

Social Behavior and Dominance of the Crowned Sifaka (*Propithecus coronatus*) in Northwestern Madagascar

Rivo Ramanamisata¹, Claire Pichon², Hanta Razafindraibe¹ and Bruno Simmen²

¹Department of Animal Biology, University of Antananarivo, Antananarivo, Madagascar

²Eco-anthropologie et Ethnobiologie, Centre National de la Recherche Scientifique (CNRS) and Museum national d'Histoire naturelle (MNHN), Brunoy, France

Abstract: We carried out a study of the social behavior and dominance hierarchy in three groups of crowned sifaka (*Propithecus coronatus*) in the Antrema Forest Station in north-west Madagascar. Data were collected from April to June 2009 and October to November 2009 using all-occurrence sampling. During 273 hours of observation, the majority of social behaviors observed were grooming interactions (39%), followed by agonistic behavior (25%), play (19%), scent-marking (9%), call-localization (5%) and approach (3%). A social hierarchy was maintained in the groups of *P. coronatus*, with females dominating the males. Although different groups of *P. coronatus* defended their territories against other neighboring groups of the same species, the most frequently observed outcome of intergroup encounters was tolerance. In addition, we detected no significant change of sifaka behavior during interspecific encounters with rufous brown lemur (*Eulemur rufus*) or with mongoose lemur (*Eulemur mongoz*), suggesting these two species live in total sympatry with *P. coronatus*.

Key Words: *Propithecus coronatus*, social behaviors, female dominance, intergroup encounter, interspecific relationships, Antrema

Introduction

The social behavior of primates has been the subject of many studies published across several decades (Crook and Gartlan 1966; Clutton-Brock and Harvey 1977; Dunbar 1988). Hierarchical interactions can be observed in gregarious and territorial primates (Cords 1987; Stanford 1991; Yeager 1992). In this case, different relationships between individuals of a group or between different groups can be affected by the dominance hierarchy. In most non-human primates social dominance is usually male-biased, e.g., *Cebus capucinus*, *Alouatta* spp., *Presbytis* spp., *Colobus* spp., *Cercopithecus* spp., *Nasalis larvatus*, *Erythrocebus patas* and *Gorilla gorilla* (Cords 1987; Crockett and Eisenberg 1987; Robinson and Hanson 1987; Struhsaker and Leland 1987; Stanford 1991; Yeager 1992). However, in some gregarious lemur species, the females dominate males (Richard and Nicoll 1987; Sauther *et al.* 1999) and group size is relatively small (Kappeler 1997). Although several behavioral studies have shown that social activities represent only a small part of the daily activity budget of lemurs (Hemingway 1999; Charrier *et al.* 2007; Pichon *et al.* 2010), these activities could be important

if they are beneficial to individuals and/or help maintain social structure.

There are no published accounts of the social relationships of crowned sifaka (*Propithecus coronatus*) in the wild. The crowned sifaka is classified as Endangered by the IUCN (2012; Salmona *et al.* in press). It is a diurnal, folivorous, medium-sized lemur, which lives in groups of up to eight individuals in the dry forests of north-western and central-western Madagascar (Mittermeier *et al.* 2010; Rakotonirina *et al.* in press; Salmona *et al.* in press). Here, we present the results of observations conducted on three groups of crowned sifakas in the Antrema Forest Station of north-western Madagascar. The aim of the study was to improve our understanding of the social behavior of the species, including patterns of dominance hierarchy.

Methods

Study site

The Antrema Forest Station is included in the network of protected areas in Madagascar. Four lemur species are present at the site in addition to *P. coronatus*: two diurnal (rufous

brown lemur *Eulemur rufus* and mongoose lemur *Eulemur mongoz*) and two nocturnal (Antafia sportive lemur *Lepilemur aeeclis* and a mouse lemur *Microcebus* sp.) (nomenclature following Mittermeier *et al.* 2010). Located in the north-west of Madagascar, on the Katsepy Peninsula, the station covers 12,270 ha; mostly of dry forest on sandy soil but including a 1,000-ha marine park. Ecologically, it belongs to the Western area (Humbert 1955), the vegetation of which is characterized by species particularly adapted to drought, including *Dalbergia*, *Commiphora* and *Hildegardia*. Our study was conducted in the 24-ha Badrala forest fragment (15°45.665'S, 46°12.300'E), located 3 km from the Antrema village. Fifteen groups of sifaka have been identified living in this fragment.

Observation protocol

Data were collected from April to June and from October to November 2009 on three groups of regularly monitored sifakas: G1 (two males and two females), G2 (three males and two females) and G3 (three males and three females). Each sifaka was identifiable through their unique facial markings.

Social behavior was studied using all-occurrence sampling (Altmann 1974) and was conducted in parallel with an investigation into diet and behavior (Pichon *et al.* 2010). Observations were made between 06:30 h and 18:00 h (or 18:30 h according to visibility). The three main types of social behaviors we recorded were affiliative (grooming interactions, approach, play and call-localization), agonistic and scent-marking (Table 1). To assess social dominance, the frequency of threats and/or avoidance between individuals was noted. Once an aggression was observed, the identity and sex of the individual *director* (i.e., who initiated the attack) and *receiver* (i.e., who suffered the attack) were noted, together with the context in which the aggression occurred. The individual with the highest rate of aggression toward other group members was considered dominant. During intergroup encounters, the behaviors (for example, alarm, affiliative, aggression, or other) of all individuals of the group were recorded. The

Table 1. Social behaviors recorded during the study of three groups of *Propithecus coronatus*.

Agonistic*	Slapping, biting, stealing food, avoidance, escape, recoil against another individual
Grooming interactions**	Affiliative interactions to groom another individual to remove dirt and ectoparasites in the body (hygienic function), to reduce stress, and to reinforce the social structure (social function)
Approach*	Individual going to, moving toward, getting close to, sitting or lying close to a congener
Call-localization	Search for other members of the group while making some vocalizations
Play*	Provocation action, pursuit, fight or other
Scent-marking*	Action to smell or make a scent mark with the anogenital gland (female and male) or chest gland (male)

*Definition modified from Moral (2009).

**Definition modified from Morelli (2008).

behaviors of the entire group were also noted during interspecific encounters.

Hierarchical dominance

Dominance was estimated by the number of aggressions recorded among agonistic behaviors (slapping, biting, stealing food) in which actors were identified. The dominant sex was estimated by comparing numbers of aggressions initiated against others of the opposite sex using a chi-square test (χ^2).

Results

Social behavior

During 273 hours of continuous sampling we observed 173 social interactions. Grooming was most frequently observed (39% of cases), followed by agonistic behaviors (25%) and play (19%). Scent-marking, call-localization and approach were rarely observed (9%, 5% and 3%, respectively) (Fig. 1).

Hierarchical dominance

Using the number of aggressive events recorded during agonistic behaviors in which all actors were identified, the direction of aggressive acts clearly showed a dominant female in each of the three groups. Half of the aggressions (51%; $n = 39$) were initiated by females and were directed toward males. However, tests on the overall data showed that females attacked males more than the reverse. These results suggest a female dominance over males for all groups ($\chi^2 = 6.593$, $p < 0.0103$). For group G1, the dominant individual was the female F2, and she initiated 65% ($n = 20$) of attacks in the group (Table 2). The dominant individual of group G2 was the female F1 (63% of attacks, $n = 8$; Table 3), and in group G3 female F1 was dominant (73% of attacks, $n = 11$; Table 4).

More aggressive interactions were observed in the smallest group, G1 ($n = 20$), compared to the two other groups ($n = 8$ for G2 and $n = 11$ for G3). Also the number of intersex aggressions (female-male and male-female) was higher in G1 ($n = 11$) than in G2 ($n = 5$) or G3 ($n = 9$). Twenty-one percent of all aggressive acts (intra- and intergroup) were food-related, that is to say,

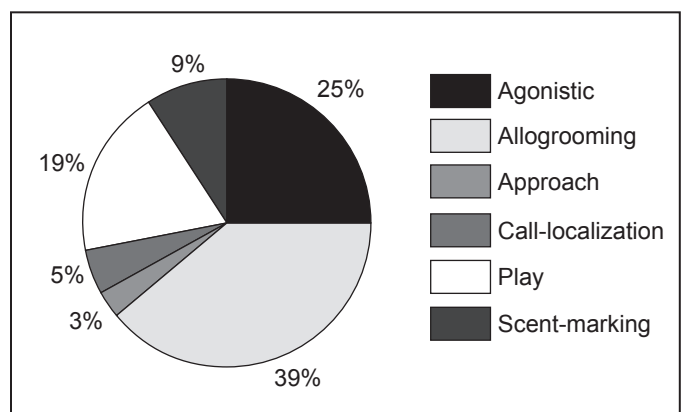


Figure 1. Proportions of social behaviors of crowned sifakas recorded during our study ($n = 173$).

Table 2. Dominance matrix for group G1 (♀: female; ♂: male). Dominant individual: female F2 with 63% (n = 20) of aggression within the group.

Director Receiver	F1♀	F2♀	M1♂	M2♂
F1♀		5	2	
F2♀				
M1♂		6		1
M2♂	1	2	3	

Table 3. Dominance matrix for group G2 (♀: female; ♂: male). Dominant individual: female F1 with 63% (n = 8) of aggression within the group.

Director Receiver	F1♀	F2♀	M1♂	M2♂	M3♂
F1♀				1	
F2♀	1				
M1♂	1				
M2♂	2				
M3♂	1		1	1	

Table 4. Dominance matrix for group G3 (♀: female; ♂: male). Dominant individual: female F1 with 73% (n = 11) of aggression within the group.

Director Receiver	F1♀	F2♀	F3♀	M1♂	M2♂	M3♂
F1♀						
F2♀						
F3♀	1			1		1
M1♂	2					
M2♂	3					
M3♂	2			1		

the director or the receiver of the attack was either feeding or approaching food. Otherwise, the contexts were variable.

Intergroup relationships

Only 19 intergroup encounters were recorded, giving a rate of 0.07 encounters per hour. Meeting areas were often limited to up to 10 m. In most cases (63%), meetings with other groups did not affect the activity of the observed group. Sometimes an intergroup encounter was followed by a temporary interruption of the activities of group members to observe the neighboring group without direct contact between individuals. In the remaining cases (37%), reactions included aggressive pursuit of individuals of the other group, scent-marking, flight of the focal group or jumping from tree to tree, all of which may be attributed to the defense of territory.

Interspecific relationships

Interspecific encounters were very rare, with two recorded cases each with *Eulemur rufus* and *Eulemur mongoz*. In all cases, the presence of these two species did not seem to affect the behavior of the crowned sifakas. An encounter with a dog, however caused flight and temporary splitting of the focal sifaka group.

Discussion

This study describes social behaviors observed in three crowned sifaka groups in the Antrema Forest Station over a five-month period. As our study was conducted in parallel with other studies, we probably overlooked some interactions, and some behaviors were not observed due to the timing of our study. Lactation, for example, was not observed because no young were present during our field observations, and no reproductive behavior was observed as the study did not take place during the mating period (the mating period of the closely-related Verreaux's sifaka *P. verreauxi* in Kirindy, an environment similar to Antrema, is between late January and March; Kraus *et al.* 1999).

Social organization and behavior of primates are influenced in part by the distribution of resources (van Schaik and van Hooft 1983; van Schaik 1989; Barton *et al.* 1996). The highly seasonal environment at Antrema would, therefore, be expected to result in different social behaviors of *P. coronatus* between the dry and wet seasons, and we recommend future studies of social behavior in Antrema to investigate this.

The dominance of female crowned sifaka observed in the present study suggests that the social organization of this species is similar to that reported in other sifakas such as *P. verreauxi* (see Richard and Nicoll 1987), diademed sifaka *P. diadema* (see Hemingway 1999) and Milne-Edwards' sifaka *P. edwardsi* (see Pochron *et al.* 2003). In this study, we used only aggressive behaviors to measure the dominance hierarchy. Since the rate of aggression in this species is low, however, there could be other behaviors, more complex and difficult to identify, that indicate dominance; two possibilities would be scent-marking and submission (Kraus *et al.* 1999; Lewis 2006; Pochron *et al.* 2005). Our analysis of the contexts in which aggressions were initiated by female crowned sifakas, with most observed aggressions happening outside the feeding phases, confirms that female dominance in lemurs is not related only to priority access to resources (Kappeler 1990).

Despite the limited number of observation days, the low intergroup encounter rate we report is consistent with observations in other sifaka species (Irwin 2006; Benadi *et al.* 2008). On the other hand, the reactions of all individuals of *P. coronatus* observed during intergroup encounters in Badrala differed from those reported by Irwin (2006) for *P. diadema* in Tsinjoarivo and by Benadi *et al.* (2008) for *P. verreauxi* in Kirindy. In these two studies the most frequently observed reactions were agonistic among neighboring groups. In our study of *P. coronatus*, even though territorial defense was evident in some intergroup encounters, tolerance between groups was most frequently observed. This may be due to neighboring groups being related or due to a mutual habituation of the groups in response to small forest fragments and a high population density (Pichon *et al.* 2010; Salmons *et al.* in press).

Concerning interspecific relationships, the tolerance we observed in *P. coronatus* when encountering *Eulemur rufus* and *E. mongoz* is probably associated with their different

diets. While *P. coronatus* is folivorous (Pichon *et al.* 2010), *E. rufus* and *E. mongoz* are frugivorous-folivorous (Curtis and Zaramody 1998; Simmen *et al.* 2003). However, the reaction of crowned sifaka that we observed during an encounter with a dog suggests that research is needed to determine whether the presence of dogs in Badrala Forest is a threat to the sifaka population.

Acknowledgments

We thank Antrema's project staff for assistance with the fieldwork. We also thank C. A. Gauthier, E. Roger, Vavindrana, A. Hladik and C. M. Hladik for logistic support and collaborative work. This study was funded by the Museum national d'Histoire naturelle, Paris, and conducted under the cooperation agreement between the Université d'Antananarivo and the museum. Special thanks to A. Andrianarimisa for helpful comments on the statistical analysis. We are most grateful to Richard K. B. Jenkins, Lounès Chikhi, Tony King and Christoph Schwitzer for improving the English of this article, and to an anonymous reviewer for their constructive comments on our manuscript.

Literature Cited

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.
- Barton, R. A., R. W. Byrne and A. Whiten. 1996. Ecology, feeding competition and social structure in baboons. *Behav. Ecol. Sociobiol.* 38: 321–329.
- Benadi, G., C. Fichtel and P. Kappeler. 2008. Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). *Am. J. Primatol.* 70: 956–965.
- Charrier, A., B. Simmen and A. Hladik. 2007. Stratégie alimentaire et dominance des femelles propithecus de Verreaux (*Propithecus v. verreauxi*) dans la forêt à Didie-reaceae du sud de Madagascar. *Rev. Écol. (Terre et Vie)* 62: 257–263.
- Clutton-Brock, T. H. and P. H. Harvey. 1977. Primate ecology and social organization. *J. Zool., Lond.* 183: 1–39.
- Cords, M. 1987. Forest guenons and patas monkeys: male-male competition in one-male groups. In *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp.98–111. University Of Chicago Press, Chicago.
- Crockett, C. M. and J. F. Eisenberg. 1987. Howlers: variation in group size and demography. In *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp. 54–68. University Of Chicago Press, Chicago.
- Crook, J. H. and J. C. Gartlan. 1966. Evolution of primate societies. *Nature* 210: 1200–1203.
- Curtis, D. J. and A. Zaramody. 1998. Behavior and ecology of the mongoose lemur. *Lemur News* 3: 20–21.
- Dunbar, R. I. M. 1988. *Primate Social Systems*. Cornell University Press, Ithaca, NY.
- Hemingway, C. A. 1999. Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? *Behav. Ecol. Sociobiol.* 45: 311–322.
- Humbert, H. 1955. Les territoires phytogéographiques de Madagascar. *Année Biologique* 31(3): 439–448.
- Irwin, M. T. 2006. Ecological Impacts of Forest Fragmentation on Diademed Sifakas (*Propithecus diadema*) at Tsinjoarivo, Eastern Madagascar: Implications for Conservation in Fragmented Landscapes. PhD Thesis, Stony Brook University, Stony Brook, NY.
- IUCN. 2012. 2012 IUCN Red List of Threatened Species. International Union for Conservation of Nature (IUCN), Species Survival Commission (SSC), Gland, Switzerland and Cambridge, UK. Website: <<http://www.redlist.org>>.
- Kappeler, P. M. 1990. Female dominance in *Lemur catta*: more than just female feeding priority. *Folia Primatol.* 55: 92–95.
- Kappeler, P. M. 1997. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biol. Rev.* 72: 111–151.
- Kraus, C., M. Heistermann and P. M. Kappeler. 1999. Physiological suppression of sexual function of subordinate males: a subtle form of intrasexual competition among male sifakas (*Propithecus verreauxi*)? *Physiol. Behav.* 66: 855–861.
- Lewis, R. J. 2006. Scent marking in sifaka: no one function explains it all. *Am. J. Primatol.* 68: 622–636.
- Mittermeier, R. A., E. E. Louis Jr., M. Richardson, C. Schwitzer, O. Langrand, A. B. Rylands, F. Hawkins, S. Rajabolina, J. Ratsimbazafy, R. Rasoloarison, C. Roos, P. M. Kappeler, and J. Mackinnon. 2010. *Lemurs of Madagascar* (3rd ed.). Conservation International, Arlington, VA.
- Moral, L. 2009. Etude des Interactions Sociales et de l'Activité d'un Groupe de Propithecus Couronnés (*Propithecus verreauxi coronatus*) en Captivité. Master éthologie spécialité éthologie appliquée, Université Paris 13, France.
- Morelli, T. L. 2008. Dispersal, Kinship, and Genetic Structure of an Endangered Madagascar Primate, *Propithecus edwardsi*. PhD thesis, Stony Brook University, Stony Brook, NY.
- Pichon, C., R. Ramanamisata, L. Tarnaud, F. Bayart, A. Hladik, C. M. Hladik and B. Simmen. 2010. Feeding ecology of the crowned sifaka (*Propithecus coronatus*) in a coastal dry forest in northwest Madagascar (SFUM, Antrema). *Lemur News* 15: 42–45.
- Pochron, S. T., J. Fitzgerald, C. C. Gilbert, D. M. Lawrence, M. Grgas, G. Rakotonirina, R. Ratsimbazafy, R. Rakotosoa and P. C. Wright. 2003. Patterns of female dominance in (*Propithecus diadema edwardsi*) of Ranomafana National Park. *Am. J. Primatol.* 61: 173–185.
- Pochron, S. T., T. L. Morelli, P. Terranova, J. Scirbona, J. Cohen, G. Kunapareddy, G. Rakotonirina, R. Ratsimbazafy, R. Rakotosoa and P. C. Wright. 2005. Patterns of male scent-marking in *Propithecus edwardsi* of

- Ranomafana National Park, Madagascar. *Am. J. Primatol.* 65: 103–115.
- Rakotonirina, L. H. F., F. Randriantsara, A. H. Rakotoarisoa, R. Rakotondrabe, J. Razafindramanana, J. Ratsimbazafy and T. King. In press. A preliminary assessment of sifaka (*Propithecus*) distribution, chromatic variation and conservation in western central Madagascar. *Primate Conserv.* In press.
- Richard, A. F. and M. E. Nicoll. 1987. Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi verreauxi*. *Am. J. Primatol.* 12: 309–314.
- Robinson, J. G. and C. H. Janson. 1987. Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp. 69–82. University of Chicago Press, Chicago.
- Salmona, J., E. Rasolondraibe, F. Jan, A. Besolo, H. Rakotoarisoa, S. Viana Meyler, S. Wohlhauser, C. Rabarivola and L. Chikhi. In press. Conservation status and abundance of the crowned sifaka (*Propithecus coronatus*). *Primate Conserv.* in press.
- Sauther, M. L., R. W. Sussman and L. Gould. 1999. The socioecology of the ringtailed lemur: thirty-five years of research. *Evol. Anthropol.* 8: 120–132.
- Simmen B., A. Hladik and P. Ramasiarisoa. 2003. Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, southern Madagascar. *Int. J. Primatol.* 35: 949–968.
- Stanford, C. B. 1991. The capped langur in Bangladesh: behavioral ecology and reproductive tactics. *Contrib. Primatol.* 26: 1–179.
- Struhsaker, T. T. and L. Leland. 1987. Colobines: infanticide by adult males. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds), pp.83–97. University of Chicago Press, Chicago.
- van Schaik, C. P. and J. van Hooff. 1983. On the ultimate causes of primate social systems. *Behaviour* 85: 91–117.
- van Schaik C. P. 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology*, V. Standen and R. A. Foley (eds.), pp.195–218. Blackwell, Oxford, UK.
- Yeager, C. P. 1992. Proboscis monkey (*Nasalis larvatus*) social organization: nature and possible functions of intergroup patterns of association. *Am. J. Primatol.* 26: 133–137.

Authors' addresses:

Rivo Ramanamisata and **Hanta Razafindraibe**, Department de Biologie Animale, Faculté des Sciences, PO Box 906, University of Antananarivo, Antananarivo 101, Madagascar, **Claire Pichon** and **Bruno Simmen**, UMR 7206, Eco-anthropologie et Ethnobiologie, Centre National de la Recherche Scientifique and Museum national d'Histoire naturelle, 4 avenue du Petit Château, 91800 Brunoy, France. E-mail of first author: <ramanamisata1@hotmail.fr>.

Received for publication : July 2011

Revised : May 2013