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Male Mate Choice in Captive Stump-Tailed Macaques (*Macaca Arctoides*)

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Abstract:
In order to determine the factors influencing male mating choice in captive stump-tailed macaques (Macaca arctoides), the group composition was manipulated in which confounding social context were controlled. Each adult male was given the opportunity to mate with any of the estrous female during the mating season between September 2010 and February 2011. Number of successful copulation between adult male and each female was used as a proxy for male mating choice. The number of successful copulation received by each female was found to be positively correlated with the female sexual attractivity. No significant correlation was found between the number of successful copulation received by the females and their dominance status, reproductive success and ages. Social interaction between adult male and female did not seem to influence the male mating choice. Sexual swelling has no influenced on the male mating choice and it was suggested to be a developmental stage of sexual skins among stump-tailed macaque females. Despite the lack of proximate explanation, females with bright red genital skin colour were found to be more attractive than females with paler and darker genital skin colour.

Keywords: *Attractivity, copulation, dominance, mate choice, stump-tailed macaques*

1. Introduction

It has become increasingly clear that neither competition over access to mates nor mate choice is restricted to one sex (Johnstone et al., 1996; Cunningham and Birkhead, 1998). Mate choice is most common in monogamous species (Anderson, 1994), but there is also some evidence of mutual mate choice in promiscuous species (Kraak and Bakher, 1998; Parga, 2006). Generally, male primate prefers older-experienced females and high-ranking females (Samuels et al., 1984; Anderson, 1986; Keddy, 1986; Keddy-Hector, 1992; Kuester and Paul, 1996), or females with large perinial swelling (Domb and Pagel, 2001). However, some studies reported that male do not prefer the females with highest dominance status or the highest reproductive success, rather female reproductive potential appears to be an important variable determining male mating efforts (Parga, 2006).

The stump-tailed macaque (*M. arctoides;* I. Geoffroy Saint-Hillaire, 1830) is a primarily arboreal species. This species occurs in Bangladesh and North-East India in the South Asian region, from South China to West Malaysia, Thailand, and North Myanmar. In Bangladesh the species is now locally extinct, and in India its population is critically endangered (Molur et al., 2003). The results presented here are part of a larger study being conducted on the breeding behaviours of this species in captivity.

Unlike other macaques, stump-tailed females lack prominent visual signals of receptivity (Fooden, 1990; pers. obs.). Sexual interactions in stump-tailed males include a large repertoire of socio-sexual acts involving sniffing and licking the perineum of the female or its products deposited on their hands (Estep et al., 1984; Schenck and Slob, 1986; Fooden, 1990). Linnankoski et al. (1981) suggested that stump-tailed males rely on non visual cues to assess female reproductive status. However, no study has been performed to show that this kind of information is mediated by chemical signals. Since the adult stump-tailed macaques females of the group exhibited a high variation in their genital skin colours, visual signals might even be an important determinant of the female attractivity. Thus, the male mate choice in stump-tailed macaques was measured using experimental manipulation in which confounding social context are controlled by exposing each adult male to the females. Successful copulation between adult male and each female was used as a proxy for the male choice.

2. Materials and Methods

2.1. Subjects and Data Collection

The study was conducted on a group of captive stump-tailed macaques *(M. arctoides)* in the Aizawl Zoological Park, India. The group consisted of 24 individuals (3 adult males, 8 adult females, 4 immature males, 3 immature females and 6 infants). The monkeys were housed in an enclosure with 2 indoor rooms and 1 outdoor enclosure covering 850 m^2. Individuals of the study group could be readily observed at all times. The composition of adult males in the study group was manipulated into sub-groups to examine the male mate choice and the factors leading to copulation. Each adult male were allowed to stay with all females for a total of 25 days where the other males could not interact with the group during the mating season between September 2010 and February 2011.

We recorded the observations in 2 sessions, viz., morning (0600–1130 h) and afternoon (1130–1700 h) on focal individual. Observations were recorded every 5 min via focal individual sampling (Altmann 1974). Thus we recorded 12 entries on the focal individual in an hour. The frequencies of the female approach to male, present to male, grooming and look-back to male were used as the indices of female sexual proceptivity. The frequencies of the male approach to female and grooming to female were considered as the indices of female sexual attractivity. Copulation was defined as an instance in which a male mounts a female with intromission and thrusting, with or without ejaculation. Two types of copulations were observed: (a) Unsuccessful copulation- mounting with vaginal intromission and thrusting without ejaculation (b) Successful copulation- mounting with vaginal intromission and thrusting terminated with ejaculation. *Approach*- when animal moves close to another within 1 m of distance (non-aggressive contexts only) (Soltis, 1999). *Groom*- when animal cleans or combs through the pelage of another with the hands (Kurland, 1977). *Look-back*- when a female looks over her shoulder at a male while within 3 m of him without showing submission (Enomoto, 1974). *Present*- when the female orients her perineal region toward male within 1 m of proximity (Enomoto, 1974). Dominance index of the female was calculated based on the direction of aggressive and submissive behaviours between all possible paired combinations of females within the group (Zumpe and Michael, 1986) which represent the relative dominance status of each female. The reproductive success of each female was calculated as the number of her infants that survived to ≥ 2 yrs of age divided by the number of reproductive years during which she could have produced an infant. Stump-tailed macaque females attained reproductive age at 5 years owing to provisioning (per. obs). The Zoo manager maintained records of births and deaths in the captive group of stump-tailed macaques since 1995. The record was used to calculate values of female reproductive success.

2.2. Data Analyses

Spearman correlation was performed to determine whether the number of successful copulation correlated with: 1) female dominance status, 2) female reproductive success, 3) female age, 4) number of interaction between adult male and females, 5) female sexual proceptivity, and 6) female sexual attractivity. For all the tests, the significant level was set at 0.05 and analyses were done using SPSS 17.0.

3. Results

Age, dominance index and reproductive success of adult females in the group were given in table 1. Interactions between each adult male and adult female were given in table 2, 3 and 4. Male mating choice was found to be associated with the female sexual attractivity. Spearman correlation index for various female activities and number of successful copulation received by adult females are given in table 5. In all the three sub-groups, the number of successful copulation received by the females was found to be positively correlated with the frequencies of approach and grooming received from the adult males. The sexual proceptive behaviour exhibited by females did not show positive correlation with the number of successful copulation received. No significant correlation was found between the number of successful copulation received by the females and their dominance status, reproductive success, age, and the number of social interactions. Females with bright red genital skin colour attracted male and received more copulation than females with paler and darker genital skin colour. The genital colours of different females were given in Figure 1.

Female	Age(yrs)	Dominance index	Reproductive success
Buangi	16	100	0.54
Hnupi	12	85.714	0.57
Dali	8	71.429	0.33
Nutei	12	57.143	0.57
Kci	15	42.857	0
Seni	8	28.571	0.66
Mci	8	14.286	0.33
Nui	5	0	0

Table 1: Age, dominance index and reproductive success of the adult females

Male	Female	No. of interactions	Female sexual perceptivity				Female sexual attractively		Unsuccessful Copulation	Successful copulation
			% approaches by female	Presents/hr	Groom by female (min/hr)	Lookback/hr	% approaches by male	Groom by male (min/hr)		
Alpha-male	Buangi	27	77.7	7.7	20	5	22.2	4.01	3	2
	Hnupi	25	76	7.3	20.3	7	24	3	2	3
	Dali	19	63	8.1	22.5	6	37	2	-	2
	Nutei	16	25	3.2	10.2	1	75	8.5	2	9
	Kci	15	13	2.4	8.8	-	87	11	2	12
	Seni	12	33	3	15	2	67	7.2	-	6
	Mci	35	88.5	8.1	30.2	9	11.4	2.01	-	2
	Nui	8	75	6.1	26.9	3	25	1.5	2	-

Table 2: Incidents of social and sexual interactions between alpha-male and adult females

Male	Female	No. of interactions	Female sexual proceptivity				Female sexual attractivity		Unsuccessful Copulation	Successful copulation
			% approaches by female	Presents/hr	Groom by female (min/hr)	Lookback/hr	% approaches by male	Groom by male (min/hr)		
Beta-male	Buangi	21	76.2	7.2	15	3	23.8	4	-	-
	Hnupi	18	83.3	6.6	13.3	3	16.6	3.2	-	-
	Dali	13	82.6	6.8	19.6	5	17.3	2	-	-
	Nutei	10	30	3.1	7.3	-	70	7.5	2	3
	Kci	12	16.6	4.5	4.4	-	83.3	9.2	4	5
	Seni	8	37.5	3.8	10.2	1	62.5	4.5	1	-
	Mci	25	80	7.8	20.3	7	20	-	-	-
	Nui	6	83.3	5	23	-	16.6	-	-	-

Table 3: Incidents of social and sexual interactions between beta-male and adult females

Male	Female	No. of interactions	Female sexual proceptivity				Female sexual attractivity		Unsuccessful Copulation	Successful copulation
			% approaches by female	Presents/ hr	Groom by female (min/hr)	Lookback/hr	% approaches by male	Groom by male (min/hr)		
Gamma-male	Buangi	31	67.7	7.8	33.33	5	32.25	5.5	-	3
	Hnupi	27	66.6	6.6	25.5	5	33.3	7	-	3
	Dali	23	78.2	7.1	26.31	7	21.7	4	-	2
	Nutei	15	20	3.6	12	-	80	12.5	1	8
	Kci	17	17.6	3.2	10.11	-	82.35	15.2	3	11
	Seni	21	33.3	3.4	13.14	2	66.6	10.5	-	6
	Mci	38	81.5	7.9	25.39	7	18.4	3	-	-
	Nui	12	75	6	25	4	25	2	-	-

Table 4: Incidents of social and sexual interactions between gamma-male and adult females

Activities	α-male		β-male		γ-male	
	r_s	p	r_s	p	r_s	p
Female dominance status	0.17	0.69	-0.01	0.97	0.31	0.45
Reproductive success	0.33	0.42	-0.21	0.62	0.32	0.43
Age	0.53	0.18	0.48	0.23	0.65	0.08
No. of interaction	-0.17	0.69	-0.23	0.58	-0.31	0.45
Female Approach	-0.73	0.04*	-0.77	0.02*	-0.95	0.01*
Female Present	-0.71	0.04*	-0.59	0.12	-0.75	0.03*
Female Grooming	-0.88	0.01*	-0.77	0.02*	-0.59	0.12*
Female Lookback	-0.63	0.09	-0.64	0.08	-0.79	0.01*
Male Approach	0.73	0.03*	0.76	0.02*	0.95	0.01*
Male Grooming	0.92	0.01*	0.76	0.02*	0.98	0.01*

Table 5: Spearman correlation between the number of successful copulation and the different activities

4. Discussions

Among the genus *Macaca*, males also gain a long-term direct benefit from choosing dominant females (Smith and Smith, 1988: rhesus macaques; Paul et al., 1992: Barbary macaques; van Noordwijk and van Schaik, 1999: long-tailed macaques). High dominance status and high reproductive success are two variables thought to indicate female quality (Koyama et al., 2001; Nishida et al., 2003). Contrary to expectation, the group males did not preferred females with high dominance status or with high reproductive success (Table 5). In addition, neither dominance status nor age of female stump-tailed macaques has correlation with the reproductive success (Table. 1). The three most preferred females in each sub-group were subordinates. Nutei and Seni were middle-aged females with high reproductive success whereas Kci was old-aged female with no report of giving birth. Thus, age of the females seemed to have no influence on male mate choice.

Sexual swellings have the potential to convey accurate and valuable information about female fertilization potential (Emergy and Whitten, 2003; Deschner et al., 2004). Domb and Pagel (2001) suggested that female sexual swelling is a reliable signal of their long-term reproductive value and thus perhaps an index of a female`s heritable reproductive quality. Female Savannah baboons with large swellings were reported to produce larger number of offspring per year and their offspring were also more likely to survive (Domb and Pagel, 2001). However, stump-tailed macaque females did not show any sexual swelling (Cerda-Molina et al., 2006; pers. Obs.) and could not be one of the factors influencing male mating choice in stump-tailed macaques. In the study group, only the youngest,

nulliparous female (Nui) showed sexual swelling during the observation period (Fig. 1H), this could be attributed to one of the development stage of sexual skins among females. Smuts (1987) have reported that male primates often resist mating with young, nulliparous females, despite persistent attempts by the latter. Similarly, none of the adult male successfully mated with Nui despite the regular proceptive behaviours exerted by her.

Grooming is a service that can be interchanged against other benefits, including mating opportunity (Barrett and Henzi, 2006). Generally, male grooms receptive females more frequently than non-receptive females, and may mount these females subsequently (Kurup, 1988; Gumert, 2000). The present study supported grooming as a mating strategy where all the adult males groomed the females prior to copulation. In addition, females that received more successful copulation were found to received more grooming from the adult males in every sub-group (Table 2, 3, and 4). Mating choice may also be based on former affiliative relationships in nonsexual contexts (Smuts, 1985). However, it has been argued that affiliative relationships are typically established as a result of prior sexual activity (Bercovitch, 1991; Polombit et al., 1997) and that they rarely have a positive impact on future matings (Bercovitch, 1991; Huffman, 1991; Manson, 1994b). Similarly, the number of social interaction between the adult male and female did not seem to influence the sexual interaction between male and female stump-tailed macaques (Table 5). Female proceptive behaviours like presenting and lookback to the male showed no positive correlation with the number of successful copulation received. When females present to the male, the behavioral sexual consequence of the male were mostly sniffing and fingering the perineum of the female that did not always result in mounting. In the present study, adult male mostly approached, groomed and mounted to the estrus female. Male mate choice was found to be associated with female sexual attractivity and females with bright red genital skin colour were found to be more attractive than females with paler and darker genital skin colour (Fig. 1). Although it is not currently possible to provide a proximate explanation, it is suggested that females with red genital skin colour were more attractive to male, receiving more approached, grooming and eventually more successful copulation than the females with darker and paler genital skin colour irrespective of their dominance status, reproductive success, age and sexual behaviours.

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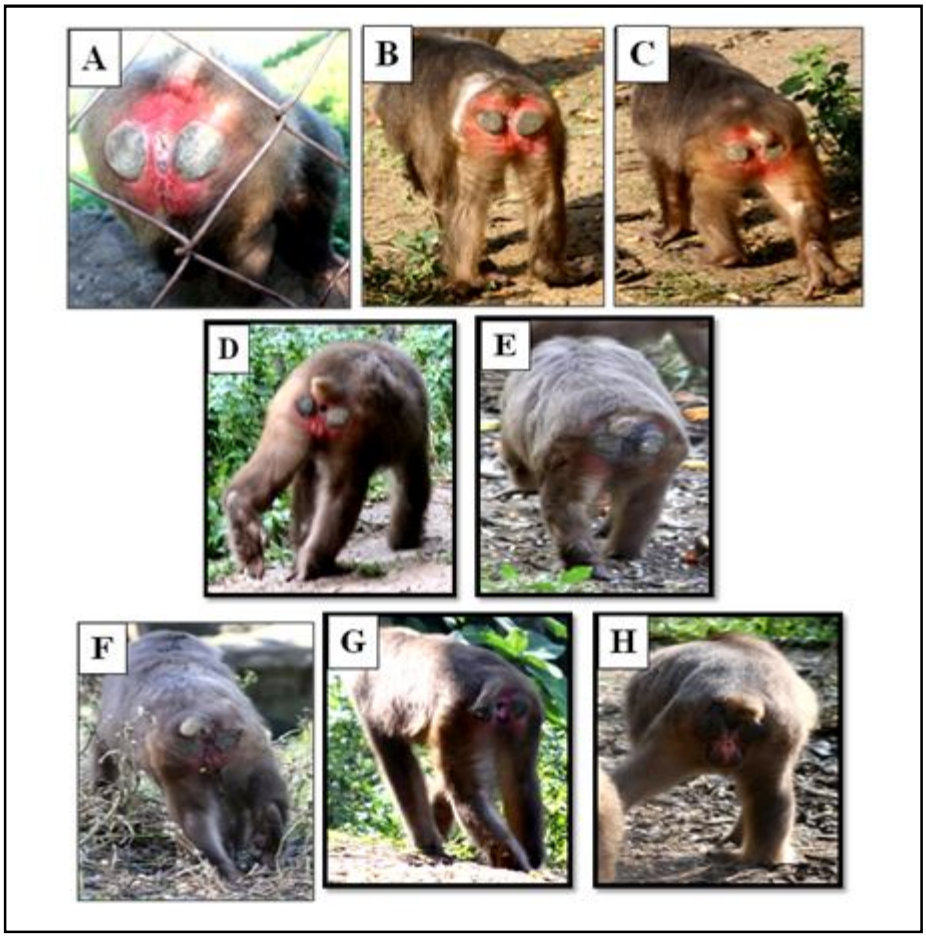

Figure 1: Genital colour of different females. (A): Seni. (B): Kci. (C): Nutei. (D): Hnupi. (E): Buangi. (F): Mci. (G): Dali. (H): Nui

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