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A Preliminary Study of Selective Visual Attention in Female Mountain Gorillas (*Gorilla gorilla beringei*)

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ABSTRACT. Visually attending to conspecifics can give group-living primates important ecological information, help them to anticipate the behavior of others and to regulate interactions with them, and provide other valuable social information. Variation in the importance and quality of social relationships should influence the way individuals selectively attend to fellow group members. Preliminary data on visual monitoring of conspecifics by wild female mountain gorillas (*Gorilla gorilla beringei*) show that selective attention mirrors variation in social relationships. Social bonds between males and females are central to gorilla society; correspondingly, females are more likely to stop feeding and focus their attention on males who walk into view than on females, especially when males give displays. Females are more likely to focus on other females with whom they have antagonistic relationships than those (mostly close relatives) with whom they have affiliative, cooperative ones. Further research on the context and consequences of visual monitoring could help to address questions about the regulation of social relationships and about social cognition in gorillas.

Key Words: Mountain gorillas; Attention; Visual monitoring; Social relationships.

INTRODUCTION

Gregarious diurnal primates can gain important social and ecological information by visually monitoring conspecifics (ALTMANN, 1967; CHANCE, 1967; VAN SCHAIK et al., 1983; STRAYER & GARIEPI, 1986; CAINE & MARRA, 1988). Monitoring allows them to identify neighbors and to note their location and activities. Correspondingly, individuals who are the objects of others' attention can directly or indirectly provide information via facial expressions, head and body orientation, vocalizations, posture, and other means (ALTMANN, 1967; GREEN & MARLER, 1979). Visual information can be purely informational or "adventitious" (i.e. influence the observer's behavior without codified signals: GREEN & MARLER, 1979) or can be communicative (i.e. involve signals designed to influence others' behavior: GOMEZ, 1994). Adventitious information can help individuals to predict whether neighbors will initiate interactions with them, and what kinds of interaction, and to decide whether, and how, to interact with them. It also may help them to anticipate and suppress interactions between their rivals (BYRNE & WHITEN, 1992).

Individuals usually have differentiated social relationships with others in their groups. Relationship quality and history can influence responses to visual information. For example, a baboon female may respond differently to an unrelated, higher-ranking female who enters her field of view than to her daughter, to a male friend, or to a recently-immigrated and unfamiliar male (SMUTS, 1985). Failure to attend to her daughter would probably not be costly; failure to focus on a higher-ranking female could lead to a mild threat or a fight; failure to focus on a

newly-immigrated male could increase her exposure to physical aggression and her infant's vulnerability to infanticide.

Visual monitoring may also give individuals useful information about others' attention. Great apes can use others' visual attention to direct their own and to get information (BYRNE, 1995; GOMEZ, 1996; POVINELLI & EDDY, 1996a, b), and can use eye contact to draw others' attention to their own attention (GOMEZ, 1996). They may vary attempts to signal their own intentions depending on whether they have a target's visual attention (TANNER & BYRNE, 1996). No compelling evidence exists that great apes attribute mental states to others on the basis of visual attention, but simply "reading" attention could be socially advantageous in many ways (POVINELLI & EDDY, 1996a, b).

Here, I present data from a preliminary study of visual monitoring by mountain gorillas (*Gorilla gorilla beringei*). Mountain gorillas are gregarious primates with variable dispersal by both sexes. Closely related females who reside together maintain long-term affiliative and cooperative relationships, but female natal and secondary transfer are common and groups usually contain mostly unrelated females whose relationships are neutral to hostile (HARCOURT, 1979a; STEWART & HARCOURT, 1987; WATTS, 1994a, 1996). Female dyads often lack dominance relationships, and aggression in many dyads is common in both directions (WATTS, 1994b). This may lend unpredictability to approaches between females, especially those with hostile relationships. Females typically spend more time close to adult males (silverbacks) and have more affiliative interactions with their top male partners than with most or all females. However, they also typically receive more aggression from males than from most or all females, although male aggression less often involves damaging physical contact (HARCOURT, 1979b; STEWART & HARCOURT, 1987; WATTS, 1992, 1994b). Given the social importance of silverbacks and of variation in relationships between females, I predicted that: 1) Adult females attend more to silverbacks than to females who enter their field of view, and more often follow silverbacks; and 2) Adult females pay more attention to other females with whom they have bad social relationships than to those with whom their relationships are good.

METHODS

STUDY SITE AND SUBJECTS

I collected the data at the Karisoke Research Centre in June–August 1991 and June–August 1992. Karisoke is in the Parc National des Volcans, Rwanda, and has been the site of research on mountain gorilla ecology, behavior, and life histories since 1966. The study area extends into the adjacent Parc des Virungas, Zaire and comprises a mix for bamboo forest, *Hagenia–Hypericum* woodland, Afro-alpine vegetation, and other types of tropical moist montane vegetation.

The data come from Karisoke Group 5 and Group B. Group 5 had 4 silverbacks (all natal males) and 12 adult and adolescent females. Four females had been born in the group and were maternal and/or paternal relatives; seven were known immigrants; and one had been present as an adult in 1966 and was the mother of three of the natal females. Group B had two silverbacks and seven adult females, including two mother-daughter pairs. The daughters and two other females were presumed paternal half-sisters, while other females were unrelated (WATTS, 1992, 1994a).

Data Collection

The data concern female responses to the appearance of others in their visual fields. I collected them opportunistically during focal samples on females, along with continuous data on social interactions (e.g. agonistic behavior: Watts, 1994b). An "appearance" was an approach by a second individual to within 5m of the focal female, while she was seated and in which the approacher came from behind her and crossed an imaginary line perpendicular to her direct line of sight. I used only approaches when focal females were feeding and in which the vegetation was sufficiently open that focal females could see approachers clearly if they looked. In analyzing the effects of sex and relationship quality on responses, I omitted appearances if the approacher had vocalized within the preceding five seconds. Mountain gorilla short range vocalizations convey information on proximity tolerance, likely changes in activity state, and, probably, individual identity (Stewart & Harcourt, 1994; Harcourt & Stewart, 1996), and could provide much of the information available from looking at approachers. I analyzed appearances accompanied by "cough grunts" (mildly aggressive vocalizations: Harcourt & Stewart, 1996) or displays separately.

In the field, I categorized responses as:

1) *None*: Focal subject does not look at the approacher.

2) *Glance*: Focal subject gazes at approacher for up to about one second, without fixing her gaze on them and without interrupting feeding or food processing.

3) *Look*: Focal subject gazes at approacher for more than one second, with no change in posture or orientation except, perhaps, to turn her head, and without interrupting feeding.

4) *Watch*: Focal subject orients towards approacher and fixes her gaze on them for more than one second, tenses, and interrupts activity (females sometimes stood while watching the approacher).

However, I combined the first three categories in the analyses, and classified responses as "watch" and "other."

I also calculated the percentages of appearances after which females "followed" approachers — i.e. watched, then immediately stood and walked after approachers who were moving away.

I noted the identity of the approacher for every appearance. A focal female had a "good" relationship with a female approacher if she had more affiliative than agonistic interactions with her and interacted affiliatively with her at a rate above her median with all females, and/or if they gave each other agonistic support. Otherwise their relationship was "bad." Although not all bad relationships were markedly antagonistic, this category includes all females who had serious fights; no partners with good relationships fought seriously. Neither group had a female dominance hierarchy, and most female dyads did not have clearly decided agonistic relationships (Watts, 1994b).

I used paired *t*-tests (with each female paired against herself) to test predictions. The dependent variable was the arcsine-transformed percentage of appearances in which females watched approachers. Sex of approacher and, for females, relationship quality were independent variables. Tests were of directional predictions, and were thus one-tailed. I included all

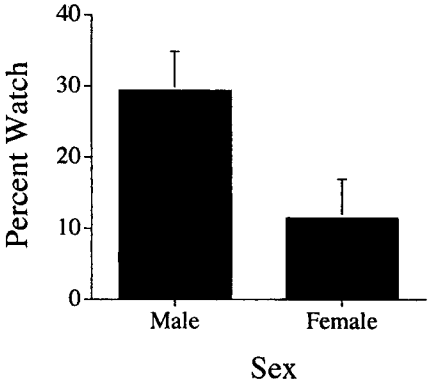

Fig. 1. Percent of appearances by males and by females to which focal females responded by watching the approaching individual (see text for definitions).

females for whom I had at least 100 non-aggressive appearances by females and 50 by males, and 50 and 25 aggressive appearances, respectively (Group 5: $n=10$; Group B: $n=7$).

RESULTS

SEX OF APPROACHER

Females were significantly more likely to watch males as they appeared than to watch other females as they appeared (Fig. 1: $t=15.73$, $df=16$, $p<0.001$). All females watched males more often than they watched females.

Females were also significantly more likely to follow males after they appeared than they were to follow females after they appeared (Fig. 2: $t=8.72$, $df=16$, $p<0.001$). All females followed males more than they followed other females.

Females were particularly likely to watch males when males displayed as they appeared, and

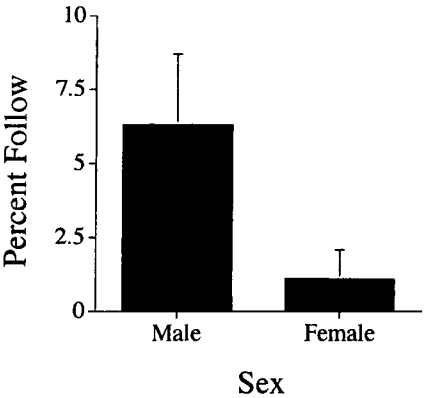

Fig. 2. Percent of appearances by males and by females to which focal females responded by stopping their feeding and following the individual who had approached. Column height indicates the mean for 17 females in the two study groups. Bars indicate 1 s.d.

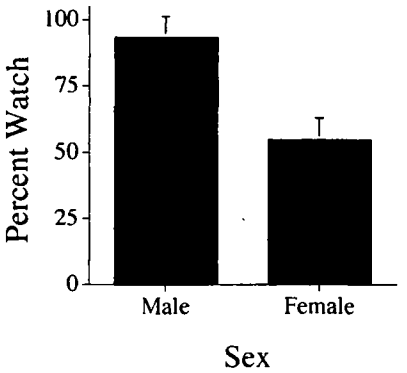

Fig. 3. Percent of appearances by males and by females to which focal females responded by watching the approaching individual, when that individual gave a display or a mildly aggressive vocalization as it approached. See Figure 2 for caption.

were significantly more likely to watch males than females when appearances were accompanied by aggression (Fig. 3: $t=10.61$, $df=16$, $p<0.001$). All females more often watched males than other females.

Effects of Relationship Quality

Females were significantly more likely to watch females with whom they had bad relationships than those with whom they had good relationships (Fig. 4: $t=6.67$, $df=16$, $p<0.001$). All females watched other females with whom they had bad relationships more often.

Females with bad relationships often appeared tense, both as approachers and when the others approached them, even when they made no eye contact or no visual contact at all. For example, *Sb*, a Group 5 immigrant, and *Pu*, a natal female, directed aggression at each other at relatively high rates (Watts, 1994a). In 1991, I once watched *Sb* as she approached *Pu* from behind while *Pu* fed. *Sb* stopped several meters from *Pu*, who did not respond and almost certainly had not seen her. She watched *Pu* closely and scratched herself repeatedly (an indication

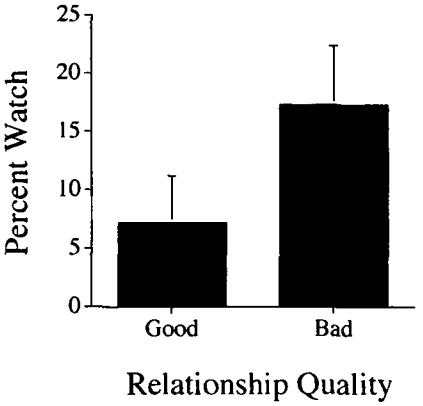

Fig. 4. Percent of appearances by females to which focal females responded by watching the approaching individual, partitioned according to relationship quality (see text for definitions). See Figure 2 for caption.

of tension: MAESTRIPIERI et al., 1992). When *Pu* stopped feeding and lay supine to rest, *Sb* quickly and calmly passed her.

DISCUSSION

Female mountain gorillas are often close to other group members while they feed, an activity that occupies about 50% of daylight hours (WATTS, 1988). However, females may lack visual information about neighbors until they walk into sight at close range because of the dense ground cover. Females make no overt response to such many approaches, or just glance briefly and perhaps briefly turn their heads. However, they are more likely to stop feeding and to focus their attention on approaching adult males than females. They watch approaching females more often if the females give aggressive acts or signals, but less often than males: females almost always stop feeding and focus intently on males who display or give mildly aggressive vocalizations within 5m. Also, they fairly often leave feeding spots to follow males who walk by, but rarely follow females. Finally, females more often focus their attention on approaching females with whom they often interact aggressively, infrequently interact affiliatively, and do not exchange agonistic support, than on those with whom their relationships have the opposite characteristics.

These results reinforce others that show the social centrality of males for females. For example, females usually stay close to males and bear most responsibility for proximity maintenance (HARCOURT, 1979b; WATTS, 1992). They react submissively to more non-aggressive approaches by males than by other females, and respond to most male displays with submissive and reassurance seeking behavior (WATTS, 1995). Males usually lead group movements (SCHALLER, 1963; STEWART & HARCOURT, 1994; BYRNE, in press; WATTS, in press). When females interrupt feeding at the approach of males, they may be anticipating possible decisions to move as well as possible interactions with the males.

Agonistic relationships between female mountain gorillas are often unresolved and unpredictable (WATTS, 1994b). Much aggression, including opposition in polyadic conflicts, is bidirectional, and females frequently retaliate against each other; this was true for many female dyads in Groups 5 and B (ibid.: WATTS, 1997). Close proximity between females with antagonistic relationships carries a risk of fights in which one or both opponents can be wounded (ibid.). Serious aggression is uncommon between some other females, especially co-resident relatives, who have more tolerant relationships and may be allies. Visual monitoring varies correspondingly, as if approaches by antagonistic partners are more threatening than those by more friendly partners.

Other researchers have documented social effects on the rate, amount, and/or quality of visual monitoring in primate groups. Differential visual monitoring of approaching males by female anubis baboons resembles the differential response of mountain gorilla females to other females (SMUTS, 1985): females are much more nervous with non-"friends" than with "friends"; they and their infants are at less risk of aggression from friends, who, in fact, protect them against other males and females. CAINE and MARRA (1988) found that the time that captive squirrel monkeys (*Saimiri sciureus*) devoted to "social looking" during a foraging experiment varied inversely with rank; they argued that all individuals needed to monitor others frequently to maintain dyadic or subgroup affiliation, but that low-ranking individuals particularly needed to do so to avoid aggression (cf. STRAYER & GARIEPI, 1986). Tamarins (*Saguinus labiatus*), in which aggression rates are lower and cooperation more important, did less social looking in the same situation (CAINE & MARRA, 1988). Among Amboseli yellow baboons, infant daughters of low-ranking females in had particularly high glance rates; they received

more aggression, and less effective agonistic support, than daughters of higher-ranking females. Predation risk also seemed to influence glance rates ALBERTS (1994).

Unresolved questions about gorilla visual monitoring include: 1) How activity state, group size, sex, and relationship quality affect time spent in social looking and monitoring rates; 2) How watching varies within female dyads in correspondance with variation in female agonistic relationships. For example, if two females have a resolved dominance relationship, or an unclear one in which the rate of aggression is considerably higher in one direction, the subordinate female/more common target of aggression may watch her partner more than the reverse; 3) How often individuals make eye contact, and how its consequences vary among social partners; 4) How often and how, individuals use the attention of others to redirect their own. Do they use attentional contact (GOMEZ, 1994) to try to redirect others' attention, or to modify their own behavior in predictable ways? Gorillas can understand that humans who are not visually attending to their communicative acts will not respond to them (GOMEZ, 1994, 1996). They may also understand that in situations in which another's behavior could affect them adversely, this will not happen, and they can ignore the other, if its visual attention is not on them; and 5) How do gorillas integrate visual and vocal information to regulate inter-individual spacing and coordinate group movements (cf. STEWART & HARCOURT, 1994)? Study of "double grunts," which seem to announce presence, to attract attention, and to give information about conditional future activities (ibid.), would be particularly valuable in this regard.

Such data, particularly on attention monitoring, would provide a rich naturalistic background for the controlled, experimental studies of great ape cognition possible in lab settings (e.g. GOMEZ, 1996; POVINELLI & EDDY, 1996a, b).

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