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

Cite as:
Hongo, S. (2023). Females Move in Tight Crowds, Males Roam: Socioecology and Movement Ecology of Mandrills. In: Reyna-Hurtado, R., Chapman, C.A., Melletti, M. (eds) Movement Ecology of Afrotropical Forest Mammals. Springer, Cham. https://doi.org/10.1007/978-3-031-27030-7_10

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 Dixson 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 (Dixson 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 (Dixson 2015), where dense vegetation would complicate the coordination of ground movement by large groups.

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

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

This temporary immigration of many males into the group is termed *male influx*. In mandrills, the male influx is thought to occur during every dry season (Hongo et al. 2016). Therefore, most males would move around in the forest yearly in search of groups. Due to their large group home ranges of about 50 km^2 (White et al. 2010) and the low group density (White 1994), however, this annual search for groups at the right time of year for mating seems quite challenging for solitary males. How do they 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 km^2, with 46 km^2 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 km^2 (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).

Acknowledgments

I appreciate the Institut de Recherche en Écologie Tropicale (IRET) for the long-lasting collaboration. Etienne François Akomo-Okoue and Fred Loïque Mindonga-Nguelet worked with me for long-term camera trapping. I am also grateful to the Centre National de la Recherche Scientifique et Technologique (CENAREST) and Agence National de Parcs Nationaux (ANPN) in Gabon for permission to conduct the study. I sincerely thank all researchers, staff and field assistants of the PROCOBHA project for providing advice and assistance. Namely, no work of mine would have been possible without the help and cooperation of Yoshihiro Nakashima, Yuji Takenoshita, Shiho Fujita and Chieko Ando. My gratitude also goes to Rafael Reyna-Hurtado, Colin Chapman and Mario Melletti for inviting me to contribute to this exciting edited volume. Jessica Rothman and an anonymous reviewer provided many constructive comments on an earlier version of this chapter. Lastly, I express my sincere appreciation and condolences to Jiro Hoshino, a Japanese pioneer in mandrill research who passed away in June 2022. My studies of mandrills in the Moukalaba-Doudou National Park were funded by JSPS KAKENHI (grunt numbers JP19107007 and JP12J01884), Kyoto University Global COE Program (A06), and JST/JICA-SATREPS.

References

Abernethy, K., and F. Maisels. 2019. *Mandrillus sphinx*. The IUCN Red List of Threatened Species 2019:e.T12754A17952325.

Abernethy, K. A., and L. J. T. White. 2013. *Mandrillus sphinx* Mandrill. Page 192–196 *in* T. Butynski, J. Kingdon, and J. Kalina, editors. Mammals of Africa. 2. Primates. Bloomsbury Publishing, London, United Kingdom.

Abernethy, K. A., L. J. T. White, and E. J. Wickings. 2002. Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. Journal of Zoology **258**:131–137.

Ariel, G., and A. Ayali. 2015. Locust collective motion and its modeling. PLoS Computational Biology **11**:e1004522.

Aureli, F., C. M. Schaffner, C. Boesch, S. K. Bearder, J. Call, C. A. Chapman, R. Connor, A. Di Fiore, R. I. M. Dunbar, S. P. Henzi, K. Holekamp, A. H. Korstjens, R. Layton, P. Lee, J. Lehmann, J. H. Manson, G. Ramos-Fernandez, K. B. Strier, and C. P. van Schaik. 2008. Fission-fusion dynamics: new research frameworks. Current Anthropology **49**:627–654.

Biondo, C., P. Izar, C. Y. Miyaki, and V. S. Bussab. 2014. Social structure of collared peccaries (*Pecari tajacu*): does relatedness matter? Behav Processes **109**:70–78.

Brockmeyer, T., P. M. Kappeler, E. Willaume, L. Benoit, S. Mboumba, and M. J. Charpentier. 2015. Social organization and space use of a wild mandrill (*Mandrillus sphinx*) group. American Journal of Primatology **77**:1036–1048.

Byers, J. A., and M. Bekoff. 1981. Social, spacing, and cooperative behavior of the collared peccary, *Tayassu tajacu*. Journal of Mammalogy **62**:767–785.

Chapman, C. A., and L. J. Chapman. 2000. Determinants of group size in primates: the importance of travel costs. Page 24–41 *in* S. Boinski and P. A. Garber, editors. On the move: how and why animals travel in groups. The University of Chicago Press, Chicago, USA.

Charpentier, M., P. Peignot, M. Hossaert-McKey, O. Gimenez, J. M. Setchell, and E. J. Wickings. 2005. Constraints on control: factors influencing reproductive success in male mandrills (*Mandrillus sphinx*). Behavioral Ecology **16**:614–623.

Chivers, D. P., G. E. Brown, and R. J. F. Smith. 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. Canadian Journal of Zoology **73**:955–960.

Clutton-Brock, T. H., and P. H. Harvey. 1977. Primate ecology and social organization. Journal of Zoology **183**:1–39.

Clutton-Brock, T. H., P. H. Harvey, and B. Rudder. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature **269**:797–800.

Cords, M., and J. L. Fuller. 2010. Infanticide in *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya: variation in the occurrence of an adaptive behavior. International Journal of Primatology **31**:409–431.

Cuarón, A. D., K. Helgen, F. Reid, J. Pino, and J. F. González-Maya. 2016. *Nasua narica*. The IUCN Red List of Threatened Species:e.T41683A45216060.

Darwin, C. R. 1871. Descent of man, and selection in relation to sex. Vol. I. John Murray, London, U.K.

Dixson, A. F. 2015. The mandrill: a case of extreme sexual selection. Cambridge University Press, Cambridge.

Fragoso, J. M. V. 1998. Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the northern Brazilian Amazon. Biotropica **30**:458–469.

Gompper, M. E. 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. Behavioral Ecology **7**:254–263.

Gompper, M. E., and J. S. Krinsley. 1992. Variation in social behavior of adult male coatis (*Nasua narica*) in Panama. Biotropica **24**:216–219.

Grueter, C. C., X. Qi, D. Zinner, T. Bergman, M. Li, Z. Xiang, P. Zhu, A. B. Migliano, A. Miller, M. Krutzen, J. Fischer, D. I. Rubenstein, T. N. C. Vidya, B. Li, M. Cantor, and L. Swedell. 2020. Multilevel organisation of animal sociality. Trends Ecol

Evol **35**:834–847.

Harrison, M. J. S. 1988. The mandrill in Gabon's rain forest — ecology, distribution and status. Oryx **22**:218–228.

Hemelrijk, C. K., and H. Hildenbrandt. 2008. Self-organized shape and frontal density of fish schools. Ethology **114**:245–254.

Hemingway, C. A., and N. Bynum. 2005. The influence of seasonality on primate diet and ranging. Page 57–104 *in* D. K. Brockman and C. P. van Schaik, editors. Seasonality in primates: studies of living and extinct human and non-human primates. Cambridge University Press, New York.

Henschel, P., L. T. B. Hunter, L. Coad, K. A. Abernethy, and M. Mühlenberg. 2011. Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters. Journal of Zoology **285**:11–20.

Hongo, S. 2014. New evidence from observations of progressions of mandrills (*Mandrillus sphinx*): a multilevel or non-nested society? Primates **55**:473–481.

Hongo, S. 2016. Socioecology of mandrills (*Mandrillus sphinx*): mating and feeding tactics in a primate with extremely large group. Kyoto University, Kyoto, Japan.

Hongo, S., Y. Nakashima, E. F. Akomo-Okoue, and F. L. Mindonga-Nguelet. 2016. Female reproductive seasonality and male influxes in wild mandrills (*Mandrillus sphinx*). International Journal of Primatology **37**:416–437.

Hongo, S., Y. Nakashima, E. F. Akomo-Okoue, and F. L. Mindonga-Nguelet. 2018. Seasonal change in diet and habitat use in wild mandrills (*Mandrillus sphinx*). International Journal of Primatology **39**:27–48.

Hongo, S., Y. Nakashima, E. F. Akomo-Okoue, and F. L. Mindonga-Nguelet. 2022. Seasonality in daily movement patterns of mandrills revealed by combining direct tracking and camera traps. Journal of Mammalogy **103**:159–168.

Hoshino, J. 1985. Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo Animal Reserve, Cameroon. Primates **26**:248–273.

Hoshino, J., A. Mori, H. Kudo, and M. Kawai. 1984. Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. Primates **25**:295–307.

Jouventin, P. 1975. Observations sur la socio-écologie du mandrill. La Terre et La Vie

4:493–532.

Keuroghlian, A., D. P. Eaton, and W. S. Longland. 2004. Area use by white-lipped and collared peccaries (*Tayassu pecari* and *Tayassu tajacu*) in a tropical forest fragment. Biological Conservation **120**:411–425.

Kiltie, R. A., and J. Terborgh. 1983. Observations on the behavior of rain forest peccaries in Perú: Why do white-lipped peccaries form herds? Zeitschrift für Tierpsychologie **62**:241–255.

Kudo, H. 1987. The study of vocal communication of wild mandrills in Cameroon in relation to their social structure. Primates **28**:289–308.

Kudo, H., and M. Mitani. 1985. New record of predatory behavior by the mandrill in Cameroon. Primates **26**:161–167.

Lahm, S. A. 1986. Diet and habitat preference of *Mandrillus sphinx* in Gabon: implications of foraging strategy. American Journal of Primatology **11**:9–26.

Leigh, S. R., J. M. Setchell, M. Charpentier, L. A. Knapp, and E. J. Wickings. 2008. Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). Journal of Human Evolution **55**:75–85.

Mayer, J. J., and R. M. Wetzel. 1987. *Tayassu pecari*. Mammalian Species **293**:1–7.

Morelli, T. L., P. Wright, S. King, and S. Pochron. 2009. The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. Behaviour **146**:499–523.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences **105**:19052–19059.

Nsi Akoue, G., W. Mbading-Mbading, E. Willaume, A. Souza, B. Mbatchi, and M. J. E. Charpentier. 2017. Seasonal and individual predictors of diet in a free-ranging population of mandrills. Ethology **123**:600–613.

Poirotte, C., D. Basset, E. Willaume, F. Makaba, P. M. Kappeler, and M. J. Charpentier. 2016. Environmental and individual determinants of parasite richness across seasons in a free-ranging population of Mandrills (*Mandrillus sphinx*). American Journal of Physical Anthropology **159**:442–456.

Poirotte, C., S. Benhamou, A. Mandjembe, E. Willaume, P. M. Kappeler, and M. J. E. Charpentier. 2017a. Gastrointestinal parasitism and recursive movements in free-ranging mandrills. Animal Behaviour **134**:87–98.

Poirotte, C., F. Massol, A. Herbert, E. Willaume, P. M. Bomo, P. M. Kappeler, and M. J. E. Charpentier. 2017b. Mandrills use olfaction to socially avoid parasitized conspecifics. Science Advances **3**:e1601721.

Reyna-Hurtado, R., and C. A. Chapman. 2019. Movement ecology of Neotropical forest mammals: Focus on social animals. Springer Nature Switzerland AG, Cham, Switzerland.

Reyna-Hurtado, R., E. Rojas-Flores, and G. W. Tanner. 2009. Home range and habitat preferences of white-lipped peccaries (*Tayassu pecari*) in Calakmul, Campeche, Mexico. Journal of Mammalogy **90**:1199–1209.

Sabater Pi, J. 1972. Contribution to the ecology of *Mandrillus sphinx* Linnaeus 1758 of Rio Muni (Republic of Equatorial Guinea). Folia Primatologica **17**:304–319.

Setchell, J. M. 2016. Sexual selection and the differences between the sexes in mandrills (*Mandrillus sphinx*). Yearbook of Physical Anthropology **159**:S105–S129.

Setchell, J. M., M. Charpentier, and E. J. Wickings. 2005. Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. Animal Behaviour **70**:1105–1120.

Setchell, J. M., M. J. Charpentier, K. M. Abbott, E. J. Wickings, and L. A. Knapp. 2010. Opposites attract: MHC-associated mate choice in a polygynous primate. Journal of Evolutionary Biology **23**:136–148.

Setchell, J. M., and A. F. Dixson. 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. Hormones and Behavior **39**:177–184.

Setchell, J. M., J. Kendal, and P. Tyniec. 2011. Do non-human primates synchronise their menstrual cycles? A test in mandrills. Psychoneuroendocrinology **36**:51–59.

Setchell, J. M., L. A. Knapp, and E. J. Wickings. 2006a. Violent coalitionary attack by female mandrills against an injured alpha male. American Journal of Primatology **68**:411–418.

Setchell, J. M., P. C. Lee, E. J. Wickings, and A. F. Dixson. 2001. Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). American Journal of Physical Anthropology **115**:349–360.

Setchell, J. M., E. J. Wickings, and L. A. Knapp. 2006b. Life history in male mandrills (*Mandrillus sphinx*): physical development, dominance rank, and group association. American Journal of Physical Anthropology **131**:498–510.

Treves, A., and C. A. Chapman. 1996. Conspecific threat, predation avoidance, and resource defense: Implications for grouping in langurs. Behavioral Ecology and Sociobiology **39**:43–53.

van Schaik, C. P., and J. A. R. A. M. van Hooff. 1983. On the ultimate causes of primate social systems. Behaviour **85**:91–117.

van Schaik, C. P., and M. A. van Noordwijk. 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). Behaviour **105**:77–98.

White, E. C. 2007. Ecology of *Mandrillus sphinx*: ranging, diet and social structure of a mandrill horde in Lopé National Park, Gabon. University of Exeter, Cornwall, UK.

White, E. C., J.-T. Dikangadissi, E. Dimoto, W. B. Karesh, M. D. Kock, N. Ona Abiaga, R. Starkey, T. Ukizintambara, L. J. T. White, and K. A. Abernethy. 2010. Home-range use by a large horde of wild *Mandrillus sphinx*. International Journal of Primatology **31**:627–645.

White, L. J. T. 1994. Biomass of rain forest mammals in the Lopé Reserve, Gabon. Journal of Animal Ecology **63**:499–512.

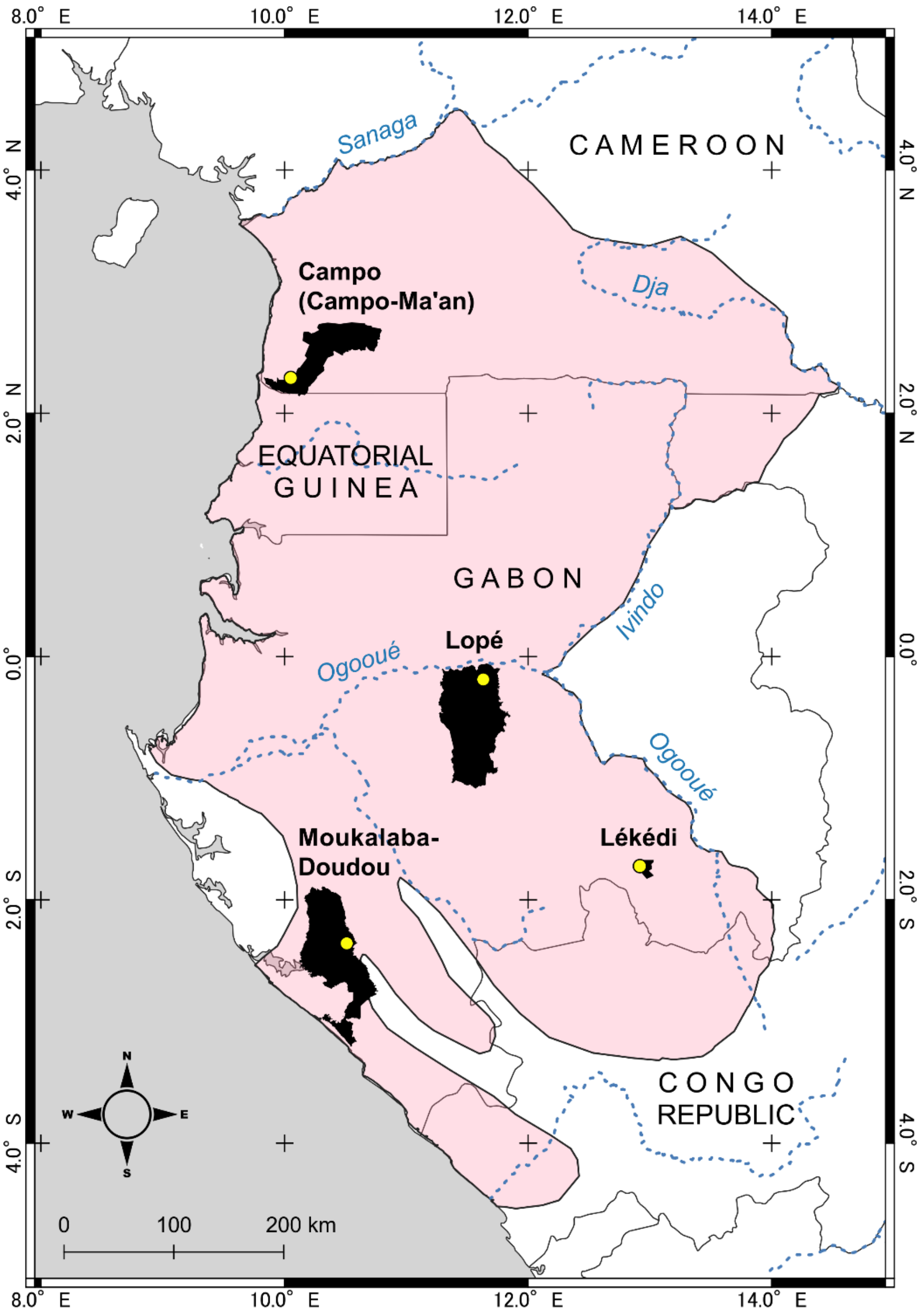

Fig. 1 Distribution range of wild mandrills (*Mandrillus sphinx*) (pink area) derived from The IUCN Red List of Threatened Species (Abernethy and Maisels 2019). Yellow circles represent their intensive research sites.

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

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).