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BRIEF REPORT

Female Sooty Mangabeys (*Cercocebus torquatus atys*) Respond Differently to Males Depending on the Male’s Residence Status—Preliminary Data

FRIEDERIKE RANGE

Department of Psychology, University of Pennsylvania, Philadelphia, Pennsylvania

I tested the hypothesis that free-ranging female mangabeys (*Cercocebus torquatus atys*) differentiate between males depending on their residence status. Adult males in this species employ two group-membership strategies: they are either full-time residents or part-time residents (i.e., present for several weeks at a time, then gone for several weeks, then present again, etc.). In a playback experiment I tested whether adult females with young infants responded differently to calls of adult males that were group members during the previous mating season as compared to males that belonged to neighboring groups during the mating season or were complete strangers. Males whose calls were played were present residents, part-time residents (absent for at least 3 months), neighbors, or complete strangers. Because infanticide is a potential risk in mangabeys, I predicted that females would respond differently to males that had resided in the group when their infant was conceived than they would to those that had not been present. The females showed a clear difference in their reaction to the playbacks of vocalizations from resident and part-time resident males as opposed to nonresidents. Am. J. Primatol. 66:000–000, 2005. © 2005 Wiley-Liss, Inc.

Key words: recognition; memory; group membership; primates; playback experiments

INTRODUCTION

Individual recognition is thought to be a prerequisite for establishing and maintaining a complex social system with different relationships [Falls, 1982]. To date, many studies have provided evidence for individual recognition by acoustic cues in several species (e.g., birds [Hopp et al., 2001; Nowicki, 1983], bats

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Although individual recognition has received much attention, few studies have investigated the ability of animals to recognize and remember individuals in systems in which group members may be absent for long periods of time. Since most animals live in social groups that are not closed (e.g., males transfer and may return), recognition and memory of individuals that have not been encountered recently has important implications for the evolution of animal behavior (Godard, 1991; Mateo & Johnston, 2000; Stoddard, 1996).

Sooty mangabeys (*Cercocebus torquatus atys*) are terrestrial monkeys that live in West Africa. Whereas the females are philopatric, the males immigrate into other groups (Range & Noé, 2002). Within groups, adult males form linear dominance hierarchies, and although the highest-ranking male will attempt to monopolize receptive females, sneaky copulations are common (unpublished data). Although most aspects of male behavior in mangabeys resemble those observed in other monkey species, mangabeys differ with respect to their group-membership strategies. Some males are always resident, while others join and leave the group for several months at a time (Range et al., in press). These part-time residents are also often encountered in the center of the group, interacting with females and, during the mating season, copulating with them. Thus, it is likely that the females are familiar with these males.

Encounters with neighboring males occur frequently (once or twice a week), as do brief incursions by solitary unknown males (“strangers”). During encounters, nonresident males walk through the group for up to 30 min, displaying, grunting, and/or behaving aggressively toward females and infants. Since neighbors are encountered frequently, it is assumed that females recognize neighbors (as has been shown for vervets [Cheney & Seyfarth, 1982]).

Like other Old World monkey species, sooty mangabey females are exposed to the risk of infanticide from males (usually nongroup members) that are not potential sires [Busse & Gordon, 1983, unpublished data]. Females retrieve their infants more often in the presence of these males and react more aggressively toward nongroup members than toward potential fathers. However, whether females recognize part-time resident males that were present during the mating season but then absent for a long period of time is not clear. The different group-membership strategies pursued by males create social pressures such that it would be adaptive for females to remember the identities of former group members.

Here I describe a playback experiment designed to test whether adult females respond differently to calls from resident or part-time resident males (group members), and neighbors or strangers (nongroup members). The subjects were adult females with infants (<6 months old). If females categorize males according to their residence status, I predicted they would react less to the grunts of group members than they would to those of nongroup members. Equal responses toward grunts of neighbors and strangers were expected, since they both pose a potential infanticide risk. Because the females frequently heard the grunts of neighbors during group encounters, I assumed that they would be more familiar to the females compared to strangers (see also Cheney and Seyfarth [1982]). Thus, if the females’ responses were simply a function of familiarity vs. novelty, stronger responses toward strangers than neighbors were expected.

**MATERIALS AND METHODS**

The study was carried out on a group of free-ranging sooty mangabeys in the Tai National Park in Ivory Coast, where visibility ranges from 5 to 20 m. During
the time the playback experiments were conducted (April–August 2002), the
group consisted of six to 10 adult males, 34 adult females (six females with young
infants), and juveniles. All of the animals were well habituated to human
observers and had been individually recognized since 1998. Two other mangabey
groups whose ranges overlapped extensively with the study group’s home range
were partly habituated to humans. I could individually recognize three males
from one group and two males from the other group.

Beginning in September 2000, I recorded the presence of all males that were
with the group on observation days (total of 356 days). Moreover, I kept detailed
descriptions of all observed encounters with neighboring groups and stranger
males. I recorded 58 intergroup encounters. In 24 of those encounters, the groups
either avoided each other or fed next to each other. Thirty-four of the encounters
involved aggressive interactions, such as chasing, threatening, and fighting.
Moreover, 24 intrusions by strangers were recorded. In 18 cases I observed high
levels of aggression between the intruder and the males of the study group.

**Experimental Design**

In trials separated by at least 6 days, females with infants (<6 months old)
listened to the playback of a grunt vocalization from 1) a resident male; 2) a part-
time resident male that was present during the last mating season, but had been
absent for 3 months at the time of the experiment; 3) a male from a neighboring
group; or 4) a stranger that had never been seen in the study group, and thus was
assumed to be unfamiliar. Males in groups 1 and 2 were “group members” (e.g.,
potential sires), and males in groups 3 and 4 were “nongroup members” (e.g., not
potential sires).

I conducted four trials with each of the six subjects. In a given trial, one
grunting bout from a male belonging to one of the four subgroups was played back
to the subject. Each bout consisted of six to 13 grunts (average=8.13 grunts) and
was 2.06–2.92 sec long (average=2.33 sec). The sequence of the presented calls
was varied between females.

**Recording of Vocalizations**

Male grunts are low-amplitude vocalizations that are always given as bouts
and are individually distinguishable [Range & Fischer, 2004]. They are the most
frequent vocalizations of sooty mangabey males, and are mainly given in
nonaggressive interactions, such as greetings, or as contact calls during foraging.
The grunts were recorded with a Sony-DAT PCM-M1 recorder and a Sennheiser
directional microphone (ME 68). The vocalizations of resident males (two males,
two grunting bouts each), a neighboring male (one grunting bout), and a stranger
(two different grunting bouts from one male) were recorded within 4–8 weeks of
the playback experiments. Vocalizations of the part-time resident (three grunting
bouts from one male) were recorded approximately 9 months before the
experiments were conducted. Grunts from the stranger were obtained from an
adult male in a group that lived well outside the study group’s home range (>3
km). All grunts were recorded while the male emitting the call was foraging in its
own group. While the grunts were recorded, nearby group members (including
females) occasionally responded with a grunt themselves, or looked briefly in the
direction of the male, but in all cases continued to feed or rest. The playback
amplitude was set to mimic an adult male grunting at a distance of 5–7 m (50 dB
at 2 m).
Playback Experiments and Analysis

Trials were conducted opportunistically in contexts assessed as relaxed (i.e., no alarm calls within 60 min, and no intergroup encounter that day). The females were required to be sitting and feeding or resting with no other possible female subject closer than 20 m. When I played the call of a resident male, no interaction between the subject and the male had occurred for at least 5 min, and the male had to be at least 20 m away. The speaker was placed on a line between the subject and the male. Once these conditions were met, the playback equipment (a Sony-DAT PCM-M1 recorder and a Nagra battery-powered loudspeaker) was placed 4–7 m away from the subject. The playback was initiated when the subject had been looking away from the loudspeaker for at least 10 sec and was facing in the opposite direction. I filmed the behavior of the subject using a Sony DCR-PC5 digital camcorder for 10 sec prior to playback and 10 sec thereafter. After the call was played back, the subject was followed for 15 min, and looks toward the speaker (scanning) were recorded. Since the speaker was not always hidden, I often went through the experimental protocol without playing a vocalization to ensure that the subjects did not associate the setup of the experiment with an impending vocalization.

Responses to playback were analyzed on a frame-by-frame basis with the use of a frame accurate digital video recorder (Sony DSR-30). I assigned a random code to the digitized video clips (25 frames \(^{-1}\)) and marked the onset of the calls. Responses were then scored blind to the experimental design with the audio channel turned off. I measured the latency to respond (time between onset of call and onset of response), the duration of looks toward the speaker (at least 90\(^\circ\)), and the time required to settle down (defined as the time it took for individuals to return to their prior activity).

Statistics and Sample Size

Statistical analyses were performed with SPSS (version 7.5.1.). All tests were one-tailed, since the predictions were directional. Alpha was set at 0.05, and trends were reported for 0.1 > alpha > 0.05. For multiple comparisons, I used the post hoc tests for Friedman ANOVAs as described in Siegel and Castellan [1988].

Because of the political situation in Ivory Coast in 2002–2003, I was unable to return for the second field season, and thus had to conduct the experiment with only six females rather than 14 as planned. Moreover, because few part-time resident males were available during the study period, and it was difficult to obtain high-quality recordings of nonhabituated males, the vocalizations used for playbacks were drawn from only one male per category (except for resident male, for which I obtained calls from two different males). The responses of the females toward the two different resident males were similar and thus were lumped.

RESULTS

Overall, there was a significant difference in duration of looking toward the speaker when the subjects heard calls from the different males (Friedman, df=3, \(P<0.008\)). Post hoc paired comparisons showed a significantly weaker response to the vocalizations of the part-time resident (mean \(\pm SD=0.12\pm0.20\) sec) compared to the neighbor’s vocalization (mean \(\pm SD=2.43\pm2.11\) sec), and a trend toward a weaker response to the resident males (mean \(\pm SD=0.27\pm0.53\) sec) compared to the neighbor. The shorter duration of looking after hearing the stranger (mean \(\pm SD=1.15\pm0.52\) sec) compared to the neighbor is partly due to the fact
that most females got up immediately and left their position when they heard the call.

The overall difference in time taken to settle down after responding to the four experimental conditions was significant (Friedman, df=3, $P<0.002$). Post hoc comparisons revealed significant pairwise differences in the responses to calls of nongroup members (neighbor: mean $\pm$ SD = 10.74 $\pm$ 10.37 sec; stranger: mean $\pm$ SD = 10.21 $\pm$ 6.18 sec) vs. group members (resident: mean $\pm$ SD = 0.85 $\pm$ 1.62 sec; part-time resident: mean $\pm$ SD = 1.13 $\pm$ 2.14 sec).

I also found, across the experimental conditions, an overall significant difference in the latency to react (Friedman, df=3, $P<0.01$). In post hoc tests, significant differences were obtained between the responses to the resident male (mean $\pm$ SD = 10.70 $\pm$ 6.77 sec) and both responses to the neighbor (mean $\pm$ SD = 2.66 $\pm$ 5.66 sec) and the stranger (mean $\pm$ SD = 1.61 $\pm$ 1.59 sec). The average latency ($\pm$ SD) toward calls of part-time residents was 10.16 $\pm$ 7.50 sec.

Finally, the females also showed significant differences in the number of times they scanned the area around them (Friedman, df=3, $P<0.009$). Post hoc comparisons revealed a significant difference between the responses to the resident males (mean $\pm$ SD = 0.0 $\pm$ 0.0) and the neighbor (mean $\pm$ SD = 4.5 $\pm$ 3.0), and a trend toward a difference between the responses to the part-time male (mean $\pm$ SD = 0.1 $\pm$ 0.4) and the neighbor. The average ($\pm$ SD) number of scans after calls from strangers was 2.0 $\pm$ 2.4.

**DISCUSSION**

The playback experiments showed no difference in the responses of female sooty mangabeys toward the grunts of a resident or part-time resident male, or toward the grunts of a neighbor or stranger. However, the females differed significantly in their responses to the grunts of group members and nongroup members. These preliminary results suggest that female sooty mangabeys can differentiate between group members and nongroup members, even if a group member has been absent for several months. The recognition of a male’s residence status is likely to be based on past social interactions. Group members are considered to be different from nongroup members because females have associated, groomed, and copulated with them. Memory of the vocalizations of familiar conspecifics for up to 1 year has been demonstrated for great tits (*Parus major*) [McGregor & Avery, 1986] and hooded warblers (*Wilsonia citrina*) [Godard, 1991]. In previous studies, female elephants remembered the vocalizations of a family member for up to 23 months after it died [McComb et al., 2000], and Northern fur seals remembered their mother’s call for 4 years after they were separated [Insley, 2000].

No significant difference in the reaction of females toward the grunts of a neighbor and a stranger was found. This may be surprising in the light of the extensive literature on neighbor–stranger recognition in birds [e.g., Beecher et al., 1996; Godard, 1991; Molles & Vehrencamp, 2001] and amphibians [e.g., Bee & Gerhardt, 2002]. However, for female sooty mangabeys with infants, neighbors and strangers represent equal infanticidal threats. Another possible explanation is that sooty mangabeys (unlike, for example, vervet monkeys [Cheney & Seyfarth, 1982]) do not recognize their neighbors by voice. However, if future experiments show that sooty mangabeys do recognize their neighbor’s voice, these results would suggest that females do not base their behavioral response on familiarity alone, but categorize males according to some other dimension—possibly infanticidal risk.
Even though past interactions may facilitate the recognition of group vs. nongroup members, individual females may perceive group members differently. For example, in 2001, two of the subjects associated equally often with the resident and the part-time resident male, two other subjects clearly preferred the resident male over the part-time resident male, and the latter two females associated more with the part-time resident male (unpublished data). Moreover, even when preferences were the same, the time females spent associating with the same male sometimes varied from 15% to 40%. In 2002, females also varied extensively in association time spent with the two resident males. One female spent up to 54% of the observation time with one male, whereas another female spent as little as 13% of the time with the same male. These differences in female–male association also argue against the problem of pseudoreplication in this study. Even though vocalizations from the same individuals were used, the subjects associated at different rates with the males, and therefore familiarity might have differed. Nonetheless, responses across group and nongroup members were significant, suggesting that differences in association rate did not affect female responses to males of different residence status.

Because of problems related to pseudoreplication and the small sample size in this study, the results provide only preliminary evidence that female sooty mangabeys differentiate between group members and nongroup members. Further experiments will have to be conducted to elucidate female mangabeys’ knowledge about male residence status.

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REFERENCES


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