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## RESEARCH ARTICLE

# Alpha Male Replacements and Delayed Dispersal in Crested Macaques (*Macaca nigra*)

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In species with a high male reproductive skew, competition between males for the top dominant position is high and escalated fights are common between competitors. As a consequence, challenges incur potentially high costs. Selection should favor males who time an alpha male challenge to maximize chances of a successful outcome minimizing costs. Despite the importance of alpha male replacements for individual males, we know little about the timing of challenges and the condition of the challenger. We investigated the timing and process of alpha male replacements in a species living in multi-male groups with high male reproductive skew, the crested macaque. We studied four wild groups over 6 years in the Tangkoko Reserve, North Sulawesi, Indonesia, during which 16 alpha male replacements occurred. Although unusual for cercopithecines, male crested macaques delayed their natal dispersal until they attained maximum body mass and therefore fighting ability whereupon they emigrated and challenged the alpha male in another group. Accordingly, all observed alpha male replacements were from outside males. Ours is the first report of such a pattern in a primate species living in multi-male groups. Although the majority of alpha male replacements occurred through direct male-male challenges, many also took place opportunistically (i.e., after the alpha male had already been injured or had left the group). Furthermore, alpha male tenures were very short (averaging ca. 12 months). We hypothesize that this unusual pattern of alpha male replacements in crested macaques is related to the species-specific combination of high male reproductive skew with a large number of males per group. Am. J. Primatol. 9999:1–8, 2015.

**Key words: alpha male replacement; dispersal**

## INTRODUCTION

In primates, as well as in other mammals living in multi-male groups, high- and especially top ranking males normally have higher reproductive success than other males in the group [e.g. Alberts et al., 2003; Ostner et al., 2008; Schülke & Ostner, 2008]. However, the difference in reproductive success between top ranking (alpha) and lower ranking males varies among species [Kutsukake & Nunn, 2006]. When the reproductive benefits of being alpha are high, males compete fiercely for this position [Borries, 2000; Hamilton & Bulger, 1990; Perry, 1998; van Noordwijk & van Schaik, 1985]. Escalated fights and severe injuries are often consequences of these challenges and bear high risks and potential costs for the males involved. Selective pressures should therefore lead to males timing their alpha male challenges according to the likelihood of winning, to minimize costs. Clearly the ability of a male to attain and maintain the alpha rank position is critical to his overall reproductive success, but our understanding of how alpha male replacements take place in primates remains limited.

The potential for males to monopolize females, and therefore reproduction, directly influences the benefits a male obtains from being in the alpha position [Kutsukake & Nunn, 2006]. The higher the

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monopolization potential, the higher is the reproductive skew, leading to the evolution of high risk strategies in rank acquisition, such as individual challenges and escalated fights [van Noordwijk & van Schaik, 2004]. As a consequence of the cost and benefit trade-off, males of species in which the monopolization potential of single males is low often achieve the alpha male position through low-risk tactics, such as queuing or succession by the death or departure of the former alpha male, rather than by fighting [e.g., Huffman, 1991]. In contrast, species with a high reproductive skew show intense male-male competition over access to females, and males most often achieve alpha rank through high risk challenges leading to common escalated fights between males [Port & Cant, 2013]. Alpha rank in primate species with a high reproductive skew can also be attained opportunistically (e.g., due to the absence of the resident alpha male), however, or through succession [e.g., Jack & Fedigan, 2004].

Alpha male replacements can occur from either resident group males, that is, from within the group, or newly immigrated males, that is, from outside. For multi-male groups, predation risk may play a role in this regard [Pradhan & van Schaik, 2008]. According to this hypothesis, younger, low-ranking males grow to full strength within a non-natal group only if they stay at the periphery: in the group's center they would face frequent harassment by the alpha male. In species facing high predation risk, young-, non-natal males thus face the trade-off between achieving safety from predators versus avoiding alpha male aggression. For this reason, males of such species, should grow into their physical prime within their natal group and only subsequently emigrate to challenge alpha males in other groups. By contrast, if predation risk is low, even on the group's periphery, males can afford to grow into their prime and challenge the alpha male from within a non-natal group. Evidence that supports this hypothesis so far comes from chacma baboons, a species facing high predation risk [Alberts & Altmann, 1995], where males grow to full strength within their natal group and then emigrate to challenge alpha males in other groups [Beehner et al., 2005; Hamilton & Bulger, 1990].

Regardless of whether a male challenges from within the group or from outside, he generally acts on his own [Borries, 2000; Hamilton & Bulger, 1990; Suzuki et al., 1998; van Noordwijk & van Schaik, 1985]. There are some known exceptions, however, in which coalitions of several males take over a group [Pope, 1990] or where male bonds within a group are useful for a challenger to achieve a high rank [Schülke et al., 2010]. These exceptions aside, individual fighting ability characterizes the general pattern of acquiring alpha status in males, and therefore physical condition and fighting ability are the principal determinants of male rank in the majority of primate species [e.g., Borries, 2000; Henzi & Lucas, 1980; Marty et al., in revision; Perry, 1998; van Noordwijk & van Schaik, 2001]. Accordingly, challengers are generally described as in their prime [van Noordwijk & van Schaik, 2004].

The decision by a male to challenge a resident alpha male is a trade-off between the derived benefits of a successful challenge and the potential costs of an escalated fight. A well-timed challenge will increase the chances of success, whereas an ill-timed challenge may lead to defeat, severe injuries, and a reduced chance of success in the near future. The potential to win a challenge depends on both the physical condition of the challenger and that of the challenged male. As such, males should time their challenges according to their own physical condition in relation to the potential strength of the alpha male. In long-tailed macaques (*Macaca fascicularis*), for example, the chances of winning a challenge increase with tenure length of the alpha male [van Noordwijk & van Schaik, 2004].

Since information on the alpha male's condition is easier to obtain from within a group, pre-prime males of many species immigrate into non-natal groups where they may soon achieve a high rank [Pusey & Packer, 1987]. In some species challenges from outside are common, however, and males of these species may also acquire knowledge on the group structure and potential benefits of a migration by surreptitiously observing a group prior to an immigration [Cheney & Seyfarth, 1990; Teichroeb et al., 2011; van Noordwijk & van Schaik, 2001]. Once established in the top dominant position, a male will strive for long tenure to increase his reproductive benefits [van Noordwijk & van Schaik, 2004].

The overall aim of this study was to investigate alpha male replacements in a primate species with a high reproductive skew and intense male-male competition, the crested macaque (*Macaca nigra*). We were particularly interested in the correlation between male condition and variables of the target group. In crested macaques, the fitness benefits of being alpha are extensive because both groups contain many females and male reproductive skew is high [Engelhardt et al. in revision; Marty et al., in revision]. We assume predation pressure is relatively low because of the absence of diurnal predators [e.g., van Schaik, 1989], though we know that large reticulated pythons prey on crested macaques (pers. obs.). Attacks from birds of prey have never been observed nor do crested macaques give alarm calls after spotting any birds.

Here, we investigated the timing of alpha male replacements, and determined both internal and external factors leading to alpha male challenges. Based on the knowledge obtained on comparable species regarding the social system and reproductive skew (e.g., long-tailed macaques), we predicted that (1) alpha males would be replaced by challengers from within the group: (2) the longer the tenure of the alpha male, the more likely he would be challenged:

and (3) challengers would be in their physical prime when challenging.

A secondary aim of our study was to investigate the alpha male tenure in male crested macaques. In a recent study, the number of females in a group, sex ratio, and inter-birth interval were all identified as predictors of alpha male tenure and the frequency of alpha male replacements in mammals living in multi-male multi-female groups [Lukas & Clutton-Brock, 2014]. We tested whether this pattern held true for our study species. Since the number of females in groups of crested macaques is high, [Marty et al., in revision] but the inter-birth interval is long [Mittermeier et al., 2013], we predicted (4) an intermediate (ca. 50 months [Lukas & Clutton-Brock, 2014, supplementary material]) alpha male tenure compared to other primates.

## METHODS

### Study Species

Crested macaques (*Macaca nigra*) live in large multi-male multi-female groups with up to 100 individuals [Reed et al., 1997]. The sex ratio is around three adult females per male [O'Brien & Kinnaird, 1997]. Females are philopatric whereas all males leave their natal group [Neumann et al., 2010]. Males often migrate several times during their lives and males with low fighting ability immigrate into a new group along with males who have high fighting ability [Marty et al. in revision]. Migrations are not restricted to certain times but occur year-round. Crested macaques are frugivorous and spend the majority of their time on the ground [O'Brien & Kinnaird, 1997]. Males and females both show linear dominance hierarchies [Duboscq et al., 2013; Neumann et al., 2011; Reed et al., 1997]. While females are described as socially tolerant [Duboscq et al., 2013] according to the four grade scale designed for macaques [Thierry, 2007], males show intense male-male competition and high reproductive skew, because high-ranking males have priority of access to fertile females [Engelhardt et al., in prep.]. Male body mass is highly correlated with rank and therefore a reliable predictor of fighting ability in this species [Marty et al. in revision]. Females show large sex skin swellings of the anogenital region, which relatively reliably indicate the fertile phase of the ovarian cycle [Higham et al., 2012]. Crested macaques are moderately seasonal breeders as per the definition of van Schaik [1999] [Engelhardt et al., in prep]. Because of a high monopolization potential of females during the fertile phase, especially during the conceptive cycle, infanticide is likely to occur in this species. Although we have not yet directly observed infanticide, the mortality rate of infants increases after new alpha males immigrate into a group, which hints that sexually selected infanticide may occur [Kerhoas et al., 2014].

### Study Site and Subjects

We collected our data in the Tangkoko Reserve in North Sulawesi, Indonesia (1°33'N, 125°10'E) as part of an ongoing long-term project (*Macaca nigra* Project, www.macaca-nigra.org). The reserve ranges from sea level to 1,350 m and spans an area of 8,867 ha of lowland rainforest [Rosenbaum et al., 1998]. The habitat of the study groups was a mixture of undisturbed primary forest, secondary forest, and regenerating former gardens.

We studied groups of wild crested macaques from mid-2006 until the end of 2012. Two of the observed groups (R1 and R2) were under continual observation studied during this period, whereas observations of PB started in 2008. We followed a fourth group (R3) sporadically beginning in 2006, but we collected regular data from July to December 2012. Group size varied between 60 and 90 individuals for R1, R2 and PB groups, whereas R3 consisted of ca. 25 individuals. All adult animals were individually recognizable and fully habituated to the presence of human observers.

### Data Collection

We followed groups at least once a week, but normally several times per week. We conducted all-day group follows and collected behavioral data on aggressive interactions using focal animal sampling [Altmann, 1974] and ad libitum sampling. We entered all data into hand-held computers using spreadsheet software (PTab Spreadsheet v.3.0; Z4Soft). We classified males as immigrants when they joined a group and interacted affiliatively with its members.

### Determination of the Dominance Hierarchy

We calculated dominance ranks, as David's scores [de Vries et al., 2006] with the package "Steepness" [Leiva & de Vries, 2011] in R [R Team, 2009]. As input data, we included all male-male displacements (approach/leave interactions) and dyadic agonistic interactions with a clear winner/loser outcome (e.g., target of aggression leaves/flees) in order to quantify dominance hierarchies. Depending on the available data, interactions within the first 3–6 months after the immigration were included in order to obtain an accurate rank. For some males, we did not have enough such interactions to calculate a David's score, but if these males successfully challenged and expelled a confirmed alpha male, we included them as alphas in our analyses.

### Body Mass

As body mass is a reliable indicator of dominance and thus of fighting ability in male crested macaques [Marty et al., in revision], we measured body mass of five natal emigrants, either shortly before or after their first dispersal, and of eight non-natal resident males. For our non-invasive measurements we used a hanging scale [Scalematic enterprise, 3A-DLE scale, weight step 0.01 kg: Marty et al. in revision]. We supplemented our data set with body mass data from two natal and six non-natal group males measured during a previous study [Neumann et al., 2010].

### Statistical Analyses

We used multiple Wilcoxon matched-pairs signed rank tests to investigate parameters on which a male might base his decision to challenge a group's alpha male position. Specifically, we compered selected parameters of a group during two periods: 1. on the day of the takeover and 2. on the day 90 days before the takeover. The selected parameters were: (1) the number of males and (2) the tenure length of the alpha male at this time. As the same data set was tested twice (for the number of males and the alpha male tenure) we correct for multiple testing using the Benjamini–Hochberg correction [Benjamini & Hochberg, 1995]. We used a Mann–Whitney *U*-test (in R) to determine whether the body mass of dispersing natal males (prospective alpha males) differed from the body mass of resident non-natal males. All tests were carried out with two-tailed probabilities and the alpha level set to 0.05. This research adheres to the legal requirements of the German and Indonesian governments, and adheres to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

## RESULTS

We observed 21 alpha male takeovers and could verify the alpha male position for 16 of these (Table I). For 10 males, we could determine a significant steep and linear hierarchy upon immigration. For an additional six males, we observed a fight or a direct replacement of a confirmed alpha male. All takeovers involved outside males whose alpha status was detectable within a few hours after immigration. About half (5 of 9) of the observed alpha male takeovers involved a direct challenge from a newly immigrated male, while the rest were opportunistic takeovers after the resident alpha male left the group or was injured during a previous challenge. The average tenure of an alpha male was 361 days (range: 21–1258, $n = 14$).

Most (6 of 8) of the new alpha males with known group of origin were males dispersing from their natal group. After correcting for multiple testing [Benjamini & Hochberg, 1995], neither the number of males (Wilcoxon matched-pairs signed rank test, $V = 26.5, P = 0.62, n = 15$), nor the alpha male tenure (Wilcoxon matched-pairs signed rank test, $V = 76$, $P = 0.06$, $n = 13$) were significantly different on the day of immigration compared to the control day 3 months before. Separate post hoc analyses for natal group emigrants revealed that 75% of these males achieved alpha male status upon their initial migration. The remaining males gained alpha male status within a half a year in another group (and one male after a group fission). The body mass of natal group emigrants was significantly higher than the average body mass of non-natal males in the group (Fig. 1). We found alpha male tenure in crested

**TABLE I. Characteristics of 16 Male Takeovers, Including Identity of the Male, Identity of the Group in Which the Takeover Occurred, Takeover Date, Tenure Length after Takeover, Whether the Takeover Was Opportunistic (i.e., Followed Prior Injury to/Absence of Former Alpha-Male), and Whether the Male Taking Over the Alpha-Position Had Transferred Directly From His Natal Group**

| ID | Group | Date of entry "DD/MM/YR" | Tenure length (d) | Opportunistic takeover | Natal dispersal |
|---|---|---|---|---|---|
| LL | PB | 20/07/09 | 908 | - | - |
| EL | PB | 14/01/12 | 115 | Yes | No |
| JL | PB | 19/05/12 | - | Yes | Yes |
| AJ | R1 | 26/09/07 | 159 | - | - |
| PM | R1 | 03/03/08 | 21 | No | - |
| IM | R1 | 24/03/08 | 100 | No | - |
| TJ | R1 | 13/01/09 | 371 | Yes | Yes |
| MM | R1 | 19/01/10 | 36 | Yes | Yes |
| DL | R1 | 21/02/10 | 99 | - | - |
| VL | R1 | 31/05/10 | 470 | - | Yes |
| EL | R1 | 03/09/11 | 80 | - | - |
| AN | R1 | 14/03/12 | 418 | No | - |
| ZJ | R2 | 08/03/07 | 1,258 | - | Yes |
| TL | R2 | 17/05/11 | 582 | - | Yes |
| FL | R2 | 19/12/12 | 435 | No | No |
| CN | R3 | 26/07/12 | - | No | - |

Hyphens indicate lack of data.

macaques to be very short (12 months) and the interbirth interval of crested macaques to be about 22 months [Mittermeier et al., 2013].

## DISCUSSION

Our results do not fit Pradhan and van Schaik [2008] hypothesis, which assumes that males in species with low predation pressure should challenge alpha males from within the group rather than from outside. In our study population, alpha male replacements were exclusively conducted by newly immigrated males. While extra-group replacements are obligatory in species with one-male groups, takeovers of the alpha-rank position in multi-male groups may be executed by both resident and newly immigrated males [e.g., long tailed macaques: van Noordwijk & van Schaik, 1985; tufted capuchins: Robinson, 1988; chacma baboons: Beehner et al., 2005]. Our observations suggest that predation pressure may not be the only reason that males of this species strongly prefer to challenge alpha males from outside the group.

An alternative explanation for this phenomenon may be the combination of having many males present in a group and the fitness value of high-ranking positions, related to high skew in male reproductive success [Engelhardt et al., in revision]. As a consequence, pre-prime males immigrating into a new group may not have a chance to sire offspring there before reaching physical prime, and also may face costs that are too high when they fight to move themselves up the hierarchy later on. Strong weaponry (e.g., canine size dimorphism) reflecting high male-male competition may reinforce outside takeovers by adding additional cost to each challenge. Indeed, crested macaques exhibit one of the most pronounced canine dimorphisms of all primates [Plavcan & van Schaik, 1992]. As a consequence, males involved in escalated fights often get injured and immediately drop precipitously in rank, often leaving the group (personal observation). It took months for many of our study males to recover following injuries from intrasexual competition, and others never fully recovered. A severe injury from a fight might therefore be the end of a male's reproductive career. Thus, young males may be better off gaining strength in their natal group, where they do not compete over access to females, and timing challenges to coincide with reaching their peak physical strength. Additionally, with a very high reproductive skew in this species, young males who are not in their prime are less likely to gain reproductive advantages in a new group. We therefore hypothesize that, in our study species at least, delayed dispersal is an adaptive strategy to avoid the costs of immigrating as a pre-prime male, thus maximizing fighting ability and chance of successfully challenging an established alpha male immediately upon first immigration. A similar example can be seen in chacma baboons, which are also characterized by high reproductive skew [Alberts et al., 2006], high canine dimorphism [Plavcan & van Schaik, 1992], and a large number of adult males per group [Engh et al., 2006]. Should our hypothesis be true, we would expect to find outside takeovers in other primates with high reproductive skew, and many males per group as well. However, such species are probably rare in primates, because the number of males and reproductive skew are usually negatively correlated with each other [Gogarten & Koenig, 2012]. The reason why some species do not follow this pattern is still unclear and merits further study.

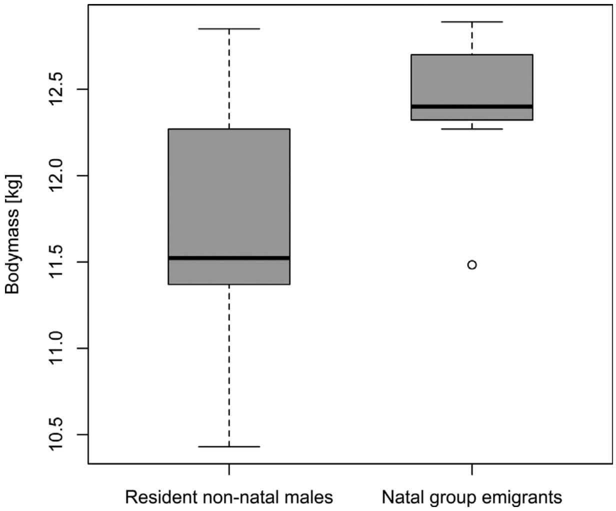

Fig. 1. Body mass (median, 1st and 3rd quartile, 95% variance and outliers) of males leaving their natalgroup (n = 7) compared to non-natal males (n = 14). Natal group emigrants were significantly heavier thanresident group members (two tailed Mann–Whitney *U*-test, $U = 81.5$, $P = 0.01$).

Although we observed that newly immigrated males often attained top rank by physical challenges, this was not always the case. A substantial number of alpha male replacements were opportunistic, in that already injured alpha males were replaced by a newly immigrating male without a fight and within a few days. These injured alpha males sometimes won a fight with an outside challenger, but their ranks dropped immediately if they were seriously injured. Even though these replacements were opportunistic, all of the newly arriving prospective alpha males were in their physical prime. Crested macaques appear regularly to observe other groups before joining them, and thus can respond quickly to changes [Marty et al., in revision]. Opportunities for learning occur during frequent intergroup encounters or when males temporarily leave their group and potentially observe other groups. Group residency may thus be less important to learn about the condition of alpha males than previously thought [van Noordwijk & van Schaik, 2004].

In addition to the challenger's physical condition, we predicted that the characteristics of the target group and the condition of the alpha male, especially the length of his tenure to date, would influence the timing of a challenge by a young prime male as seen in other species [van Noordwijk & van Schaik, 2004]. However, our data did not confirm this prediction. In our study animals, the length of alpha male tenure did not differ between the day of challenge and a control day. Furthermore, the number of males in the target group in general does not seem to have an influence on the challengers' decision to immigrate or not.

In addition to determining the process behind alpha male replacements, we were also interested in how long male crested macaques are able to defend their top position once it was won. According to a recent meta-analysis carried out across various mammalian species [Lukas & Clutton-Brock, 2014], group characteristics such as the number of females in the group, sex ratio, and inter-birth interval all influence length of alpha male tenure in multi-male groups. Following the detected pattern, we expected alpha male tenure in crested macaques to be intermediate for primates (ca. 50 months, see [Lukas & Clutton-Brock, 2014]), since the high number of females in the group and the high sex ratio predict a short tenure, whereas the relatively long inter-birth interval suggests a rather long tenure. Instead, with an average of ca. 12 months, our crested macaques showed one of the shortest tenures known for any primate species (average 50 months in multi-male, multi-female primate groups [Lukas & Clutton-Brock, 2014]), with only chacma baboons holding shorter tenures [Hamilton & Bulger, 1990; Palombit, 2003]. Here again, crested macaques do not seem to follow the general pattern possibly because the inter-birth interval has far less influence on tenure length than the other two variables. A high operational sex ratio in combination with a high number of females in the group is expected to place high pressure on outside males to reach the top dominant position. Because of this pressure, in combination with the high value of the top dominant position, males might not be able to defend the alpha male position for an extended period, regardless of inter-birth interval.

Altogether, crested macaques seem not only to show extreme patterns in alpha male replacements and tenure lengths, but also to be a species more generally at one extreme of the primate spectrum with respect to male-male competition. We think this is a consequence of different factors reinforcing each other, leading to a feedback loop. With high reproductive skew and alpha male replacements taking place only from outside males, short alpha male tenure and long inter-birth intervals, infanticide risk in this species is high and cannot be reduced by paternity confusion in group males, since all new alpha males had no chance to sire offspring before they arrived (no extra group paternities have been found in 67 tested infants, [Engelhardt et al. in revision]). As a consequence, females should provide clear signals of fertility to concentrate paternity on the highest ranking male, who is more likely to protect offspring with increasing degree of paternity certainty [Heistermann et al., 2001; Hrdy, 1979; Soltis et al., 2000]. In this way, females reinforce the existing reproductive skew and heighten male-male contest competition, thus leading to an exaggerated sexual dimorphism in weaponry. Intense male-male competition over the alpha male position should, in turn, lead to shorter tenure for top dominant males and to delayed natal dispersal. Indeed, there is particular risk of infanticide after alpha male replacements in crested macaques [Kerhoas et al., 2014], and females seem to have the clearest signals of fertility observed in anthropoid primates so far [Higham et al., 2012]. Because of these characteristics, crested macaques are excellent models for testing current predictions on the evolution of sexual selection and male-male competition. These macaques seem not to match the dispersal and alpha male replacement patterns observed in most other primate species, which yields opportunities to question current theories and to develop new ideas on the evolution of these patterns.

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