

Identification of Follower Status Based on Male Proximity Score in Crested Macaque

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ABSTRACT

Crested macaque live in multimale-multifemale social groups where temporary association (consortship) typically occurs. Current theory and these limited qualitative observations suggest the hypothesis that behavior functions as a means for males to gain access to fertile females. The aim of this study was to investigate follower status based on quantitative method. Males were classified as either “consort males,” “followers,” and “non-followers” based on proximity maintenance every 15 minute uses scan sampling. Tactics used by followers were classified into 1) individual challenge, 2) coalitionary challenge, 3) abandoned takeover, and 4) opportunistic takeover. The proportion of successful takeovers by followers was calculated by dividing the number of takeovers by followers by the total number of observed takeovers. The proportion of followers is higher than average on D-5 and earlier, D-4, and D-3. Only two of the four consort takeover tactics were used by followers. For abandoned which made up 40% and for individual tactic was made up to 11.5% of consort takeovers tactic used. This study contribute to our understanding of alternative mating strategy in primate and provide the first quantitative data demonstrating that following is an alternative mating strategy in crested macaque (*Macaca nigra*).

1. Introduction

Crested macaque live in multimale-multifemale social groups characterized by matrilineal dominance hierarchy with stable female philopatry and male emigration (Dubocq *et al.* 2017). In this system females usually mate with more than one partner and temporary association (consortship) between male and female typically occurs, lasting from minutes to several days (Altmann 1962; Hall and DeVore 1965; Bulger 1993; Engelhardt *et al.* 2004; Engelhardt *et al.* 2006; Higham *et al.* 2009; Dubuc *et al.* 2012; Girrard-Buttoz *et al.* 2014). Consortship is a predominant mating strategy in male primates in multi-male, multi-female groups in which consorting males prevent competitors from gain access to fertile females (Andersson 1994; de Ruiter *et al.* 1994). This

behaviour has been shown to significantly increase reproductive success and reproductive skew of males (Engelhardt *et al.* 2006; Pipe 2011). The duration of consortships and the number of partners which a single female may consort varies tremendously between species (Tutin 1979; van Noordwijk 1985; Manson 1992). Much of crested macaques mating during the period of likely ovulation occurs within consortships.

The link between male reproductive success and reproductive skew in primates designated as the Priority of Access (PoA) model. This model predicts male reproductive success should correlate with male dominance rank and controls for female cycle synchrony (Altmann 1962). Reproductive success and skew will be also be affected by alternative mating strategies (Danish and Palombit 2014). Previous research reveal the limits of PoA model, highlighting the potential of alternative mating strategies in a number of primates (Alberts *et al.* 2003; Wroblewski

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et al. 2009; Bissonnette *et al.* 2011; Dubuc *et al.* 2011; Danish and Palombit 2014). The alternative strategies are a means for subordinate males to queue jump, sire offspring, and reduce the ability of high ranking males to monopolize the fertile females (Abbott *et al.* 2003; Alberts *et al.* 2003; Danish and Palombit 2014). Studies of alternative strategies in primates are relatively rare, with most studies examining: sexual bimaturism in mandrills (*Mandrillus sphinx*) (Setchell and Dixson 2001; Setchell 2003) orangutans (*Pongo pygmaeus*) (Maggioncalda *et al.* 2000; Atmoko *et al.* 2002; Atmoko and van Hooff 2004) and sneak copulations and coalition formation in a number of primates living in multimale-multifemale system (Noë and Sluijter 1995; Soltis *et al.* 1997; Soltis *et al.* 2001; Alberts *et al.* 2003; van Schaik *et al.* 2004).

Recent studies indicate that “following” is an alternative mating strategies in which males maintain proximity to the consort pair for extended times. Following has been observed in olive baboons (*Papio hamadryas anubis*, Hall and DeVore 1965; Strum 1982, 1987, 1994; Bercovitch 1988; Sapolsky 1990; Forster and Strum 1994; Danish and Palombit 2014), yellow baboons (*Papio hamadryas cynocephalus*, Hausfater 1975), Barbary macaques (*Macaca sylvanus*, Kuester and Paul 1989), long-tailed macaques (*M. fascicularis*, Engelhardt *et al.* 2006) and rhesus macaques (*M. mulatta*, Kaufmann 1965). Danish and Palombit (2014) proposed “following” as an alternative mating strategy in olive baboon (*Papio hamadryas anubis*) based on quantitative method. This paper is first present for identify status of following and tactic used by followers in crested macaque (*Macaca nigra*). While following has been shown to be an alternative mating strategy in olive baboons (Danish and Palombit 2014), it has not been quantitatively examined in macaques. Here I present the first quantitative approach from wild crested macaques (*Macaca nigra*) living under natural condition in Tangkoko Nature Reserve. We first asked: 1) When does following occur more frequently? Following is likely to benefit males most during the period of likely ovulation (D-4 until D-1 before deflation of the sexual swelling) (Gesquiere *et al.* 2007; Higham *et al.* 2008). We predicted the number of followers will increase during conception period; 2) Is following an alternative mating strategy in crested macaque? Based on description of following in the literature, We predicted that males would gained access to fertile female via following since the current theory suggest

that following functions as a means to gaining access to fertile female (Danish and Palombit 2014); 3) What tactics do followers use to gain access to the fertile female? We classified the tactics used by followers based on Danish and Palombit (2014). We predicted non-followers would use individual challenge as a consort takeover tactic more than followers, and the abandoned consort takeover would be used by followers more than non follower since the first male able to reach the abandoned female, after the consort male abandons the female gains access to her (Danish and Palombit 2014).

2. Materials and Methods

2.1. Animals and Study Site

One habituated and identifiable group (R1) of crested macaques (*Macaca nigra*) was used in this study. We observed the group from May 2015 to July 2016 in the Tangkoko Nature Reserve, North Sulawesi, Indonesia (1° 34'N, 125° 14'E; an elevation of 1,350 m). The reserve was established in 1980 and comprises an area 8.867 ha (Rosenbaum *et al.* 1998). The location consists of secondary rainforest and primary rainforest and full complement of floral and animal communities as a typical in Wallacea region. The annual rainfall between October and May, with ranges between 1,550 and 2,400 mm. Monthly mean minimum air temperature was constant ca. 24°C throughout the year and the mean maximum air temperature was 27.5°C. During the study, the group consisted of 11 adult males, 33 adult females, 5 subadults, 29 juveniles, and 10 infants, in total 88 individuals. This group has been studied by other scientist since 2006. All members of the group were identified by different marks like a body features, missing fingers, scars, face etc. The study focused on adult males and swelling female during consortship period. Each observed consortship was observed from dawn to dusk at 05.00-17.30 every day for the duration of the period the females consorted; we observed 193 consortships (N=11 males; N=10 females; N=608.93 hours consortship duration).

2.2. Reproductive State of Females and Period of Likely Ovulation

All females that were not pregnant or lactating were considered cycling females. Cycling female crested macaques develop sexual swellings, which change in size throughout their cycle. Sexual swelling

cues were used as an indication they would begin consorting soon. The swelling sizes were collected on each observation day, as well as the identity of all their observed consort partners and followers were recorded using ad libitum with Wintab 10 Odys. We define inflating as beginning of the swelling which the perineal skin of female start to swollen. Swelling is a condition when the skin have fully swollen and the colour is red. Deflating was recognized with appearance of wrinkles in the perineal skin or we can said no swelling. Ovulation occurs around time when the swelling undergoes rapid detumescence (Higham *et al.* 2008). The fertile period can be determined using the day of detumescence (D-Day), with preceding days denoted as D-1, D-2, D-3, ..., D-n. The four days of preceding deflation (D-4, D-3, D-2, and D-1) are the most likely of conception period (Higham *et al.* 2012).

2.3. Follower Status

Males were classified as either “consort male”, “follower”, or “non-follower” during consortship period. Consort males were identified based on extended proximity maintenance during data collection. We considered a male consort is male that remained in close proximity to a cycling female, following her as she traveled, and mate guarded her from the other males for at least ten minutes. For remaining males in the group, we identified male status using a male proximity score (MP-score) (Danish and Palombit 2014), which was calculated for each male separately. or each observation day, we collected male-male distance data via animal scan sampling (Altmann 1974) at 15 minute interval throughout the observation day.

Distance was recorded as 1 m, 2 m, 3 m, 4 m, 5 m, 10 m, 15 m, 20 m, 25 m between consort male and each visible male. If a consort takeover occurred, we calculated the MP scores separately for each consortship period. If a consortship continued the next day, we calculated the MP score only using data from the current day. The MP score is calculated as below for each consort male-male dyad, for each scan sample intervals:

$$MP = \sum (1/\text{distance}_1) * ([1/\text{number intervals}] * 100) + \dots (1/\text{distance}_n) * ([1/\text{number intervals}] * 100)$$

The MP score components were calculated from each scan interval by taking the product of the reciprocal of the distance between males and the

percentage of time at that distance. The score is the sum of all such components, from the first scan sample to the nth scan sample. If a male was not visible during a particular scan sample, the component value for that sample was zero. Based on preliminary data, males with a score of ≥ 5.5 should be classified as followers, while males with a score less than 5.5 were classified as non-followers.

2.4. Classification of Consort Takeover Tactic

Consort takeover tactics were used by followers has been classified: 1) individual challenge, 2) coalitionary challenge, 3) abandoned takeover, and 4) opportunistic takeover (Danish and Palombit 2014). Individual challenge means a single male directed aggression at the consort male; Coalitionary challenge is the direction of aggression toward the consort male by male-male coalition; Abandoned takeover is defined when the consort male moved away without any aggression; Opportunistic takeovers is the new male gained access to the fertile female as the result of some form of external distraction.

2.5. Proportion of Successful Takeover by Followers

Female cycle day was determined using the day of detumescence (D-Day), with preceding days denoted as D-1, D-2, D-3, ..., D-10 (Gesquiere *et al.* 2007). The proportion of successful takeovers by followers was calculated by dividing the number of takeovers by followers by the total number of observed takeovers. The proportion of successful takeover before D-4 were combined because these days are not likely days of conception and females vary in the number of these days during which they consort (Bercovitch 1995; Gesquiere *et al.* 2007).

3. Results

3.1. Follower Status

The proportion of followers is higher than average on D-5 and earlier, D-4, and D-3 (Figure 1). Surprisingly, the proportion of followers is lower than average on D-1 and average on D-2. The highest proportion of following occurs at D-4 (0,1096) and the lowest proportion of followin at D-1 (0,0356). Contrary to our prediction, following occurs more only during part of the period of likely ovulation, and (contrary to our predictions) prior to that period.

3.2. Consort Takeover Tactic Used by Follower

Only two of the four consort takeover tactics were used by followers (Figure 2). For abandoned, which made up 40% of consort takeovers tactic used by followers. While abandoned consort takeovers were primarily carried out by non-followers, supported our prediction. Only 11.5% of males using the individual tactic were followers. This indicate that followers mainly used abandoned consort takeovers as a mainly a means to gain access to fertile females.

3.3. Proportion Successful of Consort Takeover

Overall, 25.4% of consort takeovers were executed by males who were followers of the targeted

consortships. Notably, the percentage of consort takeovers by followers increased up during the periods of likely ovulation, reaching a maximum at D-3, but declining after (Figure 2).

4. Discussion

Followers were most involved in several days likely conception period, between D-4 until D-2 (Figure 1). We propose that such following activity allows followers to gain access to swelling female. Following provides males with access to fertile females; our data therefore support the conclusion that following is an effective alternative mating strategy. Two consort takeover tactics were used by followers (Table 1). For

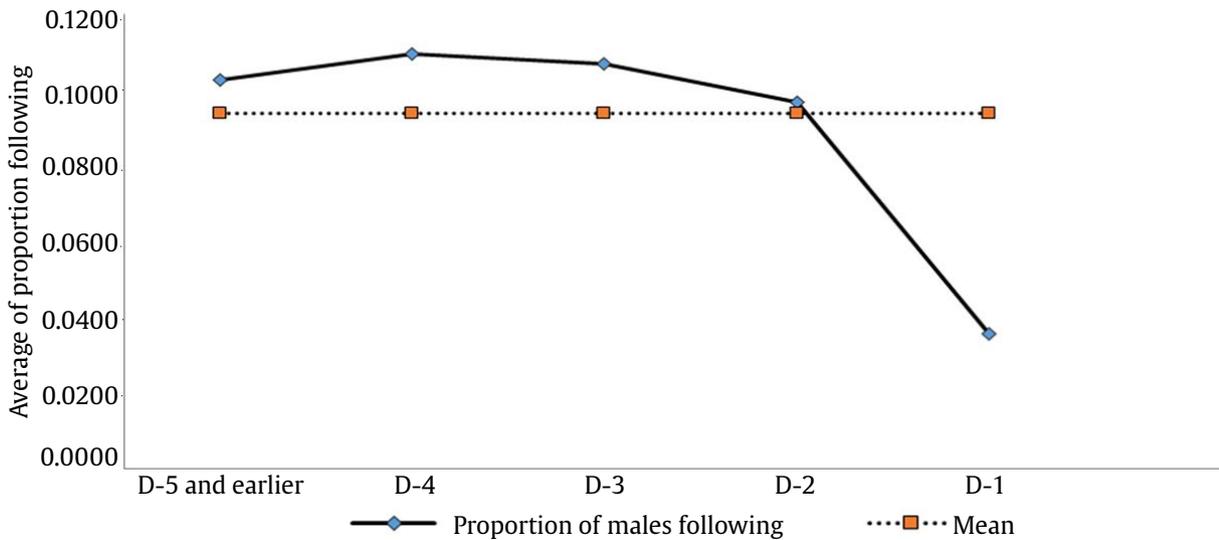


Figure 1. Cycle Day related to proportion of males following in crested macaque (*Macaca nigra*)

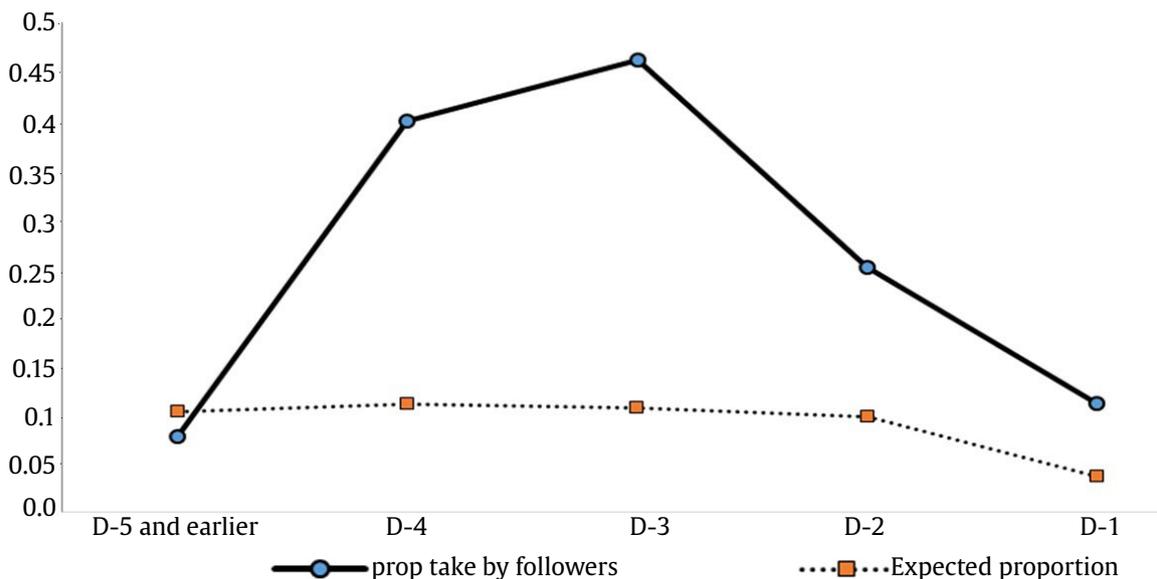


Figure 2. Proportion successful consort takeover by follower

abandoned, which the most of consort takeovers tactic used by followers. Abandoned consort takeovers were primarily carried out by followers, which partially supported my prediction. This indicate that followers used abandoned as a mainly consort takeovers tactic. Surprisingly, both of these consort takeover tactics were used more by non followers than followers (Table 1), suggesting following is not component of a non-followers strategies.

Contrary with our predictions, abandoned consort takeovers was used equally by non followers; I suggest that this pattern is due to the nature of such consort takeovers, which are categorized by seizing a chance to obtain access to a female. Since consort males typically remained in close proximity to the consort female (Pasetha pers. obs.), there appeared to be little opportunity for sneak copulations, supported by other studies of baboons (Alberts *et al.* 2003; Danish and Palombit 2014).

Based on our findings, we propose that following is an alternative mating strategy in crested macaques. While males of all dominance rank gain access to fertile female by following, my data indicate that following provides mid- and low-ranking males, who would otherwise be excluded from mating, with access to females. We suggest that strategy use by low- and mid-ranking males has impacted the strategies of high-ranking males, resulting in their adoption of the following strategy. We propose that the occurrence of following accounts for the well documented deviation from the priority of access model (Berard *et al.* 1993; Alberts *et al.* 2003; Wroblewski *et al.* 2009; Bissonnette *et al.* 2011; Dubuc *et al.* 2011, Danish and Palombit 2014) in other species, such as baboons. This study provide the first quantitative data demonstrating that following is an alternative mating strategy in crested macaques (*Macaca nigra*). Our finding that followers, rather than nonfollowers, typically pursue abandoned consort takeovers forces us to reexamine in male crested macaques.

Table 1. Percent consort takeovers tactic used by followers in crested macaque

Tactic	Follower	Non follower	Percent followers
Abandoned	6	15	40.0
Individual	3	26	11.5
Total	9	41	22.0

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