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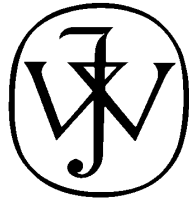
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7 BRIEF REPORT

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

15 FRIEDERIKE RANGE*

17 *Department of Psychology, University of Pennsylvania, Philadelphia, Pennsylvania*

19 I tested the hypothesis that free-ranging female mangabeys (*Cercocebus*
21 *torquatus atys*) differentiate between males depending on their residence
23 status. Adult males in this species employ two group-membership
25 strategies: they are either full-time residents or part-time residents
27 (i.e., present for several weeks at a time, then gone for several weeks,
29 then present again, etc.). In a playback experiment I tested whether adult
31 females with young infants responded differently to calls of adult males
33 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.*
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35 **Key words: recognition; memory; group membership; primates;**
37 **playback experiments**

39 **INTRODUCTION**

41 Individual recognition is thought to be a prerequisite for establishing
43 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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2 / Range

1 [Wenrick-Boughman, 1997], marine mammals [Weilgart & Whitehead, 1997], and Q6
3 primates [Cheney & Seyfarth, 1982]). Although individual recognition has received
5 much attention, few studies have investigated the ability of animals to recognize
7 and remember individuals in systems in which group members may be absent for
9 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
11 have not been encountered recently has important implications for the evolution of
13 animal behavior [Godard, 1991; Mateo & Johnston, 2000; Stoddard, 1996].

15 Sooty mangabeys (*Cercocebus torquatus atys*) are terrestrial monkeys that
17 live in West Africa. Whereas the females are philopatric, the males immigrate into
19 other groups [Range & Noë, 2002]. Within groups, adult males form linear
21 dominance hierarchies, and although the highest-ranking male will attempt to
23 monopolize receptive females, sneaky copulations are common (unpublished
25 data). Although most aspects of male behavior in mangabeys resemble those
27 observed in other monkey species, mangabeys differ with respect to their group-
29 membership strategies. Some males are always resident, while others join and
31 leave the group for several months at a time [Range et al., in press]. These part-
33 time residents are also often encountered in the center of the group, interacting
35 with females and, during the mating season, copulating with them. Thus, it is
37 likely that the females are familiar with these males. Q1

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

51 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

Recognition of Male Residence Status / 3

1 the time the playback experiments were conducted (April–August 2002), the
3 group consisted of six to 10 adult males, 34 adult females (six females with young
5 infants), and juveniles. All of the animals were well habituated to human
7 observers and had been individually recognized since 1998. Two other mangabey
9 groups whose ranges overlapped extensively with the study group's home range
11 were partly habituated to humans. I could individually recognize three males
13 from one group and two males from the other group.

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

Experimental Design

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

47 I conducted four trials with each of the six subjects. In a given trial, one
49 grunting bout from a male belonging to one of the four subgroups was played back
51 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

53 Male grunts are low-amplitude vocalizations that are always given as bouts
55 and are individually distinguishable [Range & Fischer, 2004]. They are the most
57 frequent vocalizations of sooty mangabey males, and are mainly given in
59 nonaggressive interactions, such as greetings, or as contact calls during foraging.
61 The grunts were recorded with a Sony-DAT PCM-M1 recorder and a Sennheiser
63 directional microphone (ME 68). The vocalizations of resident males (two males,
65 two grunting bouts each), a neighboring male (one grunting bout), and a stranger
67 (two different grunting bouts from one male) were recorded within 4–8 weeks of
69 the playback experiments. Vocalizations of the part-time resident (three grunting
71 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).

4 / Range

1 Playback Experiments and Analysis

3 Trials were conducted opportunistically in contexts assessed as relaxed (i.e.,
5 no alarm calls within 60 min, and no intergroup encounter that day). The females
7 were required to be sitting and feeding or resting with no other possible female
9 subject closer than 20 m. When I played the call of a resident male, no interaction
11 between the subject and the male had occurred for at least 5 min, and the male
13 had to be at least 20 m away. The speaker was placed on a line between the
15 subject and the male. Once these conditions were met, the playback equipment (a
17 Sony-DAT PCM-M1 recorder and a Nagra battery-powered loudspeaker) was
19 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.

21 Responses to playback were analyzed on a frame-by-frame basis with the use
23 of a frame accurate digital video recorder (Sony DSR-30). I assigned a random
25 code to the digitized video clips (25 frames⁻¹) and marked the onset of the calls.
27 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°), and
the time required to settle down (defined as the time it took for individuals to
return to their prior activity).

29 Statistics and Sample Size

31 Statistical analyses were performed with SPSS (version 7.5.1.). All tests were
33 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
35 post hoc tests for Friedman ANOVAs as described in Siegel and Castellan [1988].

37 Because of the political situation in Ivory Coast in 2002–2003, I was unable to
39 return for the second field season, and thus had to conduct the experiment with
41 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
43 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.

45 RESULTS

47 Overall, there was a significant difference in duration of looking toward the
49 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
51 the vocalizations of the part-time resident (mean \pm SD = 0.12 ± 0.20 sec) compared
to the neighbor's vocalization (mean \pm SD = 2.43 ± 2.11 sec), and a trend toward a
weaker response to the resident males (mean \pm SD = 0.27 ± 0.53 sec) compared to
the neighbor. The shorter duration of looking after hearing the stranger
(mean \pm SD = 1.15 ± 0.52 sec) compared to the neighbor is partly due to the fact

Recognition of Male Residence Status / 5

1 that most females got up immediately and left their position when they heard the
2 call.

3 The overall difference in time taken to settle down after responding
4 to the four experimental conditions was significant (Friedman, $df=3$,
5 $P<0.002$). Post hoc comparisons revealed significant pairwise differences in
6 the responses to calls of nongroup members (neighbor: $\text{mean} \pm \text{SD}=10.74 \pm 10.37$
7 sec; stranger: $\text{mean} \pm \text{SD}=10.21 \pm 6.18$ sec) vs. group members (resident:
8 $\text{mean} \pm \text{SD}=0.85 \pm 1.62$ sec; part-time resident: $\text{mean} \pm \text{SD}=1.13 \pm 2.14$ sec).

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

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

22 DISCUSSION

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

39 No significant difference in the reaction of females toward the grunts of a
40 neighbor and a stranger was found. This may be surprising in the light of the
41 extensive literature on neighbor-stranger recognition in birds [e.g., Beecher et al.,
42 1996; Godard, 1991; Molles & Vehrencamp, 2001] and amphibians [e.g., Bee &
43 Gerhardt, 2002]. However, for female sooty mangabeys with infants, neighbors
44 and strangers represent equal infanticidal threats. Another possible explanation
45 is that sooty mangabeys (unlike, for example, vervet monkeys [Cheney &
46 Seyfarth, 1982]) do not recognize their neighbors by voice. However, if future
47 experiments show that sooty mangabeys do recognize their neighbor's voice,
48 these results would suggest that females do not base their behavioral response on
49 familiarity alone, but categorize males according to some other dimension-
50 possibly infanticidal risk.

6 / Range

1 Even though past interactions may facilitate the recognition of group vs.
2 nongroup members, individual females may perceive group members differently.
3 For example, in 2001, two of the subjects associated equally often with the
4 resident and the part-time resident male, two other subjects clearly preferred the
5 resident male over the part-time resident male, and the latter two females
6 associated more with the part-time resident male (unpublished data). Moreover,
7 even when preferences were the same, the time females spent associating with the
8 same male sometimes varied from 15% to 40%. In 2002, females also varied
9 extensively in association time spent with the two resident males. One female
10 spent up to 54% of the observation time with one male, whereas another female
11 spent as little as 13% of the time with the same male. These differences in female-
12 male association also argue against the problem of pseudoreplication in this
13 study. Even though vocalizations from the same individuals were used, the
14 subjects associated at different rates with the males, and therefore familiarity
15 might have differed. Nonetheless, responses across group and nongroup members
16 were significant, suggesting that differences in association rate did not affect
17 female responses to males of different residence status.

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

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Recognition of Male Residence Status / 7

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