sizes ranged from 338 to 845, with a mean of 620 individuals, representing the largest size of stable groups observed in wild primates. Hongo (2014) subsequently conducted a field study in the Moukalaba-Doudou National Park, southern Gabon, and filmed a group of 350 mandrills and two subgroups of 169 and 442 individuals, suggesting that group size of hundreds is a general social feature of this species.

The evolution of such large groups in a rainforest-dwelling primate is surprising—it seems to challenge existing theories for the classic socio-ecological model, which argues that the primate group size is determined by food distribution and predation pressure (van Schaik and van Hooff 1983). Mandrills are considered to have historically been confined to Central African rainforests (Dixon 2015), where dense vegetation would complicate the coordination of ground movement by large groups.

107 Additionally, their dietary preference for fruits is generally less compatible with very
108 large groups than folivorous diets: Many rainforest fruits are patchily distributed, which
109 would lead to intense competition for foods between group members directly (called
110 *interference* or *contest* competition) and indirectly (*exploitation* or *scramble*
111 competition) (van Schaik and van Noordwijk 1988, Chapman and Chapman 2000).
112 Further, predation risk in rainforests is usually considered lower than in open habitats,
113 so the benefit of large groups in avoiding predators seems limited. All the environmental
114 conditions predict mandrills living in small groups. However, they form larger groups
115 than savanna-dwelling baboons—why?

116 Second, male sociality deviates from the standard of group-living primates, in
117 which males stay with females all year round and typical adult sex ratios in a group are
118 2 to 10 females per male (Clutton-Brock et al. 1977). Mandrill groups include multiple
119 males and females, but the adult sex ratio was largely female-biased: the Lopé groups
120 had less than 17 adult males (i.e., >10-year-old males), and the mean adult sex ratio was
121 24.6 (Abernethy et al. 2002); the Moukalaba group of 125 adult females included just
122 five adult males (adult sex ratio = 25) (Hongo 2014). Moreover, this female-biased
123 composition is more pronounced in fruit-rich, rainy seasons, when many females give
124 birth and most males presumably live in solitary (Brockmeyer et al. 2015, Hongo et al.
125 2016). During dry seasons, on the other hand, many solitary males join groups after the
126 number of sexually active females increases, competing with each other for mating
127 (Hongo et al. 2016).

128 This temporary immigration of many males into the group is termed *male*
129 *influx*. In mandrills, the male influx is thought to occur during every dry season (Hongo
130 et al. 2016). Therefore, most males would move around in the forest yearly in search of
131 groups. Due to their large group home ranges of about 50 km² (White et al. 2010) and
132 the low group density (White 1994), however, this annual search for groups at the right
133 time of year for mating seems quite challenging for solitary males. How do they
134 navigate themselves to rejoin a group, and why do they leave it?

1.3. Purpose of this chapter

As we have seen in the previous section, critical questions about mandrill social and movement behaviors are summarized as follows:

- How do female groups move around in the forest with poor visibility while maintaining their huge size?;
- How do solitary males find groups in the vast forests?; and
- What are the adaptive advantages of these behaviors?

Unfortunately, all the questions are not entirely resolved yet, and this review may not provide clear answers. So instead, I summarize and analyze the evidence provided by a variety of mandrill studies, while comparing and contrasting them with Neotropical social forest mammals (Reyna-Hurtado and Chapman 2019) to find potential explanations and identify further questions. This is because, like mandrills, they form social groups in tropical rainforests and have interesting similarities with mandrills in their socioecology and movement ecology.

2. Movement coordination and adaptive significance of large groups

2.1. How do group members coordinate their movement?

Mandrills predominantly move on the rainforest floor, where visibility is only about 20–30 m. Large mandrill groups forage without prolonged interruption for 10 to 11 hours from dawn to dusk, ranging for long distances up to 10 km per day (White 2007, Hongo et al. 2022). Nutritional, energetic and social demands are most likely different for each individual, depending on its age, reproductive status and individual history—if so, how can members of mandrill large groups travel together without scattering?

Group crowdedness

Observing small wild groups of 15–95 mandrills in the Campo Faunal Reserve (now

part of the Campo-Ma'an National Park), southern Cameroon, Hoshino et al. (1984) reported that group members keep very close inter-individual distances during group movement. Hongo (2016) hypothesized that this proximity among group members—he termed it the high *crowdedness* of the group—contributes to the coordination of group movement. Highly crowded groups are observed not only when animals are on alert but also when undisturbed. At Moukalaba-Doudou, for example, an unalarmed subgroup of 169 individuals passed on a fallen tree crossing a river in only 4 m 20 s (Hongo 2014). Camera traps also recorded often crowded groups in the forest (Fig. 3).

Similarly to mandrills, crowded social groups are also observed in Neotropical ungulates. Collared peccaries (*Pecari tajacu*) and white-lipped peccaries (*Tayassu pecari*) are rainforest-dwelling social animals, although group size and home range are, in general, much larger in the latter (Keuroghlian et al. 2004). Groups of both species move with close inter-individual distance in dense forests (Byers and Bekoff 1981, Fragoso 1998, Reyna-Hurtado et al. 2009, Biondo et al. 2014).

These observations suggest that mandrills and peccaries coordinate their speed and direction of movement with neighboring individuals to maintain crowded groups, as seen in locust and fish swarms (Hemelrijk and Hildenbrandt 2008, Ariel and Ayali 2015). Byers and Bekoff (1981) hypothesized that collared peccaries rely on olfaction to determine their spatial position relative to other group members. And white-lipped peccaries are considered to use *togetherness* vocalizations to keep close inter-individual distances (Mayer and Wetzel 1987). On the other hand, I speculate that mandrills, a primate species supposed to have good eyesight, may visually measure the distance from neighboring animals in the group. Regardless of the type of sensory cue, crowded groups may be adaptive for mammals living in large groups to move collectively across the dense rainforest floor. Since behavioral mechanisms and adaptative benefits of group crowdedness have been understudied in terrestrial mammals, future work should focus on their communication for maintaining inter-individual distances and the relationship between group size and crowdedness.

Subgrouping and long-distance calls

Although mandrill groups keep crowded during the movement, they also frequently engage in fission and fusion. All the groups studied in the wild have been observed to split into two or more subgroups regularly but temporarily during movement, keep apart for several hours to a few days, and eventually reunite together (Hoshino et al. 1984, Abernethy et al. 2002, Shun Hongo unpublished data). Since the social composition and membership stability of the subgroups are still unknown, we can not conclude whether they are stable social units or more flexible, temporary aggregations. If the former is the case, then mandrills are suggested to live in a unique multi-level society: Multi-level societies that are not based on one-male reproduction units are not observed in the other primates (Grueter et al. 2020). If the latter is true, then the fission-fusion dynamics of mandrills will be highly variable in subgroup composition and size, as known in many social mammals (Aureli et al. 2008), including white-lipped peccaries (Keuroghlian et al. 2004). In any case, the subgrouping would be beneficial to efficient foraging between fruiting trees.

Auditory communication seems to play an essential role in the fission-fusion of mandrill subgroups. Kudo (1987) followed the movement of the Campo groups while recording their vocal exchanges and identified 11 vocal types. Among them, two long-distance calls—*two-phase grunt* and *crowing*—were emitted during the group movement and were much more frequently vocalized than the other types. Kudo (1987) also discussed the differences in their functions. The two-phase grunts are continuously emitted only by adult males, probably helping coordinate the group movement, whereas the crowing is vocalized by all group members except adult males. Since group members emit crowing mainly before and after feeding behavior, this call may have the function of coordinating the formation of subgroups and reintegrating subgroups into a large group. Interestingly, the other savanna-dwelling African papionins (baboons and geladas) do not have vocalizations phonetically equivalent to crowing, implying that this long-distance call reaching >500 m has evolved with frequent and dynamic fission-fusion behavior in dense rainforests. Future research should test Kudo's above hypotheses on the functions of long-distance calls.

2.2. Why do mandrills move in extremely large groups?

Potential disadvantages of large groups

Mandrills appear to be paying a great cost to maintain their large groups. For example, a huge group of *ca.* 700 individuals at Lopé forage in a large home range of 118 km², with 46 km² of forested area (White et al. 2010). The large size of its home range could be a result of a patchy habitat with forest–savanna mosaic, where mandrills need to cross many gallery forests and bosquets to forage. However, the group home range fitted the predicted relationship between primate group mass and home range size demonstrated by Clutton-Brock and Harvey (1977), suggesting that mandrills pay an energetic cost of increasing group size at a similar rate as other primates. Also, mandrill groups need to move extended distances to meet food requirements. At Moukalaba-Doudou, groups move 6–7 km on average during the day (Hongo et al. 2022). Even a small group of *ca.* 120 animals at Lékédi Park, southeastern Gabon, ranges a mean of 2.4 km per day within a home range of 8.7 km² (Brockmeyer et al. 2015). The ecological constraints model in primate groups (Chapman and Chapman 2000) predicts that increased group size will lead to an increased home range and an extended day range, particularly in fruit-eating species, which apparently seems to be the case for large mandrill groups.

In addition, large, crowded groups of mandrills may generate particularly fertile ground for parasite transmission, possibly imposing additional travel costs through the need for parasite infection avoidance. Brockmeyer et al. (2015) found that the Lékédi group moved longer distances when group members showed high richness in short-life cycle parasites (e.g., protozoans) and suggested a strategy to escape contaminated habitats on a local scale. Protozoan richness in female mandrills at Lékédi varies seasonally, with more protozoa in the early gestation period (i.e., ~2 months after fertilization) (Poirotte et al. 2016). Interestingly, this parasite-rich period at Lékédi corresponds to the dry season, when groups at Moukalaba-Doudou forage through much broader areas (Hongo et al. 2018). The Lékédi group also avoided returning to areas with high contamination levels of gastrointestinal parasites, particularly during the dry season (Poirotte et al. 2017a). Since mandrills seem to distinguish parasitized group members via fecal odors and avoid grooming conspecifics infected with orofecally

transmitted parasites (Poirotte et al. 2017b), large mandrill groups may shift locations frequently to avoid foraging in areas with their own feces containing high parasite loads.

Possible adaptive benefits

As seen in the above section, large mandrill groups have to travel long distances and use large home ranges to find enough food, and their high crowdedness may increase the risk of parasite infections. Although they display temporary subgrouping and seasonal diet changes to efficiently forage in large groups (Hongo et al. 2018), such behavioral flexibility would have been unnecessary if they lived in smaller groups. So, what adaptive benefits would trump the disadvantages?

Of course, the large group size is well known to be generally beneficial in predation avoidance. Leopards (*Panthera pardus*) and central African pythons (*Python sebae*) are known predators of mandrills (Henschel et al. 2011, Abernethy and White 2013), and crowned eagles are also likely to kill mandrills (Shun Hongo, personal observation). In fact, mandrill groups avoid traveling through open savannas, sleep high in trees, and almost wholly avoid terrestrial activity at night (Brockmeyer et al. 2015, Hongo et al. 2022), all suggesting predator avoidance. However, as I discussed in the Introduction, a counter-strategy against predators alone is insufficient to explain the formation of groups of hundreds in rainforests, where the predation risk should be generally lower than in open habitats. Interestingly, Kiltie and Terborgh (1983) have asked similar questions about large herds of white-lipped peccaries. They argued that an increased predator-detection rate and per-capita predator avoidance were the most likely adaptive benefits of forming large herds. But it is still questionable whether peccaries weighing 30–40 kg have to live in groups of up to 300 animals just to avoid solitary carnivores such as cougars (*Puma concolor*) and jaguars (*Panthera onca*).

Here, I would like to discuss the two social benefits of large groups in female reproduction, although the evidence is still inadequate. First, larger groups might be adaptive in reducing the infanticide risk. Female mandrills are seasonal breeders, where frequent infanticide is generally considered unlikely, but killing unrelated infants may

nevertheless be beneficial for most males performing seasonal influxes to enhance their siring probability. Indeed, cases of highly suspected infanticide have been reported from the CIRMF colony: Three infants were found dead with injuries following the introduction of unrelated adult males into the colony (Setchell et al. 2006b). Extremely large groups may prevent the infanticidal males from detecting and approaching infants through the dilution effect and increased vigilance. The high crowdedness of the group may also allow infants and their mothers to avoid male aggression through the confusion effect, an anti-predatory strategy found in fish schools (Chivers et al. 1995). Moreover, large groups may benefit females in coalitionary attacks against unfavorable males (Morelli et al. 2009, Cords and Fuller 2010). A coalitionary attack by multiple females on a recently-immigrated male was observed at CIRMF (Setchell et al. 2006a). Female mandrills may form large coalitions to cope with males with much larger bodies and longer canines (Treves and Chapman 1996). Altogether, forming large, crowded groups may be adaptive for female mandrills as a counter-strategy against infanticide by males.

Second, large groups may increase the possibility of polyandrous mating for females. In mandrills, polyandrous mating would be difficult in small groups because dominant males rigorously guard females when receptive (Setchell et al. 2005), and females can't synchronize their ovulation cycles precisely (Setchell et al. 2011). Charpentier et al. (2005) reported that the paternity skew by alpha males decreased as the number of females increased, even in the small CIRMF colonies. Moreover, forming large groups would lower group densities (White 1994), which may, in turn, result in a certain number of solitary adult males being unable to find and join groups at the most appropriate time for mating. This delay in adult male influxes makes the ratio of receptive females to adult males higher than 1 (Hongo et al. 2016), possibly allowing low-ranking males to mate with receptive females. Therefore, females in large groups can mate with many males, including low-ranking and sub-adult males. This polyandrous mating may confuse the paternity of infants and increase the chances for females to choose males, both of which should be adaptive for females. Further, female mate choice is suggested to be beneficial in terms of the immune system, such as major

histocompatibility complex (MHC) diversity (Setchell et al. 2010).

3. Seasonal influxes of solitary males

3.1. How do solitary males find groups?

Most male mandrills live alone during the birth (rainy) season, so they must find groups to mate with females at the onset of the mating (dry) season. So far, it is not at all clear how the males meet this challenge—here, I present several keys that may be relevant to their navigation capacity (Nathan et al. 2008).

First, female long-distance calls (crowing) may be key for males to localize groups. As mentioned above, the exchange of crowing vocalization by many female foraging groups can reach more than hundreds of meters in dense forests (Kudo 1987). Indeed, female crowing has almost always triggered researchers to find mandrill groups. Second, the nomadic movement of groups in the mating season observed at Moukalaba-Doudou may also help solitary males join the groups (Hongo et al. 2018). During the dry season, group members have a more diverse dietary repertory and travel more widely than during the rainy season. This home range expansion may favor seasonal male influxes. Future studies should compare the movement patterns of groups and solitary males to test these hypotheses.

3.2. Why do males join and leave groups seasonally?

The adaptation of seasonal male influx can be relatively well explained. First, living as a solitary male will substantially reduce the energetic costs of traveling and the time spent foraging. Because of their much larger body size compared to females, living in groups may be more costly for males than for females in terms of long-distance movements and intragroup food competition. Second, group living enhances the risk of intensive male competition and resulting injuries (Setchell et al. 2006b). In particular, the mating season, when males live in the group, corresponds to the dry season with lower fruit production. By feeding on energy-rich fruits alone during the rainy season, males may

need to compensate for the large energetic loss due to intra-group food competition and inter-male mate competition during the dry season.

Nonetheless, Hongo et al. (2016) reported that camera traps at Moukalaba-Doudou observed adult males in the group all year round, although the percentage of adult males among all individuals decreased from 5.2% to 0.9% during the rainy (birth) season. This suggests that a small number of adult males stay in groups even during the birth season. Moreover, these males tended to position near females with sexual swellings, implying that they are dominant males capable of mating with a few receptive females outside the mating season to increase their offspring (Hongo et al. 2016). Long-term studies with individual identification and behavioral observation are indispensable to examine the above hypotheses.

An interesting example of concordance with male mandrills is found in a Neotropical carnivore—the coatis. The white-nosed coati (*Nasua narica*) is a social carnivore mainly living in Central America's forests (Cuarón et al. 2016). Similarly to mandrills, this terrestrial procyonid is sexually dimorphic in body size, with males larger than females. In addition, males are solitary most of the year and enter social groups composed of females and immatures only during the mating season. Solitary males enjoy high foraging success compared to social females and sub-adult males (Gompper 1996), supporting my hypothesis on the benefits of solitary living in male mandrills. Moreover, a few adult males who join groups in non-mating season are also reported in white-nosed coatis (Gompper and Krinsley 1992). Clarifying the social behavior of these exceptional male coatis may provide clues to the puzzle of the sociality of male mandrills.

4. Potential keys to unraveling the puzzle

Wild mandrill groups are extremely difficult to locate, identify and follow for direct behavioral observation due to their large size and low group density. On the other hand, tracking male movement is nearly impossible without using GPS telemetries as they seasonally leave the group and range alone. As I have discussed through this chapter,

major questions of mandrill social organization are strongly related to their movement ecology: group crowdedness, patterns and frequency of subgrouping, inter-male variations in the seasonal male influx, and fission-fusion dynamics between female-led large groups and solitary males. Therefore, intensive research of movement and positioning behavior using GPS telemetries and remote sensing is crucially needed to disentangle the social system of this intriguing monkey.

In addition, comparing mandrill ecology with a broader range of taxa, as I briefly attempted in this chapter with some Neotropical forest mammals, will help unravel the mandrill mysteries. Taking a broader perspective, we'll be able to comprehensively understand the various characteristics of the social movement in forest mammals, with signposts of the socio-ecological models and the movement ecology framework (Nathan et al. 2008).

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583 **Fig. 1** Distribution range of wild mandrills (*Mandrillus sphinx*) (pink area) derived from
 584 The IUCN Red List of Threatened Species (Abernethy and Maisels 2019). Yellow
 585 circles represent their intensive research sites.

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590 **Fig. 2** Sexual size dimorphism in mandrills in the Moukalaba-Doudou National Park,
591 Gabon: (a) a subadult male inspecting genital sexual swelling of an adult female; (b) an
592 adult male mate-guarding an adult female with sexual swelling.

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Fig. 3 Crowded mandrill groups observed in the Moukalaba-Doudou National Park, Gabon: (a) a subgroup of 169 individuals traveling on a tree crossing a river; (b) a group traveling on the ground; (c) a subgroup of 442 individuals crossing a logging road. Photos (a) and (c) are captured from video recordings used in Hongo (2014).