SHORT COMMUNICATION

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Male–immature interactions seem to depend on group composition in white-headed langur (*Trachypithecus leucocephalus*)

Abstract In primates, male–immature interactions are always multifacetted. We studied male–immature interactions of white-headed langur during our long-term study in Nongguan White-Headed Langur Reserve, Guangxi, China. Male–immature interactions obviously differed between one-male groups and male–immature groups. In one-male groups, adult males behaved tolerantly or aggressively towards immatures and never carried out sociopositive behaviors. Sexual selection theory supports this phenomenon because males are predicted to bias to compete for more mating chances but not to invest in any single offspring. In male–immature groups, however, adult males carried out sociopositive behaviors and never behaved aggressively towards immatures. This is supported by kin selection theory because it will be beneficial for the males to increase the survival of the immatures if they are likely the fathers of them. Thus, we conclude that male–immature interactions differ between one-male groups and male–immature groups because the mating status of males are different between the two kinds of groups.

Keywords One-male group · Male–immature group · Aggression · Affiliation

Introduction

The average mammalian male and female live largely separate lives. Due to the inherent female bias toward infant care as a result of internal gestation and female-only lactation, male mammals generally benefit more from pursuing additional matings than from caring for their offspring (Maynard Smith 1977; Clutton-Brock and Parker 1992; Hawkes et al. 1995). But in most primate groups, males live permanently with females and their offspring (van Schaik and Kappeler 1997) providing ample opportunity for males to interact with immature individuals.

Data indicated tremendous interspecific variation in male–immature interactions (Taub 1980; Silk and Samuels 1984; Whitten 1987; Menard et al. 2001). Males in some monogamous species, such as titi monkeys, night monkeys, marmosets, tamarins, and siamangs, carry out a high amount of direct paternal care (Whitten 1987; Heymann 2000). But intensive caretaking is not always correlated with paternity. Occasional affiliation between males and immatures has been reported in howler monkeys, macaques, baboons, and gorillas. Male Barbary macaques exhibit a "care-then-mate" pattern indicating male–infant caretaking is a mating strategy but not paternal investment in this species (Menard et al. 2001). The triadic interactions of baboons and macaques are probably the most controversial of all male–immature interactions among primates. These interactions have been termed as agonistic buffering (Deag and Crook 1971) or infant exploitation (Strum 1984), but still remain controversial.

Evidences also showed strong intraspecific variation of male–immature interactions. For example, in Hanuman langur one-male groups, males have an indifferent attitude towards their offspring (Sugiyama 1965; Hrdy 1974). But in some one-male groups and multimale groups, males will protect infants in infanticide events, and the protections seem correlated with high possibility of paternity (Borries 1997; Borries et al. 1999; Broom et al. 2004). But Boggess' (1982) study in Hanuman langur showed that interactions between the adult and immature males in one-male groups were considerably more relaxed than in multimale groups.

Sexual selection theory and kin selection theory make different predictions in male–immature interactions. According to sexual selection theory, males are thought biased toward the production of many offspring and against substantial investment in any single offspring (Trivers 1972). Kin selection theory, however, predicts paternal investment because individuals increase their fitness from

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the survival of their close relatives (Hamilton 1964). Nevertheless, the two theories are not mutually exclusive to each other because a male can invest in mating effort and at the same time in parental care.

White-headed langur (*Trachypithecus leucocephalus*) is a rare primate species only found in southwest Guangxi, China. Former studies have suggested various kinds of social groups in white-headed langur, including breeding groups (i.e., one-male groups), nonbreeding groups (multi-male groups, male–immature groups, all male band, etc.), and solitary males (Ran 2003). This study includes one-male groups and male–immature groups.

A male–immature group includes one adult male, subadult males (if exist), and immatures. Because male–immature groups have no adult females in them, they are considered nonbreeding group. In other langurs, ousted males leave with their sons and form an all-male band, and this may result in high survival of immatures (Newton 1988; van Schaik 2000). Evidence also shows there is a high possibility of paternity between a resident male and the infants in the same group (Launhardt et al. 2001). White-headed langurs adopt a similar way to form male–immature groups. When a new male invades a one-male group successfully, the former adult male will be ousted. An invading male will not tolerate infants and male juveniles staying in their natal group. To avoid infanticide, infants and male juveniles will leave their natal group with the ousted male. Thus, they form a male–immature group.

Because sexual selection theory and kin selection theory make different predictions in male–immature interactions, shall we expect male–immature interactions differ between breeding groups and nonbreeding groups? This study primarily aimed to answer the difference of male–immature interactions between one-male groups and male–immature groups and to find a relation between the difference and the mating status of males.

Materials and methods

Research location

We are situated between Luobai and Banli (22°15′–22°17′ N, 107°29′–107°32′E) in Chongzuo, Guangxi, China. The total area spans 16.1 km^2, which is karst terrain, is composed of limestone mountains, valleys, and low lands. The vegetation in this area is mostly deciduous broadleaf forest located in subtropical monsoon areas. White-headed langurs reside on limestone mountains scattered among the farmlands.

Study groups

Four one-male groups and three male–immature groups had been studied (group composition in Table 1). In this study, infants and juveniles were termed as immatures. Because interaction between adult and subadult males may be functionally different from male–immature interaction, it will be described and discussed in another paper (Yin et al. data in preparation).

Behavior study

We used twin telescopes (LEICA 10×42BA) and single telescopes (Nikon Field Scope, 24×60) in our field studies. Observers usually kept anywhere from 50 to 200 m away from the white-headed langurs, so not to disturb them. Because of the rough natural condition and hilly terrain, it was very difficult to monitor the langurs all day long, and most observations were carried out from 0600 to 0930 and 1700 to 2000 hours. In these two periods of time, the monkeys were typically active. From 0930 to 1700 hours, the monkeys always stayed in caves or under heavy vegetation and were very difficult to be detected.

Based on body features (body size, hair color, testis size, and face trait, etc.) and behavior traits (nipple contact, estrus, reproduction, etc.), all individuals in this study had been classified into sex/age classes. In one-male groups, infants were weaned at 19–21 months (Zhao, data submitted), and we judged an individual as an infant from its suckling behaviors as well as its body features. But in male–immature groups, because infants were forced (by invading males) to separate from their mothers, we considered those individuals who were younger than 19–21 months (judged from their body features) but did not suckle anymore as juveniles instead of infants. Juveniles

Table 1 Types, compositions, and observation time of study groups

Group type	Group name	Number of group members								Study period	Observation time (min)
		AM	AF	SM	SF	JM	JF	IM	IF		
One-male group	SHY	1	3	0	0	0	0	2	1	Feb 2, 2000–Jan 7, 2002	1,870
	WQW	1	8	3	3	3	2	6	1	Mar 24, 2001–May 13, 2001	1,015
	NQ	1	9	0	3	0	0	5	4	Feb 21, 2003–Jul 31, 2003	140
	FJC	1	4	0	3	0	0	3	1	Mar 17, 2003–Dec 29, 2003	710
Male–immature group	NBGK	1	0	2	0	2	0	1	0	Mar 14, 2003–Apr 18, 2003	125
	XNBG	1	0	2	0	0	0	2	1	Feb 8, 2004–Feb 18, 2004	95
	LTS	1	0	0	0	0	0	4	1	Feb 20, 2004–Feb 26, 2004	151

Group member: *AM* adult male, *AF* adult female, *SM* subadult male, *SF* subadult female, *JM* juvenile male, *JF* juvenile female, *IM* infant male, *IF* infant female

became subadults at about 4 years old, and subadults became adults at about 5 (females) or 6–7 (males) years old, but the exact times still remained unclear.

In this study, all male–immature interactions were recorded in focal-animal sampling (Altmann 1974). During each sample period, the adult male of the observed group was chosen focal-animal, and followed from he was detected until he disappeared from view. Data collection included the beginning and the end time of each sample period and each state behavior, and the time of occurrence of each instantaneous behavior. The actor(s) and receiver(s) of the interactions between males and immatures were also recorded. Thus, we calculated the total sampling time, the durations and time percentages of state behaviors, and the events and frequencies of instantaneous behaviors.

Adult males' behaviors included sociopositive behaviors and aggressive behaviors. Sociopositive behaviors included cofeed, allogroom, body contact (state behavior), and touch (instantaneous behavior). Aggressive behaviors included vocal threat and pushing/biting (instantaneous behavior). Aggressive behaviors served as rejections when an immature approached, touched, or tried to play with an adult male, and always resulted in the immature screaming and leaving, but never hurt.

Results

During four observation sessions in one-male groups, no cofeed, allogroom, or body contact behavior was observed. Nevertheless, adult males in male–immature groups spent 35.5% (SD ±14.7%, range from 25.6 to 52.4%) daytime carrying out sociopositive behaviors towards immatures, which was obviously different from the situation in one-male groups (Table 2).

We recorded a touch behavior on March 2nd of 2000 at 2:58 p.m.. The SHY group's adult male approached a female and her infant (2 months old). The male touched the infant briefly, then watched the infant attentively (till 3:06 p.m.). This was the only friendly interaction between male–immature recorded in one-male group.

In one-male groups, when immatures initiated affiliation towards adult males (totally 94 events), the males behaved aggressively (33 events) or tolerantly (61 events). Males in male–immature groups, however, never behaved aggressively when immatures initiated affiliation towards them

(totally 11 events). In addition, the adult male in the NBGK group was observed initiating sociopositive affiliation towards immatures (one event). So, the tolerant/aggressive trends of males were obviously different between one-male groups and male–immature groups (Table 2).

Discussion

Interactions between adult males and immatures in one-male groups and male–immature groups obviously differed. In one-male groups adult males behaved tolerantly or aggressively towards immatures. In male–immature groups, adult males carried out sociopositive behaviors and never behaved aggressively towards immatures. A Hanuman langur study also showed similar change of male–immature interactions after they migrated from a breeding group to a nonbreeding group (Rajpurohit 1991). Though our results are based on a small and imbalanced sample size, the fact that male–immature interactions differed between one-male groups and male–immature groups is clear. We have a relatively big sample size (62.25 h) in one-male groups, but discovered no sociopositive interactions (except one brief touch) between male–immature pairs. In male–immature groups, although we only have a small sample size (6.18 h) and this may lead to the deflation or inflation of the time percentages of sociopositive behaviors carried out by males, the fact that males in male–immature groups actually carried out sociopositive behaviors towards immatures will not change if we conducted more observation. So our results show differences of male–immature interactions between one-male groups and male–immature groups. And our question is: What factor made male–immature interactions so different between the two kinds of groups?

As sexual selection theory predict, males bias to compete for more mating chances but not to invest in any single offspring. Our observation in breeding groups (one-male groups) supports this prediction. White-headed langurs practise polygyny and variance of male reproductive success is higher compared with females (Pan et al., unpublished data). Therefore, males spend average 32.8% (SD ±6.5%, range from 25.3 to 37.4%) of their daytime to defend their territories (Zhao, unpublished data), which may lead to their indifference towards immatures. Also, it seemed possibly the interactions initiated by immatures

Table 2 Male–immature interactions in one-male groups and male–immature groups

Group type and name		Sociopositive behavior (min)			Aggressive behavior (event)	
		Cofeed	Allogroom	Body contact	Vocal threat	Pushing/biting
One-male group	SHY group	0	0	0	13	4
	WQW group	0	0	0	7	2
	NQ group	0	0	0	1	0
	FJC group	0	0	0	5	1
Male-immature group	NBGK group	0	7	25	0	0
	XNBG group	16	11	0	0	0
	LTS group	27	1	51	0	0

interfered the defending or mating behaviors of the males, so males are aggressive towards immatures although they are likely the fathers of them.

Our observation in nonbreeding groups (male–immature groups), on the other hand, supports the prediction of kin selection theory. Because the males are likely the fathers of the immatures in the same group (Launhardt et al. 2001), it will be beneficial for them to increase the survival of the immatures.

In Boggess' (1982) study, adult males were more aggressive and young males showed more tense behaviors in multimale groups. In contrast, interactions between adult and immature males were considerably more relaxed in one-male groups. Boggess (1982) supposed the two different social patterns between adult and immature males existed because the adult male in one-male group was likely the sire of those young, but multimale groups led to uncertainty of paternity. But in white-headed langur, because male–immature groups were formed by the individuals ousted from one-male groups, the certainty of paternity should be equal between the two kinds of groups. So, we consider that the differences of male–immature interactions between one-male groups and male–immature groups shall not be a result of paternity assessment.

In Barbary macaque, males exhibited a "care-then-mate" pattern. So male–infant caretaking was considered a mating strategy but not paternal investment in this species (Menard et al. 2001). In white-headed langur, however, males were never observed to mate again after they were ousted from breeding groups. So, we do not consider male–immature sociopositive interactions as a mating strategy of the langur males.

One explanation is that male–immature interactions differ between one-male groups and male–immature groups because the mating status of males are different between the two kinds of groups. White-headed langur males can adjust their behavioral strategy between mating effort and paternal investment flexibly. When males are in prime of age, they are competitive in mating opportunities. When they become old and go to nonbreeding groups, investing in their presumed offspring may increase their fitness. So, although male–immature interaction patterns do not change gradually, age may be an essential factor influencing the mating status of males and then male–immature interactions.

Data of the behavioral changes in the same male when he is in a one-male group and later when he is in a male–immature group are still absent. It should be our future research perspective.

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