

PRELIMINARY REPORT: ANTIPREDATOR BEHAVIORS OF MANDRILLS

Yorzinski JL, Vehrencamp SL

Key words: alarm calls, Cercopithecidae, *Mandrillus sphinx*, mobbing calls, predation, primate vocal communication

Abstract

Predation has likely been a major selective force shaping the evolution of primates. As a result of this current and past force, primates display a variety of antipredator behaviors. Because natural encounters with predators are infrequently observed, we do not have knowledge about the antipredator behaviors of many primate species. The aim of this study was to investigate how one such primate, mandrills (*Mandrillus sphinx*), responds to its predators. We presented visual models of leopards and crowned hawk-eagles to semi-free ranging mandrills and recorded their behavioral and vocal responses. The results indicated that mandrills tended to respond appropriately to different predator stimuli by running into trees for leopard presentations and seeking cover for eagle presentations; the mandrills emitted alarm calls at higher rates and for longer amounts of time in the leopard presentations compared to the eagle presentations.

Introduction

Predation has likely exerted a strong selective pressure on the evolution of primates. This pressure may have affected their group size and composition, ecological niche, reproductive and social behavior, body size, and cognitive abilities (van Schaik, 1983; Cheney and Wrangham, 1986; Cords, 1990; Hill and Dunbar, 1998; Stanford, 1998; Uster and Zuberbühler, 2001; Zuberbühler and Jenny, 2002; Isbell 2005). Because of this predation pressure, primates currently exhibit a variety of antipredator behaviors (Stanford, 2002).

The antipredator behaviors of primates include vocal and behavioral defenses. Primates often emit alarm calls that can convey specific information about the level of danger associated with the predator and the type of predator (Seyfarth et al., 1980; Pereira and Macedonia, 1991; Zuberbühler, 2000; Manser, 2001; Manser et al., 2001; Zuberbühler, 2001; Fichtel and Kappeler, 2002; Kirchhof and Hammer-schmidt, 2006). Depending on the level of danger and the type of predator, they can flee, mob, or increase their vigilance to avoid being attacked (Cheney and Wrangham, 1986). Because natural encounters with predators are infrequently observed (Isbell, 2005), we still do not know how many primate species respond to their predators.

One of these species whose antipredator behaviors are not well known is the mandrill (*Mandrillus sphinx*). Mandrills are cercopithecine monkeys that live in multimale, multifemale groups (Abernethy et al., 2002). They are mainly terrestrial

and are likely preyed on by leopards (*Panthera pardus*), crowned hawk-eagles (*Stephanoaetus coronatus*), Gabon vipers (*Bitis gabonica*), and rock pythons (*Python sebae*) (Jouventin 1975; Lahm, 1985; Harrison, 1988). Because mandrills are extremely difficult to study in the wild, few detailed reports of their behaviors exist (e.g., Kudo, 1987; Rogers et al., 1996; Setchell et al., 2006). During one reported encounter with a leopard in the wild, mandrills climbed up trees or fled on the ground and also emitted vocalizations (Harrison, 1988). We are unaware of any reports that describe how mandrills respond to their other predators.

The purpose of this study was to examine the behavioral and vocal responses of semi-free ranging mandrills to model predators. Because of the difficulty of observing mandrills in the field, we studied a semi-free ranging population. We presented model predators of leopards and crowned hawk-eagles to assess whether the mandrills reacted differently to these different classes of predators. Because these different classes of predators employ different techniques for capturing primates (Mitani et al., 2001; Zuberbühler and Jenny 2002), we expected the mandrills to display different responses to each predator class.

Materials and Methods

We studied the responses of a semi-free ranging group of mandrills (*Mandrillus sphinx*) to predator presentations between July and September 2004. Presentations were conducted between 8:00 and 17:00 h. The mandrills were housed at the Centre de Primatologie, Centre International de Recherches Médicales (CIRMF) in Gabon, Africa and enclosed within a 1.5 hectare area of rainforest that was surrounded by about 5-10 m of mowed grass. The group consisted of 25 individuals: two adult males, ten adult females, five juvenile males, three juvenile females, two infant males, and three infant females. All individuals were identifiable by their ear tags and/or tattoo markings. They were provisioned daily and habituated to the presence of the observers.

The mandrills in this study group had limited experiences with natural predators. With the exception of four individuals, all of the mandrills were born at CIRMF. The captive-born mandrills were descendants of the original 15 wild-born mandrills that established the captive colony over twenty years ago (Feistner et al., 1992). Because large eagles and raptors (e.g., crowned hawk-eagles) inhabit the study area, it is likely that the mandrills are familiar with these predators but no direct observations of predation have been observed (J. Yorzinski, pers. obs; J. Wickings, pers. com.). Leopards do not inhabit the area so the mandrills had no experience with them. The other four individuals were likely captured in the wild and brought into captivity as infants (B. Salle, pers. com.); they therefore had minimal exposure to predators in the wild.

Predator presentations

The mandrills were exposed to leopard and crowned hawk-eagle models. The leopard models were constructed by attaching a 2D paper printout to a cardboard base of the same shape. The paper printouts were copies of high quality photographs of leopards that were enlarged to approximate the actual size of the animal. Round

rhinestone crystals were glued to the eyes of the models. These types of 2D models elicit natural antipredator behaviors (Coss et al., 2005; Stankowich and Coss, 2007). Most of the crowned hawk-eagle models were also constructed similarly. However, one of the eagle models had a plastic head and a cotton-filled fabric body with eagle markings and feathers (made by Carl Gage, Bio Models, Co.). A different model was used in each presentation.

The models were presented outside of the enclosure. The leopard models were placed face-up on the ground and were revealed by pulling forwards on a stick that was attached to the backside of the model. Most of the eagle models were presented by raising the models vertically on a levy system made of clear fishing line attached to tree branches. However, one of the eagle models glided across a clear fishing line that was connected to two posts. The person revealing these models was fully concealed within the dense understory surrounding the enclosure. The models were visible for about 30-45 sec.

For each presentation, at least one observer watched the reaction of the monkeys and another person revealed the predator model. All presentations were recorded with a Canon ZR-60 and/or Canon ZR-40 digital video camcorder (Canon USA, Inc., Lake Success, NY, USA). Before the predator model was revealed, the observer(s) recorded the position and identities of all visible monkeys; after the predator model was revealed, they recorded the behavioral responses of these visible monkeys. The response of each monkey was categorized as (1) running up a tree, (2) running into cover, or (3) remaining stationary and flinching. Because it was not usually possible to observe the behavioral responses of all visible monkeys during the actual presentation, the behavioral responses of many of the monkeys were scored from the video recordings. Audio recordings were made with a Tascam DA-P1 DAT recorder (Teac America, Montebello, California, USA) and Audio-Technica (Akron, Ohio, USA) AT4071a directional microphone.

Measurements and statistical analysis

The behavioral responses of the mandrills were compared between predator classes using Fisher's exact tests with a Bonferroni correction. Selected comparisons were made by pooling the responses of individuals to a given predator class into two categories (e.g., individuals running into trees versus all other behavioral categories). Only the responses of adult females and juveniles that were initially located on the mowed grass (open area without vegetation) were analyzed. Some individuals were exposed to the same predator class on multiple occasions; because these individuals always responded in the same way to a given predator, they were only counted once per predator type. The responses of individuals that were initially located in the trees or bushes were excluded because of low sample sizes. The responses of the dominant adult male were considered separately because they were different from those of the other age-sex classes; the other adult male of the group was never visible during the predator presentations so we have no information about his antipredator behaviors.

The alarm calling behavior of the mandrills was compared between treatments. Because we were rarely able to identify the individual that was vocalizing, the acoustic analyses are based on the pooled vocalizations from all individuals. Even though the alarm calls of mandrills are sometimes emitted in a series of two syllable

bles (Kudo, 1987), each syllable of an alarm call was considered a separate alarm call. Based on the audio recordings, we calculated the total number of alarm calls given within the first 10 sec of a predator presentation (call rate). We also calculated the total amount of time that mandrills emitted alarm calls (the difference between the last and first alarm call emitted; amount of time alarm calling). Mixed models (PROC MIXED) were used to analyze the call rate and amount of time alarm calling. All analyses were performed with SAS (SAS Institute 2003). Means and SE are provided in graphs to illustrate effect sizes.

Results

Four leopard and four eagle presentations were successfully conducted. More mandrills tended to run into the trees in the leopard compared to the eagle trials (Fisher's exact test: $p=0.0310$). More mandrills tended to run into the bushes in the eagle compared to the leopard trials ($p=0.0849$) (Table 1). The responses of the dominant adult male to the predator presentations differed (his responses were only visible for three leopard presentations and three eagle presentations). In two of the leopard presentations, he remained on the ground and paced back and forth while looking in the direction of the predator; in one of the presentations, he ran away after hearing the alarm calls but never turned to look at the leopard model. In the eagle presentations, he always remained stationary and sometimes also flinched.

Table 1: Behavioral responses of adult female and juvenile mandrills after seeing different predator types. All of these mandrills were initially located on the mowed grass (open area without vegetation) when the predator was presented.

Predator	Run into trees	Run into cover	Stationary and flinch
Leopard	6	0	0
Eagle	3	4	1

Mandrills emitted many alarm calls in response to the different predator classes. The call rate was higher in response to the leopard trials compared to the eagle trials ($F_{1,6}=23.07$, $p=0.003$; Fig. 1). Mandrills continued giving alarm calls for longer in response to the leopard trials compared to the eagle trials ($F_{1,6}=38.61$, $p=0.0008$; Fig. 2).

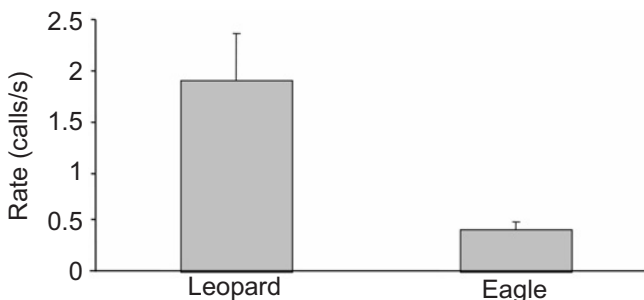


Fig. 1: Statistically significant difference in the rate of alarm calls between predator classes.

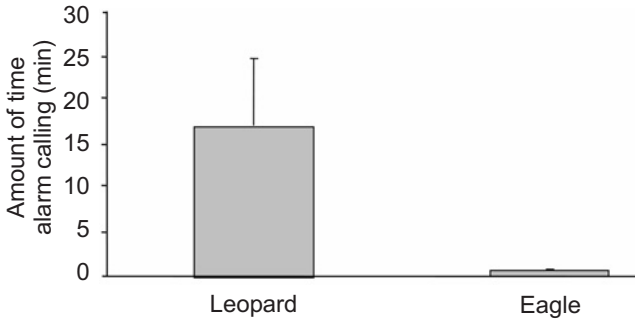


Fig.2: Statistically significant difference in the amount of time emitting alarm calls between predator classes.

Discussion and Conclusions

The results indicated that mandrills tended to run into trees for leopard presentations and to run into cover for eagle presentations. The mandrills emitted alarm calls at a higher rate and for longer amounts of time in the leopard presentations compared to the eagle presentations.

Leopards and eagles use different hunting techniques to capture primates (Mitani et al., 2001; Zuberbühler and Jenny, 2002). Many primates can evade leopard attacks by running into trees and eagle attacks by running into cover (Seyfarth et al., 1980). The behavioral responses of the mandrills were consistent with the hunting strategies of the predators presented.

The different predator classes likely represent different levels of danger to mandrills. Leopards likely represent a high level of danger to all age-sex classes because they are known to prey on juvenile and adult mandrills (Jouventin, 1975; Harrison, 1988). Crowned hawk-eagles may only prey upon juvenile and subadult mandrills (Jouventin, 1975; Lahm, 1985; Harrison, 1988) and therefore may not be dangerous to all group members. These different levels of danger could explain why the mandrills called at a higher rate and for longer amounts of time in the leopard presentations (higher overall danger) compared to the eagle presentations (lower overall danger).

The behavior of the dominant adult male of our group in response to the predator models was striking compared to the responses of the other mandrills. Rather than fleeing in response to seeing the leopard models, he remained in front of the leopards and paced back and forth; he also did not flee in response to the eagle models. Because male primates often serve an important role in defending against predators (Crook and Gartlan, 1966; van Schaik and van Noordwijk, 1989; Hill and Lee, 1998), it would be interesting to determine whether this behavior of a male mandrill is widespread within the species. This would be an especially interesting finding since it has been suggested that adult male mandrills contribute little to group protection because of their seasonal presence in mandrill hordes (Abernethy et al., 2002).

Although the mandrills had limited experience with natural predators, they still responded to all of the models. In particular, they responded to the models of leopards even though most of the mandrills had never seen this predator before. Their responses to the leopard models may represent a generalized response to novel, terrestrial animals rather than leopards per se (Yorzinski and Ziegler, 2007). Because

the mandrills continued alarm calling long after the leopard models were revealed, it is unlikely that their behaviors were simply startle responses. It would be informative to compare the responses of these mandrills to those in the wild. More research exploring the antipredator behaviors of mandrills could help us further understand their group dynamics.

Acknowledgements

We thank Jean Wickings and CIRMF for permitting us to conduct this research. Mark Laidre was extremely helpful in assisting with the predator presentations. Jean Wickings, Bettina Salle, and Olivier Bourry provided logistical support while in the field. CIRMF provided accommodation. Carl Hopkins, Jack Bradbury, John Sullivan, and Matt Arnegard offered useful advice about conducting research and traveling in Gabon. Greg Budney and Mark Reaves assisted us in borrowing recording equipment from the Cornell Laboratory of Ornithology and Carl Hopkins loaned us miscellaneous field equipment. Dieudonne Ofougou helped with some of the predator presentations. Mark Laidre and Andrew Marshall gave useful comments on the manuscript. Jerome Braun kindly assisted with the statistical analyses. This research followed the guidelines of the Cornell Institutional Animal Care and Use Committee. JLY was funded by a Cornell Presidential Research Scholars grant, an Andrew W. Mellon research grant, and a National Science Foundation Graduate Research Fellowship.

References

- Abernethy KA, White LJT, Wickings EJ (2002): Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. *J Zool* 258: 131-137.
- Cheney DL, Wrangham RW (1986): Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RM, Struhsakes RR (eds): Primate Societies. Chicago, University of Chicago Press: 227-239.
- Cords M (1990): Vigilance and mixed-species association of some East African forest monkeys. *Behav Ecol Sociobiol* 26: 297-300.
- Coss RG, Ramakrishnan U, Schank J (2005): Recognition of partially concealed leopards by wild bonnet macaques (*Macaca radiata*): the role of the spotted coat. *Behav Processes* 68: 145-163.
- Crook JH, Gartlan JS (1966): On the evolution of primate societies. *Nature* 210: 1200-1203.
- Feistner ATC, Cooper RW, Evans S (1992) The establishment and reproduction of a group of semifree-ranging mandrills. *Zoo Biol* 11:385-395.
- Fichtel C, Kappeler PM (2002): Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behav Ecol Sociobiol* 51: 262-275.
- Harrison MJ (1988): The mandrill in Gabon's rainforest: ecology, distribution and status. *Oryx* 22: 218-228.
- Hill RA, Dunbar RIM (1998): An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping patterns. *Behaviour* 135: 411-430.

- Hill RA, Lee PC (1998): Predation risk as an influence on group size in cercopithecoïd primates: implications for social structure. *J Zool* 245: 447-456.
- Isbell LA (2005): Predation on primates: ecological patters and evolutionary consequences. *Evol Anthro* 3: 61-71.
- Jouventin P (1975): Observations sur la socio-ecologie du mandrills. *La Terre et La Vie* 29: 493-532.
- Kirchhof J, Hammerschmidt K (2006): Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*): evidence from playback experiments. *Ethology* 112: 346-354.
- Kudo H (1987): The study of vocal communication of wild mandrills in Cameroon in relation to their social-structure. *Primates* 28: 289-308.
- Lahm SA (1985): Mandrill ecology and the status of Gabon's rainforests. *Primate Conservation* 6: 32-33.
- Manser MB (2001): The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proc R Soc Lond B* 268: 2315-2324.
- Manser MB, Bell MB, Fletcher LB (2001): The information that receivers extract from alarm calls in suricates. *Proc R Soc Lond B* 268: 2485-2491.
- Mitani JC, Sanders WJ, Lwanga JS, Windfelder TL (2001): Predator behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav Ecol Sociobiol* 49: 187-195.
- Pereira ME, Macedonia JM (1991): Ringtailed lemur antipredator calls denote predator class, not response urgency. *Anim Behav* 41: 543-544.
- Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, Tutin CEG (1996): Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. *Am J Primatol* 40: 297-313.
- SAS Institute (2003): SAS/STAT software. Version 9.1. SAS Institute Inc, Cary, North Carolina.
- Setchell JM, Wickings EJ, Knapp LA (2006): Life history in male mandrills (*Mandrillus sphinx*): physical development, dominance rank, and group association. *Am J Phys Anthropol* 131: 498-510.
- Seyfarth RM, Cheney DL, Marler P (1980) Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Anim Behav* 28: 1070-1094.
- Stanford CB (1998): Predation and male bonds in primate societies. *Behaviour* 135: 513-533.
- Stanford CB (2002): Avoiding predators: expectations and evidence in primate antipredator behavior. *Int J Primatol* 23: 741-757.
- Stankowich T, Coss RG (2007): The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *Proc R Soc B* 274: 175-182.
- Uster D, Zuberbühler K (2001): The functional significance of Diana monkey 'clear' calls. *Behaviour* 138:741-756.
- van Schaik, CP, van Noordwijk MA (1989): The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. *Behav Ecol Sociobiol* 24: 265-276.
- van Schaik CP, van Noordwijk MA, Warsono B, Sutriano E (1983): Party size and early detection of predators in Sumatran forest primates. *Primates* 24: 211-221.
- Yorzinski JY, Ziegler T (in press): Do naïve primates recognize the vocalizations of felid predators? *Ethology* 113: 1219-1227.

- Zuberbühler K (2000): Referential labeling in Diana monkeys. *Anim Behav* 59: 917-927.
- Zuberbühler K (2001): Predator-specific alarm calls in Campbell's monkeys, *Cerco-pithecus campbelli*. *Behav Ecol Sociobiol* 50: 414-422.
- Zuberbühler K, Jenny D (2002): Leopard predation and primate evolution. *J Hum Evol* 43: 873-886.

Corresponding author

Jessica Yorzinski, 2320 Storer Hall, Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, jyorzinski@ucdavis.edu