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Male mate choice in Tibetan macaques *Macaca thibetana* at Mt. Huangshan, China

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Abstract Though females are generally more selective in mate choice, males may also benefit from mate choice if male reproductive success is limited by factors other than simply the number of female mates, and if females differ in short-term reproductive potential. We studied male mate choice in a free-ranging troop of Tibetan macaques *Macaca thibetana* at Mt. Huangshan, China, from August 2007 to April 2008. We employed focal animal sampling and all occurrence sampling to record sexual related behaviors. Eight adult females were divided into three female quality categories according to the females' age, rank and parity. Using male mating effort as a proxy for male mate choice, we found that males do distinguish female quality and show time-variant mating strategies. Specifically, females with dominant rank, high fecundity, and middle age attracted significantly more males. Our results suggest that female short-term reproductive potential appears to be an important variable in determining male mating effort. Male Tibetan macaques do exercise mate choice for higher quality females as well as reduce useless reproductive cost, which is consistent with the direct benefits theory of mate choice [*Current Zoology* 56 (2): 213–221, 2010].

Key words Tibetan macaques, *Macaca thibetana*, Direct benefits theory, Male mate choice, Reproductive potential, Reproductive success

Darwin (1871) first put forth the idea that males are competitive and females are choosy in mating behavior. Bateman's (1948) classic study on *Drosophila melanogaster* later reinforced this understanding of sex roles. Traditional sexual selection theory predicts sexual differences because of the sexes' relative parental investment. However, the Darwin-Bateman paradigm of competitive males and choosy females may be too simplistic (Clutton-Brock, 2007). First, in species where males' parental investment is greater than that of females, typical sex roles are reversed (Andersson, 1994; Trivers, 1972; Buchan et al., 2003). Second, although single sperm are relatively less expensive than single eggs, spermatozoa are delivered not individually but by the millions, and the ejaculate also contains potentially costly accessory-gland secretions (Dewsbury, 1982). This evidence, coupled with the costs of mate searching, courtship, nuptial gifts, mate guarding, mating, sperm competition and risks of predation, suggests increased costs of male reproduction (Andersson, 1994; Bonduriansky, 2001; Dewsbury, 1982). Third, if male reproductive success is limited by more factors than simply the number of females, and the females differ in quality (specifically in their short-term reproductive potential), it would benefit males to exercise mate choice (Altmann, 1997). Therefore we would reasonably expect males to choose females based on features that indicate their potential reproductive success.

Subtle male mate choice is usually concealed by intense mate competition (Matsumoto-Oda, 1999). There is not a strict dichotomy between choosiness and competition; even the more competitive sex may also show mate choice. This selectivity has been shown in numerous systems in which males appear to make no material contribution to their offspring, including crustaceans (Jormalainen et al., 1994), insects (van Dongen et al., 1998), fish (Sargent et al., 1986), amphibians (Arak, 1983; Arntzen, 1999), reptiles (Shine et al., 2001), birds (Saether et al., 2001) and mammals (Preston et al., 2005). Nevertheless, few researchers have studied male mate choice compared to the substantial research effort devoted to female mate choice (Andersson, 1994; Bonduriansky, 2001). Consequently, there is a popular view that the intricacy of female choice far exceeds that of male choice, although it is unknown whether this is an accurate perception of sexual differences or a side effect

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of the paucity of studies focused on males (Shine et al., 2003). It is apparent that more studies would better our understanding of male mate choice.

While there is abundant evidence for male and female mate preferences and mate choice in humans (Buss, 1994; Dixson et al., 2010), and non-primate animals (Andersson, 1994), the situation appears to be much less clear in non-human primates. There are several reasons for this uncertainty. First, in contrast to many other fast-breeding species, experiments designed to test predictions derived from sexual selection theory are more difficult for long-living nonhuman primates. Second, researchers need know detailed group histories in natural settings and systematic behavioral observations on sexual interactions and mate choice. Third, because male and female reproductive interests are rarely congruent, theories of sexual conflict and sexual dialectics predict highly variable, dynamic, and often antagonistic sexual tactics (Godwaty, 1997). Several primate studies in captivity have found evidence for male sexual preference for certain females over others. The likely variables determining male sexual preference are usually female age, dominance or parity – all of which are thought to signal a female's quality or fertility. These variables frequently jointly determine a female's quality (Beach, 1976). Males often prefer older or middle-aged females, which are more likely to be multiparous (Andersson, 1986; Kuester and Paul, 1996). Males may also show sexual preference for dominant females (Kuester and Paul, 1996; Silk and Boyd, 1983). The size of a female's perineal sexual swelling is also implicated as a characteristic affecting male sexual preference in the wild (Domb and Pagel, 2001), though much controversy has surrounded whether this trait is an honest indicator of female fertility (Setchell and Wickings, 2004; Zinner et al., 2002; Nunn, 1999).

The Tibetan macaque *Macaca thibetana* is the biggest of all *Macaca* species and is currently listed as vulnerable on the World Conservation Union (IUCN) Red List (Long, 2008). Like other species of *Macaca*, Tibetan macaques live in a society containing multiple males, multiple females, and their offspring. Males transfer from their natal groups before sexual maturation, but females live within the natal group for life. A linear dominance hierarchy exists both among adult males and adult females separately (Deng and Zhao, 1987). Previous studies on births showed the species to be seasonal breeding (Li et al., 1994; Zhao and Deng, 1988), and that there is intense competition among males during the mating season (Li, 1999). Adult females have slight but detectable sexual skins in the perineal region, but the appearance of the sexual skin does not vary cyclically with the season or with the female's reproductive state. Females have no typical behaviors indicative of sexual motivation, i.e. estrus (Li et al., 2005).

Our primary goal was to test for differences in the cumulative amount of male mating effort during mating season. The null hypothesis was that males would prefer all females equally as mates. One prediction from the null hypothesis was that males would expend equal levels of mating effort during mating season. Eight adult females were divided into three classes according to female quality (age, rank and parity). If we found different levels of male mating effort in different classes (evidencing male mate choice), the next step was to ascertain how male mating effort changes during mating season (inspecting male mating strategies).

1 Materials and Methods

1.1 Study site and animals

Our study was carried out at Mt. Huangshan (118°11′W, 30°29′N), Anhui Province, China. Mt. Huangshan covers an area of 154 km^2, and is a well-known natural attraction in China. The altitude of the peak is 1841 m and straddles the border between China's temperate and subtropical zones.

There are two resident groups of Tibetan macaques *Macaca thibetana* in the area (Berman and Li, 2002). The study group, named the Yulingkeng group YA1, has been observed at least twice a year (in spring and winter) since 1986 in order to follow its demography (Li et al., 1996; Wada et al., 1987). All animals in the study group were identified by natural markings and characteristics. The ages of monkeys who were born in the study group after 1986 and their matrilineal relationships were known. The ages of immigrants were estimated from known-aged individuals. The dominance hierarchy was determined by aggressive/submissive interactions.

Provisioned food (approximately 6 kg corn/day) was given to the monkeys at the feeding site three times (10:00, 15:30, 17:30) a day to attract the monkeys to open areas at which visitors could see them easily from the platform. This provisioned feeding also facilitated our study of this group. As few tourists came during the observations, we had excellent opportunities to observe the monkeys without disturbance. In addition to the provisioned food, the monkeys mainly lived on various plants in their habitat.

The current study was based on intensive observations conducted during the mating season (Aug. 2007 – Jan. 2008) and birth season (Feb. 2008 – Apr. 2008). There were 22 individuals in the group at the beginning of the study, including 4 adult males (⩾7 years old, one left after one week) and 8 mature females (⩾4 years old). By the end of birth season (Jun. 2008), the group had increased to 28 animals, due to births and immigration. Table 1 shows the detailed composition of YA1 troop during the study. During the data collection period of the current study, the study group consisted of three adult males and eight adult females (no male-female kinship) most of time, resulting in a sex ratio (SR) of 0.375/1 (male/female), well below the previous year during which adult males and females were almost equal. The decline of the SR reduced the impact of male mate competition on mate choice and thus this was a good time to study male mate choice in this group of Tibetan macaques.

1.2 Data collection

All data of behavioral observations were conducted by a single observer (Zhang) in an intensive study for 216 days (mean: 25 days/month, range 20 – 30 days), of which 150 days were in the mating season and 66 days were in the birth season. We employed focal sampling and all-occurrence sampling for data collection (Altmann, 1974). The matrices of data obtained from two different sampling methods showed a similarity in structure (Matrix correlation test, Grimacing: Kr=53, Pr=0.031; Following: Kr=26, Pr=0.012; Sexual chasing: Kr=61, Pr=0.042; Sexual inspecting: Kr=22, Pr=0.033, based on 2000 permutations). The two sets of data were combined, because of the infrequent occurrence of these behaviors. It is believed to be representative of the proportion of mating motivation activity by all group members, as van Noordwijk (1985) and Robbins (1999) reported.

When the monkeys were in the forest (away from the feeding site), we used focal animal sampling to record details of interactions (mating, proximity, grooming, grimacing, sexual-inspect, sexual chasing, etc.) between focal animals (adult males and adult females) and other group members. Each focal sample lasted 10 minutes so that all adults could be sampled at least once each day on average, and the order of focal animals was determined at random before observations began. If a given focal monkey could not be found at its sampling time or was out of sight during sampling, we chose the next monkey on the list and returned to the previous monkey when it reappeared. Because the three feeding times divided the day into four time blocks, we attempted to observe each focal animal for equal periods of time in each time block. The total amount of time devoted to focal animal sampling was 274.07 h in the mating season (24.92 h ± 0.33 h/individual, *n*=11) and 121.11h in the birth season (11.01 h ± 0.12 h/individual, *n*=11).

When the monkey group was at or around the feeding site, we used all-occurrence sampling to record sexual interactions between the two sexes. Generally, the monkey group stayed at the feeding site for 20–40 minutes after provisioning. This sampling method allowed us to monitor each adult monkey every observational day and increased behavioral samples. Although all-occurrence sampling in the field was usually

Table 1 Composition of YA1 troop during study

Age class [a]	Male			Female			
	Animal	Rank	Date of Immigration	Animal	Rank	Age	Date of Delivery
Adult	ZL	1	2006-11-17	YZ	1	16	2008-1-24
	HL[b]			TT	2	17	2008-1-22
	GS	2		TG	3	22	2008-6-28
	HG	3	2007-8-9	TH	4	5	2008-3-17
	CT [c]	4	2008-1-14	YM	5	18	
				YH	6	5	2008-2-19 [d]
				HH	7	5	2008-3-8
				H	8	25	
Adolescent	3			2			
Juvenile	5			1			
Infant	4			1			
Total	16			12			

[a] Following LI JH (1999). [b] HL migrated out in 2007-8-7. [c] CT was not the study subject because its immigration time was in the late period of mating season. [d] The infant died just one week after born out of unknown reason.

compromised to some extent by the monkeys' comings and goings at different times, we felt the effect of this was small because the group had a cohesive structure (Li et al., 1994) and observational conditions were good around the feeding site. In total, 525.2 h of data were collected in the mating season (3.5 h ± 1.2 h/day，*n*=150) and 231.7 h in the birth season (3.6 h ± 1.7 h/day，*n*=66) using all-occurrence sampling.

1.3 Definitions

The mating pattern for male Tibetan macaques at Huangshan is a single mount ejaculation; and mating usually exhibits a pause and body/leg tremor at ejaculation (Xiong and Wang, 1991). Sexual motivation behavior is defined as the showing of the males' interest for mating, as separated from the behavior of copulating in primates by Wallen (2001). Here we define four behaviors (grimacing, following, sexual chasing, sexual inspecting) as sexual motivation behaviors in Tibetan macaques. The behavior recordings were made by observation with the following behavior categories described by Li (1999):

Table 2 Behavioral definitions

Catalog	Definition
Following	One individual follow along with another individual once it move away.
Grimacing	Male teeth-playing to the female far away, which is the behavior that adult male attract ovulation female for mating.
Sexual chasing	One male chases female and want to mate with her. It is slower than aggressive chase, and the female run away with sometime stopping and without screaming.
Sexual inspecting	Adult male uses finger or mouth to check the female's genitals.
Mating	A male mounts a female with intromission and thrusting, but not necessarily with ejaculation.

1.4 Determinants of female quality

Evolutionary psychology suggests that female quality is based on cues of health and short-term reproductive potential. Because female Tibetan macaques used "concealed estrus" strategies and mated often due to continuous estrus in the mating season (Li et al., 2005), it is hard to use sexual swelling as a cue to males about females' reproductive state. Previous studies have suggested that there were close correlations between females' age, rank and parity and short-term reproductive potential. So we chose these variables as cues instead, which can provide a reliable index of a female's quality.

During the study period, there were eight adult females in the group. Table 3 shows their age, rank and parity categories. As long as two out of the three variables were the same, two different individuals were assigned into the same group. We defined three female quality groups: Classes I, II, and III. Class Ⅰ consisted of females that had dominant rank, high fecundity and middle age (at the meridian of life). Class II was older in age and lower in rank than Class I. They also had middle fecundity (had passed their prime). Class III was the youngest, and had middle rank. They were nulliparous females (in their early adulthood). It was therefore theoretically possible that males would expend different levels of mating effort by female quality category during the mating season.

Table 3 Females grouped by age, rank and parity

Female	Age [a]	Rank [b]	Parity [c]	Category
YZ	Middle	High	High fecundity	I
TT	Middle	High	High fecundity	I
TG	Old	Middle	Middle fecundity	II
YM	Middle	Middle	Middle fecundity	II
H	Old	Low	Middle fecundity	II
TH	Young	Middle	Nulliparous	III
YH	Young	Middle	Nulliparous	III
HH	Young	Middle	Nulliparous	III

[a] Young (⩾5 years old, ⩽10 years old); Middle (⩾11 years old, ⩽20 years old); Old (⩾21years old). [b] High (1-2); Middle (3-7); Low(8). [c] Nulliparous: with no infants; Middle fecundity: with less than or equal to 3 surviving infants in recent 5 years; High fecundity: with more than 3 surviving infants in the recent 5 years.

1.5 Measuring male mating effort

Halliday (1983) defines mate choice as “any pattern of behavior shown by members of one sex that leads to their being more likely to mate with certain members of the opposite sex than others”. Under this definition, one can use the mating effort males expend during mating season as a measure of male mate choice. Unfortunately, we could not assess the actual amount of metabolic energy males expended. Instead, we used the frequency of male sexual motivation behavior as a proxy for the strength of male mating preferences.

1.6 Data analysis

A matrix correlation test was used to ensure that the two sets of behavior data obtained from different samplings were similar and combinable (de Vries, 1993). We used a row-wise correlation test to examine the correlation between two data matrices (Kr test; Hemelrijk, 1990). The Hemelrijk's Matrixtester v2.23 program was used for these computations (C.Hemelrijk, pers.comm.). The results were based upon 2000 simulations.

In order to compare differences in male mating effort among female classes, a 3 (males) × 3 (female quality categories) chi-square test based on observed frequencies of behavior was used. The expected values were calculated separately for each male as the mean values per female times the number of females in a category. If the overall chi-square was significant, the adjusted residuals (non-parametric equivalent of z-scores) for the cell were examined, which score greater than 1.96 indicated significant difference ($P<0.05$). This was done to determine whether the results were in the predicted directions and consistent for all three males. Then we performed separate analyses for each male to test for distributions of mating effort across female classes during mating season using a 3 (female categories) × 6 (months) Fisher’s exact test. The SPSS 16.0 (SPSS Inc. Chicago, Illinois, USA) package was used for these computations. All statistical analyses were two-tailed and the significance level was set at 0.05. All data were expressed as Mean ± *SD*.

2 Results

2.1 Differences in male mating effort among classes

Fig. 1 showed four measures of male mating effort by female quality categories. A chi-square test of male mating effort among classes yielded significant values for the following three categories: grimacing (Fig. 1A: $\chi^2=114.4$, *df*=8, $P<0.05$), following (Fig. 1B: $\chi^2=97.43$, *df*=8, $P<0.05$) and sexual chasing (Fig. 1C: $\chi^2=95.74$, *df*=8, $P<0.05$). The frequencies of males sexual inspecting females had no significant differences (Fig. 1D: $\chi^2=12.36$, *df*=8, $P<0.05$) because this sexual motivation behavior may have functioned to identify pregnant females (unpublished data). As can be seen in Table 4, all three males showed significant preference for females in Class I (dominant rank, high fecundity and middle age);

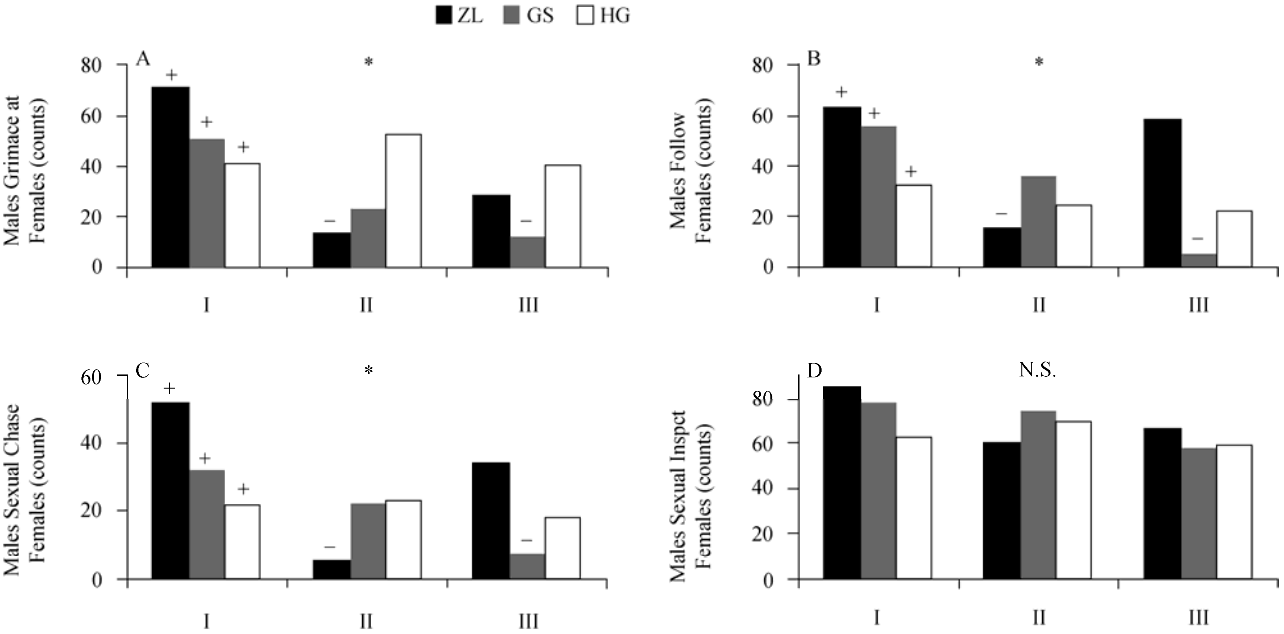

Fig. 1 Four measures of male mating effort by female quality category

A. Males grimace at females. B. Males follow females. C. Males sexual chase females. D. Males sexual inspect females (N.S.= no significance; * = $P<0.05$; + = adjusted standard residual >1.96; - = adjusted standard residual<-1.96).

Table 4 Adjusted standardized residuals of male mating effort

	I			II			III		
	G[a]	F	S	G	F	S	G	F	S
ZL	**4.08**	**3.73**	**5.17**	**–5.12**	**–4.63**	**–5.14**	0.04	0.90	–0.11
GS	**3.60**	**3.99**	**2.96**	–0.26	0.10	–1.15	**–3.34**	**–3.99**	**–2.80**
HG	**2.14**	**2.61**	**2.10**	0.40	–1.78	–1.11	–1.54	–0.93	0.09

[a] G: grimacing; F: following; S: sexual chasing. Bold face means significant difference.

whereas it was notably less than expected from the mating effort record by ZL for females in Class II and GS for females in Class III.

Despite the small sample size (only 2–3 individuals in each female quality category), our results indicate that males do distinguish differences in female quality. Specifically, females with dominant rank, high fecundity, and middle age attracted significantly more males.

2.2 Time-variant male mating strategies

A fisher's exact test for distributions of male mating effort across female classes during mating season yielded significant values for the following dominant individuals: ZL (Grimacing: $\chi^2=88.626$, $df=10$, $P<0.05$; Following: $\chi^2=97.052$, $df=10$, $P<0.05$; Sexual chasing: $\chi^2=42.899$, $df=10$, $P<0.05$), and GS (Grimacing: $\chi^2=42.33$, $df=10$, $P<0.05$; Following: $\chi^2=48.953$, $df=10$, $P<0.05$; Sexual chasing: $\chi^2=27.363$, $df=10$, $P<0.05$). As a low ranking individual, the distributions of HG's mating effort had no significant differences (Grimacing: $\chi^2=4.842$, $df=10$, $P>0.05$; Following: $\chi^2=11.607$, $df=10$, $P>0.05$; Sexual chasing: $\chi^2=8.359$, $df=10$, $P>0.05$).

The present results demonstrated that male Tibetan macaques made time-variant mating strategies by female quality category (Fig. 2): both ZL and GS expended high levels of mating effort for females in Class I from the beginning of the mating season, which declined with the seasonal change. GS's mating effort attained a peak later, at about the middle term of the mating season, for females in Class II. ZL expended low mating effort for females in Class III at the beginning of mating season, which then peaked during late term of the mating season. There were no notable rules for distributions of HG's mating effort.

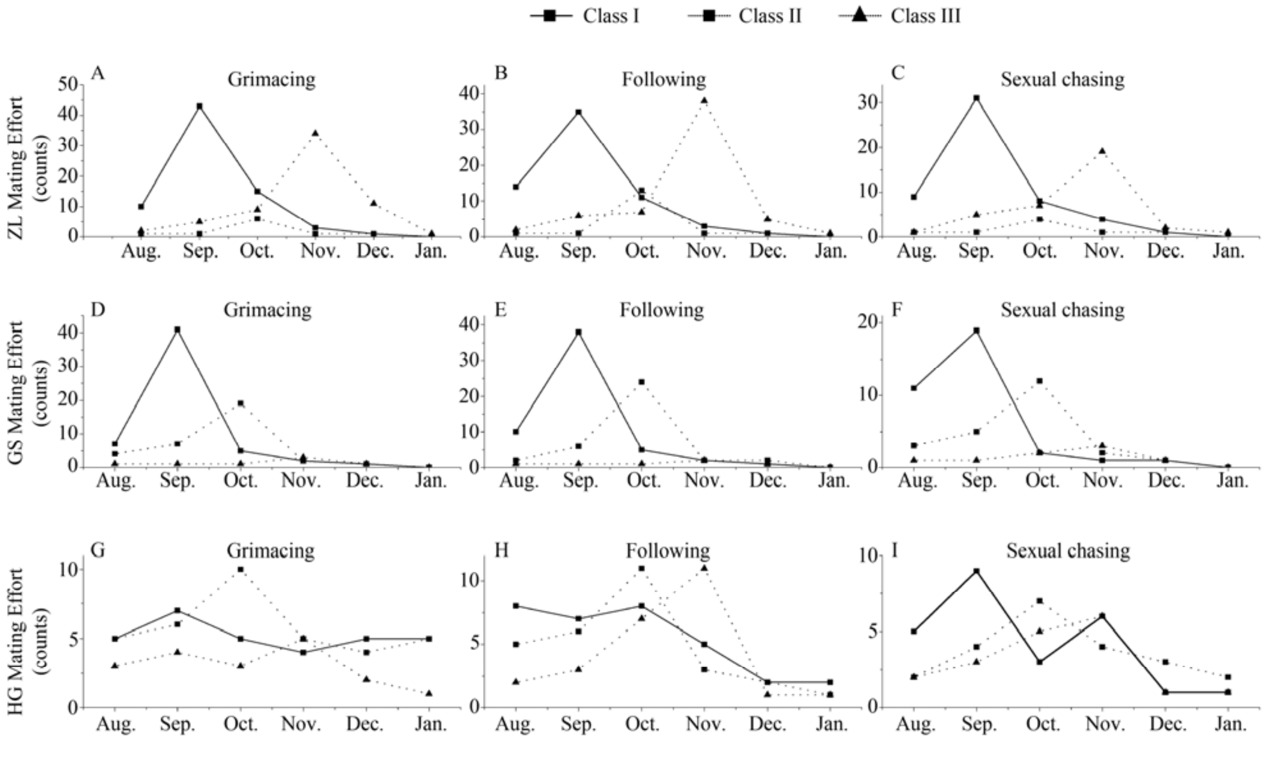

Fig. 2 Temporal variation of male mating effort by female quality category

3 Discussion

Using male mating effort as a proxy for male mate choice, we found that female short-term reproductive potential appeared to be an important variable in determining male mate choice. Males did not choose all females equally as mates. Our data clearly indicated that males could assess short-term reproductive potential of females, and they appeared to allocate significantly different amounts of mating effort based on the assessment (Fig. 1). This trend was also evident when we analyzed the distributions of male mating effort. The present data demonstrated that male Tibetan macaques made time-variant mating strategies by female quality category (Fig. 2). The results are evidence for male mate choice among Tibetan macaques at Mt. Huangshan and emphasize the importance of behavioral cues in mate assessment. These findings also contribute to a growing body of evidence which suggests that the notion of one sex being discriminating and the other competitive is overly simplistic.

The direct benefits theory of mate choice indicates that males should attempt to maximize their reproductive success by selecting females with the highest reproductive potential as preferred mates. This hypothesis has already been supported for some primates (*Macaca mulatta*: Drickamer, 1974; *Macaca radiata*: Silk et al., 1981; *Macaca sylvanus*: Paul and Kuester, 1988; *Macaca fuscata*: Altmann et al., 1988). In our study, all three males showed preference to females with dominant rank, high fecundity, and middle age. Both experienced, parous females and high rank females often have a higher reproductive rate, as well as offspring which are more likely to survive (Paul and Kuester, 1988). In our group, only the females of Class Ⅰ all gave birth and all their infants survived in three female classes. Males would benefit from mating with these females because of their increased fecundity. It suggests that males do exercise mate choice for higher quality females, and reduce useless reproductive cost. Our findings in Tibetan macaques are consistent with the direct benefits theory of mate choice.

In groups of some primate species, the highest rank individuals of each sex prefer the highest rank opposite sex individuals as their mate partners (Smith and Smith, 1988; Kuester and Paul, 1996). In current study, the social rank of males also influenced male mate choice. It was important to note that in certain circumstances, male sexual preferences may translate into actual male mating opportunities for only the most dominant males. Male Tibetan macaques live in close proximity to each other as well as to females, and the open habitat makes it difficult to conceal any activity. So it may be possible for dominant males to prevent low rank individuals from sneak copulations. This is our explanation for no notable rules in distributions of HG's mating effort, although HG showed significant preference for females in Class Ⅰ in the cumulative amounts of mating effort.

Male Tibetan macaques play the dominant role in sexual interaction (Xiong, 1991), however, we should note that females are not entirely passive and their preferences may also affect mating opportunities: Females appear to be more averse than males to copulating with relatives, perhaps because this behavior generally leads to reduced reproductive success (Zhu et al., 2008). We must also remember that animals rarely behave optimally. They make decisions with a certain degree of error, and quite often, operate with incomplete information. In addition, mate choice may depend on other factors not measured, such as genetic complementarities between prospective mates. Therefore, it should not be surprising that all three males did not consistently allocate their mating effort for females in Class Ⅱ and Class Ⅲ, and there was individual variation in mate preference.

Our results have shown quality-based male mate choice. Another interesting male-initialed mate choice strategy that remains to be resolved in Male Tibetan macaques is whether 'friendships' or special relationships occur between individual males and females, as described for other species of primate living in multi-male, multi-female groups such as baboons (Seyfarth, 1978; Altmann, 1980; Smuts, 1985), rhesus macaques (Chapais, 1983) and Japanese macaques (Takahata, 1982). It seems likely that this occurs because young ZL and old GS showed some differences in mate preference both as dominant individuals in current study, however, we need more detailed behavioral data that would allow us to determine whether long-term relationships between sexes exist, and whether these are reflected in mate preference. These questions are all of potential interests in our study species.

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