

Male-infant interactions in wild crested black macaques, *Macaca nigra*

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Direct fitness is measured as the number of surviving offspring. Thus adult males may try to produce as many offspring as possible or to increase the survival of their offspring. Recent findings have shown the many potential benefits of fathers' presence and support on infants' development and survival. However, little is known about the influence of socio-ecological factors on male-infant interactions. The main aim of this thesis was therefore to investigate male-infant interactions in wild crested macaques (*Macaca nigra*). In particular, we aimed to examine the affiliative and agonistic interactions taking place in this species, along with the factors influencing these interactions and offspring survival. Data collection for this thesis took place in the Tangkoko-Duasudara Reserve in Sulawesi, Indonesia, on 3 wild groups of crested macaques. For the first study, data were collected on migrations, births, disappearances, and encounters between groups over 5 years. We analyzed the influence of socio-ecological factors (e.g. rainfall, alpha-male position takeover, and male hierarchy stability) on pre- and post-natal loss. The results showed that high infant mortality was mainly associated to male alpha-position takeover, which suggests that infanticide may indeed occur in this species. In addition, we found that female within-group competition for food sources and between-group resource defense influenced fetal and infant loss. Based on these findings, we were interested to see whether fathers protected their own offspring against male attacks. Thus, in the second study, we investigated the social determinants and characteristics of male-infant affiliations. Our results indicate that adult males and infants form preferential association, and that infants initiate the majority of male-infant affiliations. Infants initiated affiliations mainly towards a high ranking male or a male in a close relationship with their mother. In addition, infants affiliated mainly with adult males in the absence of their mother, while males affiliated mostly with infants when the infants' mother was present in proximity. Furthermore, males initiated affiliations towards an infant when they held a high rank or when they had a strong bond with the infant's mother. Interestingly, paternity did not affect male-infant affiliations. In conclusion, these studies provide insights in the specifics of both infant survival strategies and male reproductive strategies. In addition, we show that infants are active agents in establishing and maintaining preferential relationships with males. This thesis, thus, confirm that male-infant interactions, although rare, have a strong influence both on males' and infants' direct fitness.

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Summary

Direct fitness is measured as the number of surviving offspring. To increase direct fitness, adult males may try to produce as many offspring as possible or to increase the survival of their offspring, potentially through care. In mammal species, male-infant interactions are rarely observed but may cover a wide array of social behaviors, from extensive paternal care to infanticide. In fact, infanticide by males has been found in many mammal species. Several hypotheses have been proposed to explain this behavior, but the dominant theoretical framework is the sexual selection hypothesis (van Schaik and Janson 2000), whereby males kill unrelated and un-weaned infants to accelerate their mothers' return to estrus, thus increasing mating access and the production of their own offspring. In case of infanticide, sires may try to protect their offspring, a clear form of paternal care, to increase their direct fitness. In general, infant care by adult males occurs in less than 10% of mammal species (Woodroffe and Vincent 1994), but is relatively common in primate species (up to 40%; Kleiman and Malcolm 1981). Recent findings have shown the positive effect of fathers' presence and direct care on infant development (Charpentier et al. 2008) and resource access (Huchard et al. 2013). However, no studies have thoroughly explored in one species the determinants of male-infant interactions and its associated influence on offspring survival at a pre- and post-natal stage while controlling for the interplay of several other socio-ecological factors.

Crested macaques (*Macaca nigra*) are an ideal species to investigate male-infant interactions, as infant mortality reaches 20% (Engelhardt and Perwitasari-Farajallah 2008) although there is a low predation pressure. Crested macaques live in multi-male multi-female groups with female philopatry (i.e. females stay in their birth group throughout their life) and male dispersal. The social system is very dynamic with frequent male migration (Neumann et al. 2011), short male group tenure and high alpha-male position turn-over (i.e. top ranking male in the male dominance hierarchy; Marty et al. 2015). Paternity is highly skewed towards alpha males due to their successful mate guarding, although females are promiscuous throughout their estrus cycle. Finally, breeding is aseasonal (Engelhardt and Perwitasari-Farajallah 2008). As a result, males fight fiercely for

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dominance and thus infanticide as a male reproductive strategy may emerge. Based on the high infant mortality in this species, strategies to improve survival may be critical for infants to develop. In addition, sires may protect their offspring from infanticidal males.

The overall aim of this thesis was therefore to investigate the male-infant interactions in wild crested macaques (*Macaca nigra*). In particular, our aim was to understand which type of interactions takes place in this species, along with the factors influencing these interactions and offspring survival. In study 1, we studied which ecological and social factors may directly influence pre- and postnatal offspring survival. Among diverse socio-ecological factors, such as mother parity, rainfall (proxy of fruit seasonality) or maternal dominance rank, we tested specifically whether male immigration, alpha-male position takeover and male hierarchy stability had any impact on infant survival. In study 2, we analyzed the presence and specificity of male-infant affiliations. In addition, we compared the social factors influencing male-infant affiliations initiated either by males or by infants, in order to investigate the specifics of both infant survival strategies and male reproductive strategies.

Data collection for this thesis took place within the Macaca Nigra Project in the Tangkoko-Duasudara Reserve in Sulawesi, Indonesia, on 3 wild groups of crested macaques. For study 1, ad libitum data were collected on migrations, births, disappearances, monthly female sex skin swelling cycles (i.e. a sign of monthly ovarian activity) and encounters between groups. In addition, outcomes of dyadic aggressions and displacements were recorded to determine males' and females' dominance rank. Data were collected over 5 years and comprised 99 fetuses and 78 infants from 60 females, with a total of 3894 observation days across the 3 groups. For study 2, behavioral focal data (Altmann 1974) were collected on 35 infants (i.e. from birth to 1 year of age) in 3 wild groups between 2008 and 2010. Behavioral data focused on affiliative and agonistic interactions between any group members and the focal infants. In addition, spatial proximity between the focal infants and group members was recorded using point time sampling (Altmann 1974). In total, 3611 hours of focal observations were collected with an average of $100.63 \text{ hours} \pm 23.87 \text{ (SD)}$ per infant that survived to 1 year of age. In addition, genetic samples were collected and analyzed on all infants, mothers and all adult males present in any of the 3 groups and paternity was assigned to all focal infants. Statistical methods applied during data analysis for the two studies comprised non-parametric tests, Cox proportional hazards models and linear mixed models.

The results of study 1 revealed that infant survival was most impaired after a recent take-over of the alpha-male position by an immigrant male, while infant survival probability was not influenced by male hierarchy stability or merely male immigrations. In addition, infant age, gender, maternal rank and mother parity had no effect on their survival. However, we also found that infant survival improved with an increase of number of females in the group and rainfall. Fetal survival was also improved by the interplay of these two factors, but more so in high-ranking females than lower-ranking ones. Interestingly, fetal survival was also improved with a higher occurrence of intergroup encounters. Overall, these findings suggest, thanks to a multivariate approach, that the interplay of environmental seasonality, female within-group competition for food sources (through dominance hierarchy), and between-group resource defense influenced fetal and infant loss in this species. However, they also show that factors influencing pre- and postnatal mortality may differ in details. In addition, those results highlight that high infant mortality is mainly associated to male alpha-position takeover in this species, which suggest that infanticide may indeed occur, and it is not a by-product of an increase in male-male aggressions during instable male hierarchy and male immigration events.

Study 2 provided evidence that affiliations were the most common male-infant interactions in crested macaques, and it further investigated the key factors that may influence these affiliations. Based on the results of study 1 that male alpha-position takeover greatly increases infant mortality, we were interested to investigate whether any male or paternal care was present in this species. The results revealed that most adult males and infants form preferential associations, and that infants are initiating the majority of male-infant affiliations. The multivariate analysis showed that the most influential social factors leading infants to initiate interactions with a particular male was male rank and male association with the infant's mother. Infants affiliated most with males while their mother was absent. In contrast, adult males initiated affiliations with an infant mostly when the mother was present in proximity, when they were present at conception, and when they held a high rank or associated with the infant's mother. No influence of paternity was observed in our study groups. These results suggest that adult males potentially associate with an infant to secure future mating with the mother. Infants are more likely to associate with a male to receive better support (by interacting with high ranking male or a male friend of their mother), a potential strategy to improve infant survival in a species with high infant mortality.

Summary

The results presented within this thesis provide a central contribution in our current understanding of the determinants of male-infant interactions and their influence on offspring survival. They also provide insights on the social and environmental factors influencing direct fitness in a promiscuous primate mating system. In fact, these findings highlight the strong interplay of socio-environmental factors on fetus and infant survival, and in particular the influence of male reproductive strategies in a species with high infant mortality. In addition, it emphasizes that infants are the main actor of male-infant affiliations and may use these interactions to establish bonds as a potential infant survival strategy by targeting specific affluent males. In conclusion, the male-infant interactions, although rare, were found to have strong influence both on males' and infants' direct fitness. These results also suggest that studies focusing on infant-initiated interaction towards male deserve increased attention.

Zusammenfassung

Direkte Fitness wird definiert als die Anzahl überlebender Nachkommen. Um diese zu erhöhen, können adulte Männchen entweder versuchen so viele Nachkommen wie möglich zu zeugen, oder das Überleben ihrer eigenen Nachkommen sichern, z.B durch Fürsorge. Bei Säugetieren sind Männchen-Kind Interaktionen nur bei 5% aller Arten bekannt, wenngleich sich die Ausprägung von intensiver väterlicher Fürsorge bis zum Infantizid erstreckt. Tatsächlich tritt Infantizid bei vielen Säugetierarten auf. Verschiedene Hypothesen versuchen dieses Verhalten zu erklären. Dabei ist die Hypothese der sexuellen Selektion die weithin anerkannte. Die Hypothese geht davon aus, dass adulte Männchen unverwandte, nicht entwöhnte Jungtiere töten, um den physiologischen Prozess der Fruchtbarkeit von adulten Weibchen zu beschleunigen. Tritt der Östrus bei den Weibchen nachfolgend auf, so erhöhen sich die Paarungschancen der Männchen. Im Falle von Infantizidrisiko haben Väter die Möglichkeit ihre Nachkommen zu schützen, was als echte väterliche Fürsorge bezeichnet wird und die direkte Fitness der Männchen erhöht. Generell tritt Fürsorge von Jungtieren in weniger als 10% aller Säugetierarten auf, vorrangig bei Primaten (bis zu 40%). Jüngste Beobachtungen zeigen einen positiven Zusammenhang zwischen der Anwesenheit von Vätern und (1) der Entwicklung ihrer Nachkommen und (2) deren Zugang zu Ressourcen. Jedoch gibt es bisher keine Studie, die das Auftreten von Interaktionen zwischen adulten Männchen und Kindern in Relation zum Überleben der Kinder (prä- und postnatal) untersucht und gleichzeitig den Einfluss sozio-ökologischer Faktoren berücksichtigt hat.

Aus verschiedenen Gründen eignen sich Schopfmakaken (*Macaca nigra*) als Studienobjekt zur Untersuchung von Männchen-Kind Beziehungen. Schopfmakaken leben in Gruppen aus mehreren Männchen und Weibchen, wobei die Weibchen zeitlebens in ihrer Geburtsgruppe verbleiben, wohingegen Männchen mit Erreichen der sexuellen Reife abwandern. Zusätzlich ist das Sozialsystem der Schopfmakaken sehr dynamisch, da adulte Männchen häufig zwischen den Gruppen migrieren, was die Rangfolge präsender Männchen, inklusive dem Wechsel der Alphaposition, beeinflusst. Bei Schopfmakaken korreliert die Vaterschaft positiv mit dem Rang eines Männchens. Dabei können

sich Alphas Männchen den größten Paarungserfolg sichern, wenn sie promiske Weibchen im Östrus erfolgreich bewachen. Des Weiteren verpaaren sich Schopfmakaken nicht saisonal, weshalb Männchen stark für ihren Rang kämpfen. Daraus resultierend tritt Infantizid als mögliche Reproduktionsstrategie von Männchen dieser Art auf. Insgesamt kann die Jungtiersterblichkeit bei Schopfmakaken 20% erreichen bei relativ geringem Prädationsdruck. Basierend auf diesen Fakten wäre das Schützen von Jungtieren durch ihren Vater eine kritische Strategie, die sich entwickeln sollte.

Ziel dieser Arbeit war daher die Charakterisierung von Männchen-Kind Beziehungen bei Schopfmakaken und die Untersuchung von potenziell daraus resultierenden Fitnesseffekten bei Jungtieren (Überleben). Studie 1 untersucht den Einfluss ökologischer und sozialer Faktoren auf die Interaktionen zwischen adulten Männchen und Jungtieren, sowie deren Überleben. Neben diversen sozio-ökologischen Faktoren wie z.B. Parität der Mutter, Niederschlag als Nahrung für saisonal auftretende Früchte oder maternaler Rang, haben wir untersucht, ob das Einwandern von Männchen, der Wechsel der Alphas Männchenposition und die Stabilität der Hierarchie der adulten Männchen, das Überleben von Jungtieren beeinflusst. Studie 2 betrachtet das Auftreten und die Bestimmtheit von Männchen-Jungtier-Interaktionen, sowie den Einfluss der Initiationsrichtung (von Männchen oder Jungtieren) vor dem Hintergrund möglicher Strategien zur Reproduktion von Männchen oder dem Überleben von Jungtieren.

Die Aufnahme der Verhaltensdaten für diese Studien erfolgte als Teil des *Macaca Nigra* Projekts im Tangkoko-Duasudara Reservat in Sulawesi, Indonesien an drei freilebenden Gruppen von Schopfmakaken. Für Studie 1 wurden ad libitum Daten über Migration von Männchen, Geburten von Jungtieren, Verschwinden von Individuen, weiblichen Zyklus und Aufeinandertreffen von verschiedenen Gruppen erhoben. Zusätzlich wurden Daten zur Hierarchie von Männchen und Weibchen gesammelt und analysiert. Die Datenerhebung erfolgte über 5 Jahre (3894 Beobachtungstage) und umfasste 99 Föten und 78 Jungtiere von 60 Weibchen. Für Studie 2 wurden 2008 – 2010 35 Jungtiere von der Geburt bis zum vollendeten 1. Lebensjahr beobachtet. Mittels Fokustierbeobachtungen wurden kontinuierliche Daten von affiliativen und aggressiven Interaktionen zwischen den Beobachtungstieren und allen Gruppenmitgliedern erfasst. Zusätzlich erfolgte die regelmäßige Aufzeichnung der Distanzen von Fokustieren zu Gruppenmitgliedern in unmittelbarer Nähe. Insgesamt war es möglich, mehr als 3611 Stunden Fokustierdaten zu sammeln ($100.63 \pm 23.87h(M \pm SD)$) pro Fokustier, welches das erste Lebensjahr vollendet

hat). Zusätzlich wurden genetische Proben von allen Jungtieren, Müttern und allen adulten Männchen (45) aller drei Gruppen vor und während des Beobachtungszeitraumes gesammelt und analysiert. Vaterschaften konnten für alle Fokustiere bestimmt werden. Die in dieser Arbeit angewendeten statistischen Methoden umfassen nicht-parametrische Tests, Cox-Regression und gemischte Regressionsmodelle.

Studie 1 liefert Beweise dafür, dass das Überleben der Jungtiere am stärksten durch einen kürzlich erfolgten Wechsel des Alphemännchens beeinträchtigt wird. Zusätzlich zeigt sich ein positiver Zusammenhang des Jungtierüberlebens mit einer steigenden Anzahl an adulten Weibchen in der Gruppe und mit zunehmendem Niederschlag. Hingegen wird die Überlebenswahrscheinlichkeit der Jungtiere weder von der Stabilität der Männchenhierarchie, von Migrationsvorkommen und Jungtier- oder Mutterattributen beeinflusst. Darüberhinaus ist das embryonale Überleben abhängig von der Interaktion von Niederschlag und Weibchenanzahl in der Gruppe, insbesondere in Bezug auf hochrangige denn niedrigrangige Weibchen. Interessanterweise erhöhte sich das embryonale Überleben ebenfalls durch eine erhöhte Anzahl von Aufeinandertreffen verschiedener sozialer Gruppen. Insgesamt legen diese Funde nahe, dass das Zusammenspiel von Saisonalität hinsichtlich der Umwelt, der Konkurrenz von Weibchen innerhalb einer Gruppe um Futterquellen und der Verteidigung von Ressourcen zwischen verschiedenen Gruppen, den Verlust von Embryos und Jungtieren bei dieser Makakenart beeinflusst. Jedoch zeigen die Ergebnisse auch, dass die Faktoren, welche die prä- und postnatale Sterblichkeit beeinflussen sich teilweise unterscheiden. Zusätzlich heben die Befunde hervor, dass hohe Jungtiersterblichkeit bei dieser Art vorrangig mit einem Wechsel des Alphemännchens einhergeht. Daraus folgt, dass Infantizid tatsächlich auftreten kann und dies kein Nebenprodukt von steigender Aggressivität zwischen den adulten Männchen während Zeiten instabiler Hierarchie und Migrationsvorkommen ist.

Die Ergebnisse von Studie 2 zeigen, dass Interaktionen zwischen adulten Männchen und Kindern zumeist affiliativ sind. Darüberhinaus wurde untersucht, welche Faktoren diese Affiliationen beeinflussen könnten. Basierend auf den Ergebnissen von Studie 1, dass der Wechsel des Alphemännchens die Sterblichkeit von Jungtieren deutlich beeinflusst, ging Studie 2 ebenfalls der Frage nach, inwiefern es sich bei den beobachteten Interaktionen zwischen Männchen und Jungtieren um männliche oder väterliche Fürsorge handelt. Die Ergebnisse weisen darauf hin, dass die meisten Männchen-Kind-Interaktionen

präferenziell sind und vorrangig von den Jungtieren initiiert werden. Die multivariate Analyse ergab, dass der Rang der Männchen und die Assoziation von Männchen und Müttern die einflussreichsten sozialen Faktoren sind, welche Jungtiere zur Initiation von Interaktionen mit Männchen bewegen. Dabei initiieren Jungtiere Interaktionen mit Männchen vorrangig wenn ihre Mütter abwesend sind. Im Gegensatz dazu führen Männchen Interaktionen mit Jungtieren vorrangig herbei, (1) wenn die Mütter der Jungtiere in der Nähe sind und sich die Männchen mit den Müttern assoziieren, (2) wenn sie zum Zeitpunkt der Zeugung anwesend sind oder (3) wenn sie einen hohen Rang inne hatten. Vaterschaft hatte keinen Einfluss auf das Affiliationsverhalten von Männchen und Jungtieren. Die vorliegenden Ergebnisse stützen die Hypothese, dass adulte Männchen vorrangig mit Jungtieren interagieren, um sich zukünftige Paarungschancen mit den Müttern der Jungtiere zu sichern. Dagegen sind Jungtiere zur Interaktion mit Männchen motiviert, um Unterstützung von diesen zu bekommen, was eine potentielle Strategie zur Erhöhung der Überlebenswahrscheinlichkeit von Jungtieren dieser Art darstellen kann.

Die Resultate der vorliegenden Arbeit leisten einen wichtigen Betrag zum Verständnis der bestimmenden Faktoren von Männchen-Kind Beziehungen und deren Einfluss auf das Überleben der Jungtiere bei Schopfmakaken. Sie liefern ebenfalls Erkenntnissedazu, wie soziale und ökologische Faktoren die direkte Fitness bei Primaten mit promiskem Paarungssystem beeinflussen. Tatsächlich heben die Befunde dieser Arbeit das starke Zusammenspiel zwischen sozio-ökologischen Faktoren und embryonalem sowie Jungtierüberleben hervor. Insbesondere wird der Einfluss der männlichen Reproduktionsstrategie in einer Art mit hoher Jungtiersterblichkeit deutlich. Darüberhinaus zeigt sich, dass Jungtiere vorrangig die Interaktionen mit adulten, gut situierten Männchen initiieren. Hierbei stellt dieses Verhalten eine mögliche Strategie der Jungtiere zur Erhöhung ihrer Überlebenswahrscheinlichkeit dar. Schlussfolgernd haben Interaktionen zwischen Männchen und Jungtieren, wenngleich sporadisch zu beobachten, einen starken Einfluss auf die Fitness von Männchen und Jungtieren. Die Erkenntnisse dieser Arbeit legen nahe, dass Studien mit Fokus auf Interaktionen von Jungtieren zu adulten Männchen vermehrter Aufmerksamkeit bedürfen.

Chapter 1

1 General Introduction

1.1 Infants and adult males in mammals

Direct fitness is based on the production and survival of offspring (Williams 1996). In some species, offspring survival may be improved by parental care (Clutton-Brock 1991). Parental investment is defined by Trivers (1972) as “any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring”. The cost-benefit ratio of parental investment is a central topic in evolutionary biology. Males generally attempt to acquire many mates, while females care for their own offspring. According to sexual selection theory, males should fundamentally be biased toward the production of many offspring and against substantial investment in any single offspring (Trivers 1972), since a key cost of parental care for males is a likely trade-off with investment in pursuing additional mating opportunities (Stockley and Hobson 2016). If the cost-benefit ratio is lower for males than females, then one expect that females would provide more care (Queller 1997). Moreover, in species with high cost associated to paternal care and paternal uncertainty, paternal care is predicted to be rare as the potential cost for a male to care for some unrelated offspring may exceed greatly the benefits of caring for its own offspring (Griffin et al. 2013).

Accordingly, in mammals, infant care by males occurs in fewer than 10% of the species, and female care is the predominant form of parental care (Woodroffe and Vincent 1994). Uniparental male care does not occur in mammals, but some male care is found to be relatively common in three mammalian orders: the carnivores, the perissodactyls species, and the primate (up to 40%; Kleiman and Malcolm 1981; Clutton-Brock 1991). There is a close link between male care and monogamous mating system among mammals, and a highly developed male care system is found in most monogamous species (Stockley and Hobson 2016). This type of care is expected only in an environment where infant survival with biparental care exceeds survival under uniparental care. However, it is difficult to identify male care in mammals' species as it can be quite indirect (e.g. supplying food to the mother during gestation, resource defense, anti-predator behavior, etc.; Kleiman and Malcolm 1981). Conversely, male care can be aimed primarily to increase future mating success (Barbary macaques, *Macaca sylvanus*; Ménard et al. 2001) or male's survival (e.g. infant carrying as agonistic buffer in yellow baboons, *Papio cynocephalus*; Stein 1984).

In fact, male-infant interactions observed in mammals are found to cover a wide array of social behavior, from maternal-like care (Kleiman and Malcolm 1981; Smuts et al. 1987) to infanticide (Packer and Pusey 1984; Borries 1997; van Schaik and Janson 2000). In addition, within species, male-infant relationships can vary widely (Itani 1959). Yet, tolerance and occasional affiliations seems to be the most commonly observed behaviors occurring between males and infants in primates (MacKinnon 2007). However, little is known about the determinants of male-infant interactions in many mammal species and the effect of direct and indirect male care on infant's survival.

1.2 Primate males' use and abuse of infants

Fetal and infant survival in primate gregarious species may depend on many different factors: resource availability (Altmann and Alberts 2003; Beehner et al. 2006b), hierarchy stability (Engh et al. 2002; Roberts et al. 2012), female social bonds (Silk 2007a), to name a few (reviewed in Pusey 2012). Fetal mortality is, in few mammals species, associated with the arrival of a new male. This so-called "Bruce effect", where the female terminates her pregnancy, possibly to avoid future infanticide, has been observed in mice (*Mus musculus*; Bruce 1959), and recently in Gelada baboons (*Theropithecus gelada*; Roberts et al. 2012). Infant mortality has also been associated to male attacks in several species (van Schaik and Janson 2000). Among mammals, infanticide by adult males is mostly observed in carnivores, rodents and primates (van Schaik and Janson 2000). Several hypotheses have been proposed to explain this behavior (Bartlett et al. 1993; MacKinnon 2007). The social pathology, a non-adaptive hypothesis, states that some individuals would kill infants based on maladaptive behavior. Another non-adaptive hypothesis could be male aggression by-product, where aggressions between males may kill infants as indirect collateral (Hrdy et al. 1994). Finally, the dominant theoretical framework for infanticide is the sexual selection hypothesis (Hrdy 1974; van Schaik and Janson 2000). Males kill unrelated infants in order to speed the return to fertility of females with un-weaned infants, thus aiming to increase their direct reproductive success. Infanticide occurrences has been reported in many species (van Schaik and Janson 2000). Several female counter strategies to male infanticide have been proposed, such as mother-male friendship (Palombit 1999; Soltis et al. 2000), where the male

“friend” (often a potential sire of the mother’s infant) may protect the female’s infant during males’ attacks (Moscovice et al. 2009). In addition, female promiscuity (Nunn 1999) has been proposed as a counterstrategy to infanticide by increasing paternity uncertainty.

In addition to infanticide, a wide variety of agonistic interactions can be observed between males and infants in primates’ species, especially within triadic interactions. Agonistic buffering takes place when a subordinate male, involved in an agonistic interaction with a dominant male, grabs an infant and carry it for the remaining duration of the aggression (Deag and Crook 1971; Stein and Stacey 1981). This behavior is often observed with a sharp decrease of aggressive display from the dominant male and has been observed in yellow baboons (Strum 1984) and gelada baboons (Dunbar 1984). Interestingly, one can observed triadic interaction involving two males and an infant in Barbary macaques where affiliations between the two males are “facilitated” by the presence of the infant and promote coalition formation (Taub 1984; Kuester and Paul 1986; Paul et al. 1996).

In conclusion, males may target infants with different agonistic behaviors, associated to different evolutionary reasons. However, the rate of male abuse towards infants is extremely low compared to male-infant affiliations (MacKinnon 2007).

1.3 Male care and paternal care in primates

Many monogamous primates display intensive caretaking behavior towards infants (Whitten 1987; Fernandez-Duque et al. 2009). Males may carry, groom and protect infants. However the level of care may vary among species, groups, and even among offspring. These intense caretaking behaviors are observed mostly in New World primates (Huck and Fernandez-Duque 2013), but some Old World monogamous primates, such as the siamangs, *Symphalangus syndactylus*, also display this extensive male care (Lappan 2008).

In species with a promiscuous mating system, the likelihood of male-infant affiliations is low, as a male is expected to decrease care because of the likelihood of being cuckolded by the female (Griffin et al. 2013). Interestingly, there are strong enduring male-female affiliative bonds (termed as “friendship”) that extends to the female’s unweaned infants in some baboons species (Smuts 1985; Silk 2002). Experimental studies using playback of infant’s scream even show that males’ friend

may actively protect infants from potential infanticide attacks in olive baboons (*Papio Anubis*) (Palombit et al. 1997). These “friend” males are not always the sire of the infant they protect, but they often mated with the mother around the time the infant was conceived, thus their paternity likelihood is high (Moscovice et al. 2009; Moscovice et al. 2010). These likely sires have been observed to provide protection in other promiscuous primate species. In Hanuman langurs (*Semnopithecus entellus*), fathers and likely sires protect infants against infanticidal attacks (Borries et al. 1999). Similarly, likely sires, in chacma baboons (*Papio ursinus*), carried infants when threats of infanticide or predation was high (Busse and Hamilton 1981; Anderson 1992).

In some species, only the fathers, and not likely sires, are found to provide some care towards infants. This paternal care (or mate-then-care strategy; Ménard et al. 2001) can take many forms. For example, fathers may engage in affiliative interactions with their offspring (Langos et al. 2013). Fathers have also been observed to side in favor of their offspring when involved in conflict with other juveniles in yellow baboons (Buchan et al. 2003). Fathers are found to enable their offspring to access richer food patches in chacma baboons (Huchard et al. 2013). These paternal effects can also be indirect. In yellow baboons, the sole presence of fathers in the group accelerates their daughters sexual maturation (Charpentier et al. 2008), thereby increasing their lifetime reproductive success. Paternity may be assessed through behavioral cues such as consortship and mating around the most likely day of conception (Buchan et al. 2003), or phenotype matching (Widdig 2007).

Finally, male care is also found in some species with promiscuous mating systems, as a form of mating effort (Smuts and Gubernick 1992; Ménard et al. 2001). Males give care towards unrelated offspring to increase future mating access to their mothers. This care-then-mate pattern has been observed in Barbary macaques, where males giving infant care achieved higher mating frequencies (Ménard et al. 2001). However, it remains unclear whether this reproductive strategy is widespread among primates' species (van Schaik and Paul 1996).

1.4 Crested macaques as study species

Crested macaques (*Macaca nigra*) are an ideal species to investigate the different types of male-infant interactions and their determinants, given their high

infant mortality (Engelhardt and Perwitasari-Farajallah 2008), tolerant social system (Thierry et al. 2004), and high turnover rate by immigrant males (Neumann et al. 2011). This species lives in multi-male multi-female groups and group size varies from 50 to 97 individuals (Reed et al. 1997; Kinnaird and O'Brien 2000; Saroyo and Tallei 2010). The sex ratio is around 3 adults females per adult male (O'Brien and Kinnaird 1997). Crested macaques show male dispersal around sexual maturity, after reaching maximum body mass (Marty et al. 2015), and female philopatry (i.e. females stay in their birth group throughout their life). This species is one of the few species of macaque with a tolerant social system (Thierry et al. 2000a; Thierry 2000; Thierry 2007). Females in this species have dyadic conflicts of low-intensity and moderate dominance asymmetry (Dubosq et al. 2013). In addition, mothers are predicted to have a tolerant mothering style, allowing group members to approach and interact with their infants (Thierry et al. 2004). This social system may allow males to potentially interact with infants and provide care.

Female age at sexual maturity is 49 months (Harvey et al. 1987) with an adolescent period where sex skin swellings slowly develop. Interbirth interval is 22 months (Mittermeier et al. 2013). Infant weaning starts at 5 months of age (average of first nipple access deterrence at 154.57 days of age, behavior described in Thierry et al. 2000b) and is usually completed when the infant is approximately 1-year old, as for other species of macaques (Tanaka 1992).

Infant mortality may reach 20% in this species (Engelhardt and Perwitasari-Farajallah 2008), although predation pressure is thought to be low (van Schaik 1989), due to the absence of felids in the Sulawesi Island (Whitten et al. 2001). Breeding is aseasonal (Dixon 1977; Hadidian and Bernstein 1979; Engelhardt and Perwitasari-Farajallah 2008) and several males are observed to mate with females throughout their estrus cycles (Dixon 1977). The social system is very dynamic, with frequent male migration (Neumann et al. 2011), short male group tenure, and high alpha-male position turn-over (i.e. the top ranking male in the male dominance hierarchy; Marty et al. 2015). As a result, male dominance hierarchy is often unstable (Neumann et al. 2011). However, paternity is highly skewed towards alpha males due to their successful mate guarding during the most likely period of ovulation (i.e. peak female sex skin swelling; Higham et al. 2012). This would corroborate the graded signal theory (Nunn 1999), which predicts that in species with exaggerated female swellings, alpha males guard fertile females only at peak swelling while females can mate with multiple mates outside peak swelling, thereby confusing paternity. Consequently, males fight fiercely for dominance, and infanticide as a male

reproductive strategy may emerge. Based on the high infant mortality in this species, strategies to improve survival may be critical for infants to develop. In addition, sires may protect their offspring from infanticidal males.

The geographic distribution of this endangered species is limited to the northern tip of Sulawesi and the Bacan islands (Rosenbaum et al. 1998). The study was conducted in the Tangkoko-Duasudara Nature Reserve in Sulawesi, Indonesia. This reserve, composed of primary and secondary lowland rainforest, covers an area of 8867 ha and ranges from sea level to 1350 m (O'Brien and Kinnaird 1997; Rosenbaum et al. 1998; Whitten et al. 2001). Temperatures are relatively constant throughout the year, with a monthly mean minimum and maximum of 23 and 28 °C, respectively. Annual rainfall ranged between 1410 and 2352 mm during the study period (mean of 1940 mm per year). This species is semi-terrestrial and largely frugivorous (Kinnaird and O'Brien 2000). Their daily path length is affected significantly by the seasonal availability of fruits and intergroup interactions appear to be tied to resource defense (Kinnaird and O'Brien 2000). The individuals within the 3 social groups were fully habituated to human observers with adults and infants individually identified and continuously monitored by the Macaca Nigra Project (Marty et al. 2015).

1.5 Aims of this thesis

The overall aim of this thesis was to investigate the different type of social interactions taking place between males and infants in a primate species with high infant mortality. In particular, the thesis aimed to assess the influence of social and ecological factors on fetal and infant survival and specifically test whether males are responsible for offspring loss. Furthermore, we attempted to investigate the characteristics of male-infant affiliations, and the key factors influencing those affiliations, from both a males' and infants' perspective.

In the first study, we used a powerful multivariate statistical tool, the Cox proportional hazards model, to measure the influence of social and ecological factors and their interplay on pre- and postnatal loss. This survival analysis allowed us to estimate the influence of several parameters simultaneously and over time on the risk of death. Thus, this study allowed to test whether key factors related to males' behavior (such as male immigrations, alpha-male position takeover, and male

hierarchy stability) had any impact on fetal and infant loss, while controlling for the influence of diverse socio-ecological factors (e.g. mother parity, rainfall as a proxy of fruit seasonality, or maternal dominance rank). In addition, we were able to measure the combined effect of several factors to pinpoint the determinants of offspring survival, thus providing insights into fitness costs and benefits of sociality.

The second study investigated the different characteristics of male-infant affiliative behaviors and the factors shaping these affiliations. This study aimed to examine the presence and strength of male-infant affiliations in crested macaques, and to identify whether males or infants were the main actors of this relationship. In addition, we explored whether infants would target and develop bonds with a specific male and vice versa. Finally this study analyzed, through a multivariate approach, which specific social factors held an influence on the daily occurrence of affiliations of males towards infants and infants towards males.

Chapter 2

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2 Social and ecological factors influencing offspring survival in wild macaques

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2.1 Abstract

Premature loss of offspring decreases direct fitness of parents. In gregarious mammals, both ecological and social variables impact offspring survival and may interact with each other in this regard. Although a number of studies have investigated factors influencing offspring loss in mammals, we still know very little on how different factors interact with one another. We therefore investigated fetal and infant mortality in three large groups of wild crested macaques (*Macaca nigra*) over a period of up to five years by including potential social causes such as maternal dominance rank, male immigration, between group encounters and ecological conditions such as rainfall in a multivariate survival analysis using Cox proportional hazards model. Infant but not fetal survival was most impaired after a recent takeover of the alpha-male position by an immigrant male. Furthermore, infant survival probability increased when there was an increase in number of group adult females and rainfall. Fetal survival probability also increased with an increase of these two factors, but more in high-ranking than low-ranking females. Fetal survival, unlike that of infants, was also improved by an increase of inter-group encounter rates. Our study thus stresses the importance of survival analyses using a multivariate approach and encompassing more than a single offspring stage to investigate the determinants of female direct fitness. We further provide evidence for fitness costs and benefits of group living, possibly deriving from high pressures of both within- and between-group competition, in a wild primate population.

Keywords: offspring loss, proportional hazards model, socio-ecology, *Macaca nigra*, female reproductive success, between-group encounters

2.2 Introduction

Direct fitness is defined as the number of adult offspring left by an individual in the next generation (Williams 1996). Premature loss of offspring thus limits parents' reproductive success and creates costs in terms of investment already made in progeny (Trivers 1974). There is an extensive body of literature on the factors impacting female reproduction, specifically offspring survival, in mammals (Bronson 1985; Clutton-Brock 1988; Bronson 1989) both under captive (e.g. Lim and Wang

2010; Kavanagh et al. 2011) and natural conditions (e.g., rodents: Larsen and Boutin 1994; carnivores: Bertram 1975; Frank et al. 1995; ungulates: Pluháček and Bartoš 2005; primates: Roberts et al. 2012; Wahaj et al. 2007; Watts and Holekamp 2008; Watts and Holekamp 2009). However we still know little of the influence of the interaction of social and ecological factors on offspring loss. Furthermore, most studies focused solely on a specific offspring stage, either pre- or post-natal, although the determinants of offspring death may vary between these stages. Events occurring in the pre-natal stage, such as the causes of miscarriages, have either not been reported or little investigated under natural conditions, typically due to the difficulty of monitoring spontaneous abortions (but see Beehner et al. 2006a; Beehner et al. 2006b). More comprehensive studies are therefore needed to better understand the interactions between social and ecological factors causing offspring loss in wild female mammals.

From the data available, it is clear that a number of parameters can impact offspring survival. In addition to maternal, paternal or offspring properties (e.g., female parity: Pluháček et al. 2007; female age: Packer et al. 1998; female dominance rank: Majolo et al. 2012; offspring genetic abnormalities: Wilmut et al. 1986; reviewed in Pusey 2012) especially influencing fetal loss in the first trimester of pregnancies, both ecological and social variables have been shown to influence offspring (i.e., fetus and infant) survival. One of the most important is climate, as its components such as rainfall and temperature have great impact on plant productivity (e.g., Terborgh and Janson 1986) and thus food availability (Kim et al. 2012). Since female fecundity as well as offspring survival depend highly on food availability, climatic variables can modify female reproductive success (e.g., ungulates: Kruuk et al. 1999; carnivores: Russell et al. 2002; bats: Grindal et al. 1992; primates: Beehner et al. 2006a; Dittus 1977; Altmann and Alberts 2003). Additionally, in gregarious species, social factors act through the influence of other group members and rival groups. Female competition both within and between groups is an important selective force on females (e.g., rodents: Schradin et al. 2010; carnivores: Clutton-Brock et al. 2006; primates: Sterck et al. 1997), although only few studies have addressed the reproductive consequences of between group competition. However females and their offspring also benefit from living with conspecifics, for example through enhanced allomaternal care and joint resource defense against other groups, as well as protection against predators and infanticide; hence female social bonds and support can be important determinants of female reproductive success (reviewed for mammals: Silk 2007b; and primates: Silk 2007a).

Additionally, males can have a positive effect on offspring survival by providing paternal care (e.g., some carnivores: Clutton-Brock et al. 2001; and primates: Goldizen and Terborgh 1989; Huchard et al. 2013; Charpentier et al. 2008; Langos et al. 2013). Males are however also well known to cause offspring death, particularly in species in which infanticide is a sexually selected male strategy (van Schaik and Janson 2000). They may even harm offspring before birth by increasing stress in pregnant females, particularly when newly immigrating males takeover the alpha position (e.g., equids: Pluháček and Bartoš 2005; rodents: Labov 1981; primates: Roberts et al. 2012; Engh et al. 2006).

Little is known to date about the relative importance of interaction between the aforementioned ecological and social factors in impairing offspring survival although it is clear that several of these potentially interact with each other, for example the effects of food availability and group size (Ebensperger et al. 2012). Only two studies carried out on baboons have so far used multivariate analysis to investigate the determinants of offspring survival (Cheney et al. 2004; Beehner et al. 2006a). Both found that offspring loss is influenced by both ecological conditions and social factors. However, these studies as others on the determinants of survival usually focus on a single offspring stage (either pre- or post-natal, e.g., Roberts et al. 2012; Pluháček et al. 2007; Packer et al. 1998; Majolo et al. 2012; Wilmut et al. 1986).

The aim of our study was therefore to investigate simultaneously the combined effect of social and ecological factors, using modern statistical tools, upon pre-natal and post-natal offspring survival in a wild population of crested macaques (*Macaca nigra*), living on the island of Sulawesi. In this species, miscarriages have been observed in the wild, and infant mortality reaches 20% (Engelhardt and Perwitasari-Farajallah 2008) although predation pressure is thought to be low due to the absence of large felids on Sulawesi (van Schaik 1989).

Crested macaques are categorized as one of the most socially tolerant species within the macaque genus, in which females form strong social bonds in extended social networks (Thierry et al. 2000a). We thus expect all offspring to benefit from an increased number of adult female group members due to improved chances of successful resource access and monopolization through defense against adjacent groups. In addition, female social rank seems to be of little importance in females of this species with low intensity conflicts and moderate dominance asymmetry (Duboscq et al. 2013). Hence we predict maternal rank to have relatively little effect on offspring survival probability. At the same time, intergroup encounters

should be stressful for females, given that, in wild crested macaques, intergroup encounters in which females are involved are often aggressive (Kinnaird and O'Brien 2000) and injuries inflicted to females are observed on a regular basis. In fact, between-group aggressions is predicted to be high in this species, (van Schaik 1989; Sterck et al. 1997). We thus predict spontaneous abortion to be more likely with an increasing rate of stress through more frequent intergroup encounters. Finally, the high turnover rate by immigrants males lead to frequent instability in the adult male dominance hierarchy (Neumann et al. 2011). Given that these instabilities may lead to increased tension within the group, we expect abortion to be more likely with an increasing rate of male immigration and changes in the male hierarchy. Dependent infants, on the other hand, should suffer specifically from takeovers of the alpha-male position by newly immigrating males given the potential risk of infanticide under these circumstances. We test our predictions with a Cox proportional hazards model in 3 groups over a study period of a total of 152 group months.

2.3 Methods

1. Study site and subjects

Data were collected within the *Macaca Nigra* Project on three groups of wild crested macaques (R1, R2, and PB) living in the Tangkoko-Duasudara Reserve in Sulawesi, Indonesia (1N 32'39'', 125E 12'42''). This reserve, composed of primary and secondary lowland rainforest, covers an area of 8867 hectares and ranges from sea level to 1350 meters (O'Brien and Kinnaird 1997; Rosenbaum et al. 1998; Whitten et al. 2001). Temperatures are relatively constant throughout the year, with a monthly mean minimum and maximum of 23°C and 28°C, respectively. Annual rainfall ranged between 1410 and 2352 mm during the study period (mean of 1940 mm per year).

The study groups were fully habituated to human observers (Duboscq et al. 2008), and adults and infants were individually recognized. Group sizes varied from 50 to 80 individuals and included 4-11 adult males and 13-25 adult females (Table S1).

Crested macaques in this population give birth year round, but more than 80% of births occur within five consecutive months, namely January to May (Engelhardt and Perwitasari-Farajallah 2008) and up to 59.3% within three

consecutive months. As is the case in other macaques (e.g., Tanaka 1992), infant weaning started at five months of age (average of first nipple deterrence observation at 154.57 days of age, behavior described in Thierry et al. 2000) and was usually completed when the infant was approximately one year old.

2. Data collection

Observations on groups R1 and R2 took place from March 2006 to December 2010 and for group PB from January 2008 to December 2010. Each of the three groups was followed at least once a week but usually several times per week from dawn to dusk (3894 total group observation days across the three groups, i.e., 75.5% days of the whole observation period) to record migrations, births, and disappearance/death of individuals, as well as the occurrence and size of female sex skin swellings (a sign of monthly ovarian activity; Higham et al. 2012) that lasts on average 19.4 days (Engelhardt and Perwitasari-Farajallah 2008) and encounters between groups, using *all-occurrence* sampling (Altmann 1974). In addition, outcome of dyadic aggressive interactions and displacements were recorded, during focal sampling of adult males and females (data extracted from Engelhardt and Perwitasari-Farajallah 2008; Neumann et al. 2010; Neumann et al. 2011; Duboscq et al. 2013) and *ad libitum* sampling (Altmann 1974), to determine dominance rank through Elo rating, a method robust to frequent hierarchy changes (Neumann et al. 2011). Females were considered adult after they conceived their first living infant and males were considered adults after their scrota descended and their canines erupted.

We collected data on 99 fetuses and 78 infants (126 offspring altogether from 60 females). Onset of pregnancy was determined through the cessation of regular swelling cycles (i.e. a female not displaying her monthly sexual swellings for more than two consecutive months), as sexual swellings in this species are a reliable signal of ovulation (Higham et al. 2012) and there is no post-conception swellings in this species (Hadidian and Bernstein 1979), confirmed by subsequent delivery or miscarriage. Miscarriages were detected through the observation of massive hemorrhaging from the vagina (sometimes with a protuberant umbilical cord) followed by the resumption of sexual activity and sex skin swelling (after a mean of 26.5 days \pm 20.2, N=17). Menses is difficult to detect in wild adult female crested macaques. To ensure that vaginal bleeding truly derived from fetal loss and not from menses, we only counted those cases in which the female had not displayed any swelling during the previous two months thus suggesting that she was pregnant. This means that we may have missed some early miscarriages occurring during the first

two months of the pregnancy. Pregnancy with live birth in this species last on average 170 days (Thomson et al. 1992) and we observed in this population a range of pregnancies lasting from 171 to 185 days.

Infants were observed during their earliest life phase, i.e., during the period in which infant mortality is highest in mammals (Caughley 1966). In macaques and other cercopithecine primates, this period covers the first year of life (e.g., van Noordwijk and van Schaik 1999). Accordingly, we recorded disappearances and deaths (from here on called “deaths” only) for individuals under the age of one year.

3. Data analysis

We used fetal and infant survival as a binary response variable in two separate models. The period of fetal survival was considered from conception (the last day of sexual swelling of the last estrus cycle) to birth and the period of infant survival was considered as the date of birth until one year of age. Infants were scored as alive or dead for each of up to four 90 day intervals from birth to death or one year of age and for fetus up to two 90 day intervals from the defined day of conception to miscarriage or birth (496 intervals in total) in order to incorporate time-dependent variables into the model (Perperoglou et al. 2006). Infants for which the day of conception was known (N=71), occurred twice in the analyses: once as foetus and once as infant. Each quantitative variable was calculated on a daily basis and we used the mean over each 90 day intervals per individual. We considered the following predictor variables as potentially influencing fetal and/or infant survival:

- *Mean rainfall* (with an offset of three months) as an approximation of environment seasonality. We shifted actual rainfall values back by three months, given that female crested macaques respond reproductively to environmental changes with a time lag of three months (Figure S1). It is well known that there is a link between phenology and water availability in seasonal tropical forests (van Schaik et al. 1993). Accordingly, increased rainfall leads to increased availability of fruits in the study area (Kinnaird and O’Brien 2000) and fruits are the major food source of crested macaques in Tangkoko (O’Brien and Kinnaird 1997).
- *Number of adult females* in the group as a measure of female-female within-group competition for resources (Isbell 1991) on one hand and of competitive ability during between-group competition on the other.
- *Maternal dominance rank* as a measure of individual competitive ability using Elo-ratings based on aggressive dyadic interactions as well as displacements

(Albers and de Vries 2001; Neumann et al. 2011). For each day, we standardized (range of 0 to 1) the Elo-ratings of all adult females in each group. Maternal rank is assumed to be transferred to the infant in macaques (Berman 1980).

- *Male hierarchy instability* as a measure of increased within-group aggression and stress. Male hierarchical instability was calculated using the weighted hierarchy instability index (cf. Neumann et al. 2011) based on all the adult males' daily dominance rank assessed through Elo-rating (as described above).

- *Number of male immigration* events as another measure of increased within-group aggression was scored as a binary measure “0” or “1” to balance the dataset containing mainly no occurrence.

- *Alpha-male takeovers* by a newly immigrated male (N=13 events) as yet another measure of increased within-group aggression and as a measure of the risk of infanticide. We measured the proportion of days a new alpha male was present per interval until the fetus was born or the infant reached 6 months old, as some mother start cycling again by then.

- *Intergroup encounter* daily rate (i.e. two groups in visual range, N=1126 events) as a measure of conflict resulting of between-group competition.

- We furthermore controlled for *fetus and infant age* and *Infant sex*. Miscarried fetus sexes were unknown.

We incorporated interactions into both models. An interaction between two or more predictor variables indicates that the effect on the response of one of these predictor variables is conditional on the state or value of the other predictor variable and not simply additive (Quinn and Keough 2002). We added a three-way interaction between rainfall (our measure of environmental seasonality), number of adult females in the group and maternal dominance rank, as well as all lower-order interactions between these particular variables to our model, since these variables are known to have an interdependent effect on resource access and thus offspring survival (Pusey et al. 1997; van Noordwijk and van Schaik 1999; King et al. 2005). The number of individuals within a group influences individual resource access through the degree of within-group competition as well as success of between-group resource defense (van Schaik 1989). Furthermore, fruits, being usually seasonal and patchily distributed, increase within-group contest competition, which again increases with the number of competitors. Finally, with increasing degree of within-group competition, high-ranking females get an advantage over low-ranking females in regard to resource access and reproduction. In addition, we incorporated three nested random factors

into the model to control for the multiple source of random error: group identity, mother identity and offspring identity.

4. Statistical analysis

We used a Cox proportional hazards model (Therneau and Grambsch 2000) to test the influence of the predictor variables on fetal and infant survival, respectively. The Cox model is a nonparametric survival analysis (Pletcher 1999) that allows the influence of several parameters to be estimated simultaneously and over time on the risk of death (i.e., the hazard or mortality rate), while no assumption is made concerning the shape of the hazard function. In our Cox model, the regression coefficients represent the log change in the hazard function per unit increase of the predictor variable. In other words, a negative hazard rate (β) indicates increased survival chances with increasing value of the predictor variable (Therneau and Grambsch 2000). The model was fitted in R (version 2.14.0, Fox and Weisberg 2011) using a mixed effects model variant of the Cox model, namely the function ‘coxme’ (package “coxme”, R Development Core Team 2010) in order to include the three nested random factors. We checked each predictor for its distribution. To obtain approximately symmetrical distributions, we square-rooted age and intergroup encounter rate, and double square-rooted male hierarchy stability. Subsequently, all quantitative predictor variables were z-transformed to a mean of zero and a standard deviation of one. We determine the statistical significance of the two full models by comparing their fit with the respective null model (containing only the random and control factors) with a log-likelihood ratio test. The variance inflation factors derived from a linear model containing all the predictors except the random effects (function “vif” of the R package “car”, Quinn and Keough 2002; Fox and Weisberg 2011) revealed that collinearity was not an issue for both models (largest VIF=2.1). Furthermore, we checked for model stability by excluding data points and predictor variables one by one (Clark et al. 2003). The specific time interval of 90 days for a given offspring (i.e., fetus and infants) is the unit of analysis. When a fetus was aborted or an infant died, the time interval containing this event was included in the analysis. Variables may be fixed over time (e.g., infant sex) or time-dependent (e.g., rainfall) (Beyersmann and Schumacher 2008). All the terms included in the models are specified in Table 1 and 2, except for the three nested random factors. For more information on the data and statistical analysis, see the supplementary information.

2.4 Results

1. General results

Overall, during the study, 18% of the 99 conceptions resulted in abortions and 17 of the 78 infants (22%) disappeared in their first year of life. We found the body of 8 of these 17 infants. All but one of these infant bodies showed large puncture wounds (Table S2).

2. Models

Fetal survival

Overall, the model revealed that the set of predictor variables used had a clear influence on the probability of fetal survival (integrated log-likelihood ratio test comparing the fit of the full model with the fit of a null model containing only the random effects; $\chi^2 = 24.32$, $df = 11$, $P = 0.01$). The model results indicate that the rate at which a group encountered a neighboring group had the strongest effect on fetal survival (Table 1): the more frequent intergroup encounters were, the more likely those fetuses survived. In addition, the three-way interaction between rainfall, number of adult females in the group and maternal dominance rank had a significant impact on fetal survival (Table 1). In general, fetuses were more likely to survive with an increase in rainfall and the greater the number of females present in the group (Figure 1a-c). There were, however, differences between female rank classes in terms of when and to what extent these positive effects set in. Fetuses of high-ranking females benefitted most and constantly from an increase in rainfall compared to fetuses of middle- and low-ranking females. Fetuses of middle- and low-ranking females, in contrast, only benefitted from an increase in the number of group females when rainfall was low to moderate. When both female number and rainfall were high, fetuses of high-ranking females were most likely and those of low-ranking females least likely to survive. Alpha-male takeover rate, occurrence of male immigration, male hierarchy stability, and fetal age did not have any significant impact on fetal survival (Table 1).

Table 2.1. Cox mixed model results for foetus survival (N=184). Significant effects are highlighted in boldface. β is the hazard rate coefficient; a positive value indicates an increased risk of dying with increasing value of the predictor. z and P-values not shown are uninformative because the respective term is involved in a higher order interaction.

Predictor	β	z	P- value
Rainfall	-0.504		
Number of adult females	-1.751		
Maternal dominance rank	0.336		
Male immigration	0.100	0.23	0.820
Male hierarchy stability	-0.853	-1.43	0.150
Male takeover	-0.498	-0.64	0.520
Intergroup encounter rate	-1.509	-3.09	0.002
Foetal age	-0.027	-0.07	0.940
Rainfall* Maternal dominance rank	1.009		
Number of adult females* Maternal dominance rank	1.055		
Number of adult females* Rainfall	-0.728		
Rainfall* Number of adult females* Maternal dominance rank	1.036	2.36	0.018

Infant survival

The model revealed that, overall, the full set of predictor variables used did not explain the variation in infant survival (integrated log-likelihood ratio test comparing the fit of the full model with the fit of a null model containing only the random effects; $\chi^2=20.49$, $df=14$, $P=0.11$). However, since the three-way interaction between rainfall, number of adult females in group and maternal dominance rank did not reveal significance ($\beta=0.06$, $z=0.19$, $P=0.85$) and two of the constituent two-way interactions were also not significant (maternal dominance rank*rainfall: $\beta=-0.11$, $z=-$

0.31, $P=0.75$; maternal dominance rank*number of females in group: $\beta=-0.21$, $z=-0.69$, $P=0.49$; determined from a model not comprising the three-way interaction), we excluded these interactions from the full model. Although there is a risk of multiple testing (Mundry and Nunn 2009), exclusion was conducted successively, although we did not use stepwise deletion, to ensure that none of the potentially significant interactions remained undetected.

The results of the final reduced model showed that all single parameters and the remaining significant two-way interaction (number of females*rainfall) explained the variation in infant survival (integrated log-likelihood ratio test: $\chi^2=21.83$, $df=11$, $P=0.02$). According to this model, infant survival probability was most strongly affected by takeover of the alpha-male position (Table 2). Such a takeover almost tripled the probability of infants dying ($\beta=2.9$). Interestingly, instability in the male hierarchy *per se* did not have such an effect nor did the immigration of males into a group. Rainfall and the number of adult females per group also significantly influenced the probability of infant survival (Table 2); infants were more likely to survive with increasing rainfall and the greater the number of females in the group (Figure 2). From a certain degree of rainfall and number of females onwards, however, the positive effect of each of these variables was weakened, as in the fetus model. Infant age and infant sex did not have any significant effect on survival probability.

Table 2.2. Cox final reduced mixed model results for infant survival (N=260). Significant effects are highlighted in boldface. β is the hazard rate coefficient; a positive value indicates an increased risk of dying with increasing value of the predictor. z and P-values not shown are uninformative because the respective term is involved in a higher order interaction.

Predictor	β	z	P-value
Rainfall	-0.319		
Number of adult females	0.460		
Maternal dominance rank	-0.457	-1.35	0.180
Male immigration	-0.683	-1.58	0.110
Male hierarchy stability	0.092	0.23	0.820
Male takeover	2.928	3.22	0.001
Intergroup encounter rate	-0.031	-0.07	0.950
Infant age	-0.417	-1.18	0.240
Infant gender	-0.251	-0.39	0.700
Mother parity	-0.276	-0.83	0.410
Number of adult females*			
Rainfall	0.697	2.00	0.045

2.5 Discussion

Our results strongly indicate that an interplay of social and environmental factors significantly influenced fetal and infant loss in wild crested macaques. Our results also showed that the determinants of survival may differ between offspring stages. In both models, a social variable best explained variation in survival, but the precise variable differed between fetuses and infants. Similarly, in both models the interaction between an ecological and a social factor exerted a significant effect on offspring survival, but again, our analyses revealed differences in the details of

survival determinants between different offspring stages. Our results thus stress the importance of investigations covering more than a single offspring stage.

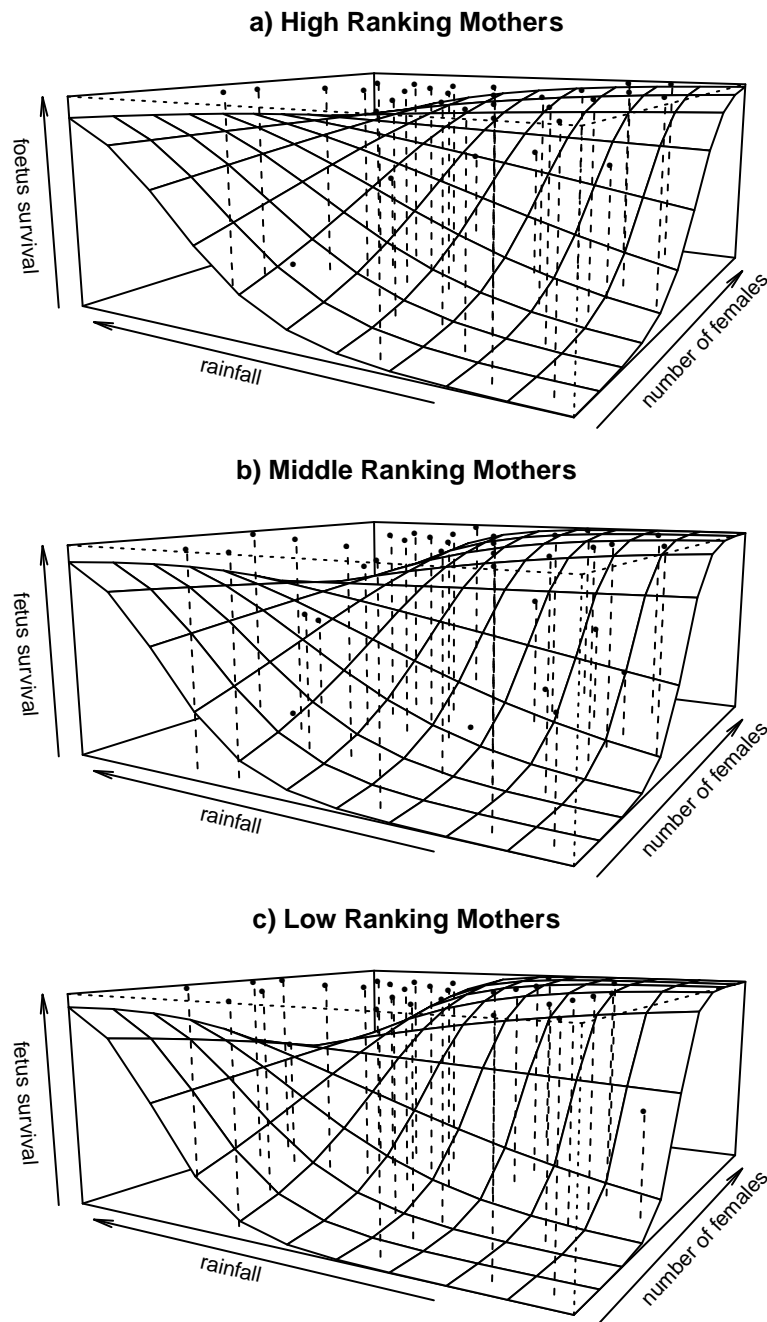


Figure 2.1a, b, c. Effect of rainfall and number of group adult females on the survival likelihood of fetuses of high (a), middle (b) and low (c) ranking mothers. The continuous variable dominance rank was divided into three categories (high, middle and low) to enable plotting. The plane depicts values predicted by the Cox mixed model with each grid representing the mean value per square of the predicted mixed model. Dots represent mean empirical survival rates value per square.

For both offspring stages, a social variable best explained variation in survival. Fetuses had a greater survival chance the more often their group was involved in intergroup encounters, whereas infants had a reduced survival chance after a new male had taken over the alpha-male position. Our finding that fetuses are more likely to survive the more often their group is involved in intergroup encounters is surprising to us. We had expected the opposite to be the case, since aggressive inter-group encounters may increase female stress levels (Pride 2005) and thus may cause pregnancy failures (reviewed in Nakamura et al. 2008). In addition, between-group aggressions have been predicted to be important in crested macaques for female social interactions (van Schaik 1989; Sterck et al. 1997), as between group competition may have an impact on resource access, hence on female dominance interaction and reproduction (Kinnaird 1994). Nevertheless, our data indicate that intergroup encounters do not impair but foster female pregnancies, a finding that is difficult to explain through direct advantages. One possible explanation may be that the rate with which a group comes into conflict with neighboring groups correlates with the quality of this group's home range. It has, for example, been shown for Japanese macaques that in areas with food of higher quality, intergroup encounters occur more often than in areas with food of lower quality (Sugiura et al. 2000). Similarly, in our study population, multiple groups compete over fruit trees and the frequency of aggression during intergroup encounters increases when fruit becomes scarce and defensible (Kinnaird and O'Brien 2000). Improved fetal survival may thus simply reflect preferential access to food by these groups during food shortages. Future studies might therefore incorporate the influence of winning or losing intergroup encounter and test the prediction that winning an intergroup encounter increases fetal survival.

f

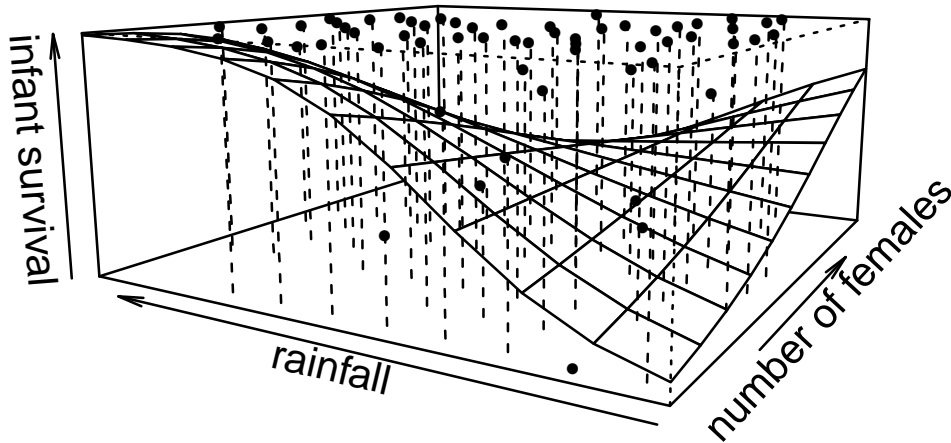


Figure 2.2. Effect of rainfall and number of group adult females on the likelihood of infant survival. The plane depicts values predicted by the Cox mixed model with each grid representing the mean value per square of the predicted mixed model. Dots represent mean empirical survival rates per square.

The assumption that between-group competition and environmental seasonality play a role in fetal survival in our study population is also supported by our finding that an increase in both the number of group adult females and rainfall in principle improved fetal survival probability. Groups with more adult females are better able to defend resources against other groups (Sterck et al. 1997). Rainfall, at the same time, may lead to an increase in fruit availability in the study area (Kinnaird and O'Brien 2000) and as such to an increase in the most important food source of crested macaques (O'Brien and Kinnaird 1997). As a consequence, pregnant females can better cope with the energetic costs of pregnancy (Small 1982). Our findings thus suggest that in terms of successful pregnancy, improved access to food outweighs the costs of stress received during intergroup encounters in crested macaques. Interestingly, there seems to be a limit to which this is the case. Our model shows that from a certain group size and degree of rainfall (i.e., environmental seasonality) onwards the positive effect is diminished in the fetuses of middle-ranking and even more so in those of low-ranking females. Fruits, particularly when occurring clumped in large trees (as is the case in Tangkoko, Kinnaird and O'Brien 2000) are highly defensible food sources that increase within-group contest competition (Mathy and Isbell 2001). Within-group contests also increase with the number of females competing for clumped food (van Schaik 1989). Our results thus suggest that under

certain conditions (patchily distributed food and many competitors) the costs of within-group competition override the positive effect of group resource defense for middle- and lower-ranking females. This may explain why dominance hierarchies remain in female crested macaques (Duboscq et al. 2013), although the species is relatively less despotic than other macaque species (Sueur et al. 2011; Micheletta and Waller 2012; Micheletta et al. 2012; Duboscq et al. 2013). When food is less clumped, on the contrary, competition between females of the same groups seems to be less detrimental and/or balanced by the positive effect of joint resource monopolization. The reason for this is most likely that females feed more on dispersed and less defensible food sources during such periods (Kinnaird and O'Brien 2000) and thus engage in fewer direct contests.

Based on the reduced model, between-group competition and seasonality also seem to influence infant survival likelihood in our study population. As in fetuses, infants in general benefit from an increase in rainfall and in the number of adult females in the group, but their survival likelihood then decreases when both parameters simultaneously increase beyond a certain point. However, in contrast to fetuses there is no rank-specific difference, suggesting that all infants suffer similarly from high levels of within-group competition. Why the infants of high-ranking females (in contrast to their pregnant mothers) should suffer equally from within-group contest remains unclear. Most likely the infants of high-ranking females are not yet able to successfully deploy their status (compare Datta 1988) during food competition. Macaque infants, as in several other Old World monkeys, do not hold a position within a dominance hierarchy during their first months of life and depend on support from others during agonistic encounters (Berman 1980; Pereira 1989).

Environmental seasonality and female group size were nevertheless not the most important determinants of infant survival in our study population. More important was whether or not the alpha-male position was taken over by a recent immigrant after the infant had been sired. In cases where a newly immigrating adult male reached alpha-rank position after an infant had been conceived, infants were three times more likely to die. We do not have direct evidence of these males having killed the respective infants -although males have been observed to attack infants- but the resemblance to cases of infanticide conducted as a male reproductive strategy is striking (e.g., Pluháček and Bartoš 2005; Hausfater 1984; Hrdy 1974; van Schaik and Janson 2000). In many of the cases in which we were able to retrieve the body, these exhibited deep punctures in the head and thorax consistent with having been inflicted by adult male canines, as it has been observed in other macaque species (cf. Ciani

1984; de Ruiter et al. 1994; Soltis et al. 2000). Since there are no large felids on the island of Sulawesi we feel justified in assuming these wounds stem from male bites. Interestingly, general immigration by males and instability in the dominance hierarchy did not have a significant effect on infant survival probability. This suggests that infants are not more likely to die as a byproduct of increased aggression between males in general (as suggested e.g., in Bartlett et al. 1993), but that infant death is specifically related to the arrival of a new alpha-male. It may well be that infanticide is a male reproductive strategy in crested macaques, given that dominant males appear easily able to monopolize access to females during the period of likely conception (Higham et al. 2012) and that new alpha-males in the vast majority of cases originate from other groups and are thus very unlikely to have fathered the infant killed (13 out of 14 takeovers during our study period).

Interestingly several parameters previously found to impact fetal and infant survival in several species did not show any effect on offspring survival in our study. Fetal age usually has an effect on survival probability with younger fetuses (e.g., Beehner et al. 2006a) being more likely to die. Given that in humans the majority of miscarriages occur in the first trimester of pregnancy (e.g., Wilmut et al. 1986), we may have missed such an age effect because we were only able to detect miscarriages from the second trimester onwards. The majority of early miscarriages, however, results from genetic aberrations (Ljunger et al. 2005), which were not the focus of our study.

We also did not find any significant effect of infant age or sex or maternal parity on infant survival probability, although all three have previously been reported in mammals (e.g., parity: infant mortality is higher for primiparous females, Pluháček et al. 2007; infant age: younger infants die more than older infants, Altmann et al. 1977; infant sex: higher mortality among male than female infants, Cheney et al. 2004). The reason for our result is possibly that in our study population infants seem to die mainly from infanticide, and that males perform infanticide opportunistically, i.e., without regard to infant sex or age (as long as the infant is still dependent), or the mother's parity. Furthermore, reports of sex differences in infant mortality are inconsistent for primates (Clutton-Brock 1991) and sex-dependent mortality seems not to apply to macaques during the first year of life (van Noordwijk and van Schaik 1999). Similarly, the impact of parity on infant survival seems to be insignificant for most primates (van Noordwijk and van Schaik 1999; Cheney et al. 2004; but see Schino and Troisi 2005). Other, more important variables (such as the number of adult females, rainfall, and alpha-male takeover) may thus have overridden any such

effect in our statistical analysis. In addition, these variables may not play a role at such an early stage, thus future studies should include older offspring stage too.

In summary, our study suggests that a combination of ecological constraints and social variables, in our case environmental seasonality, female within-group competition for food sources, between-group resource defense and male reproductive strategies, and their interactions, have an impact on offspring survival in crested macaques. It therefore reveals the direct link between fitness costs and benefits of sociality in regard to within- and between-group competition. We further show that the determinants of direct fitness have to be measured at both a pre- and post-natal level, because they cannot necessarily be extrapolated from one to the other. Future studies adopting a similar approach would further elucidate the complex interplay of social and environmental determinants of direct fitness in gregarious mammals.

Chapter 3

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3 Mother-male bond, but not paternity, influences male-infant affiliation in wild crested macaques

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3.1 Abstract

In promiscuous primates, interactions between adult males and infants have rarely been investigated. However, recent evidence suggests that male affiliation towards infants has an influence on several aspects of the infants' life. Furthermore, affiliations may be associated with male reproductive strategy. In this study, we examined which social factors influenced male-infant affiliation initiated by either male or infant, in wild crested macaques (*Macaca nigra*). We combined behavioral data and genetic paternity analysis from 30 infants living in three wild groups in Tangkoko Reserve, Indonesia. Our results indicate that adult males and infants do not interact at random, but rather form preferential associations. The social factors with the highest influence on infant-initiated interactions were male rank and male association with the infant's mother. While infants initiated affiliations with males more often in the absence of their mothers, adult males initiated more affiliations with infants when their mothers were present. Furthermore, males initiated affiliations more often when they were in the same group at the time the infant was conceived, when they held a high dominance rank or when they had a close relationship with the mother. Interestingly, paternity did not affect male-infant affiliation despite being highly skewed in this species. Overall, our results suggest that adult males potentially associate with an infant to secure future mating with the mother. Infants are more likely to associate with a male to receive better support, suggesting a strategy to increase the chance of infant survival in a primate society with high infant mortality.

3.2 Introduction

The theory of parental investment (Trivers 1972) states that differences between sexes with regard to infant care stem from females investing more time and energy per gamete than males, who instead compete with one another for access to fertile females. Accordingly, adult males (hereafter referred to as males) have been observed to provide infant care in only 10% of mammalian species (Woodroffe and Vincent 1994). Nevertheless, in the primate genera, paternal care (defined as any behaviour a father is directing to his offspring that improves the fitness of the offspring, Trivers 1972) has been observed in up to 40% of species (Kleiman and Malcolm 1981).

Infant care by male primates is most frequently observed in monogamous pair-bonded species (Whitten 1987), where paternity certainty is high (Griffin et al. 2013). In such settings, fathers maximize their fitness not just by producing a given number of offspring, but by also ensuring their survival (Hamilton 1964). In contrast, a promiscuous mating system often leads to low paternity certainty; thus father-offspring affiliations are expected to be lower than for monogamous species (Geary 2000) unless fathers are able to recognize their offspring. However, even in promiscuous primate societies, fathers, in some species, have been observed to provide care to a substantial degree, and in doing so increase the probability of their offspring's survival ("paternal investment" strategy; Smuts & Gubernick, 1992) and hence their own fitness.

Paternal care can take different forms. It can entail quite active behavior e.g., males exchanging affiliative interactions with offspring (rhesus macaques, *Macaca mulatta*, Langos et al. 2013), supporting offspring during agonistic conflict with third parties (savannah baboons, *Papio cynocephalus*, Buchan et al. 2003) or even protecting them against infanticidal males (Hanuman langurs, *Semnopithecus entellus*, Borries et al. 1999). In addition, fathers may have an influence on the fitness of their offspring through paternal effects. For example, sharing spatial proximity with offspring might increase access to food (chacma baboons, Huchard et al. 2013). Furthermore, the mere presence of the father in the infant's social group may increase the rate of infant maturation (savannah baboons, Charpentier et al. 2008).

In some species, male care can be witnessed in the context of "friendship" (Smuts 1985) between a lactating female and a male that may or may not be the sire. These males form longer-lasting bonds with a mother and may provide care and protection to her offspring (Busse and Hamilton 1981; Anderson 1992; Palombit et al. 1997; Palombit et al. 2000). However, a male friend is often a likely sire, i.e. a male present at the time of conception that also mated with the female and hence has some paternity probability (chacma baboons, Moscovice et al. 2009; Moscovice et al. 2010). An alternative strategy for males to improve their fitness could be to provide care to an unrelated infant. This could increase the male's future mating opportunities with the infant's mother in her next reproductive cycle (or mating-effort hypothesis, Smuts and Gubernick 1992; Kurland and Gaulin 1984; Clutton-Brock 1991; care-then-mate strategy, Ménard et al. 2001). Whether this is a widespread strategy in primates remains unclear (van Schaik and Paul 1996). While it has been observed in Barbary macaques (*Macaca sylvanus*, Ménard et al. 2001), no evidence has been found in white-headed langurs (*Trachypithecus leucocephalus*, Zhao and Pan 2006).

While the males' role and benefits of affiliations with infants has been the focus in previous studies, the infants' perspective is far less clear. Most studies on male-infant interactions in multi-male groups have, to date, focused on explaining male initiated affiliative behavior towards infants. In fact, very few studies have investigated the role of infants in affiliative interactions with males, and those that exist are mostly anecdotal (Ransom and Ransom 1971; Guimarães and Strier 2001; Moscovice et al. 2009). They do, however, show that infants also take an active part in their relationship with males (Langos et al. 2013; Huchard et al. 2013). Infancy is the most critical period in an individual's life in terms of survival, as it holds the highest mortality rates in many species (reviewed in Caughley 1966; see also Dunbar 1987; Cheney et al. 2004). Hence infants can be expected to have evolved survival strategies; for example by forming bonds with their fathers or with males that are friends of their mothers, either to receive protection (Nguyen et al. 2009) or to gain access to richer food patches (Huchard et al. 2013). Under these circumstances, high-ranking males may be preferred social partners for infants, particularly in species in which the risk of infanticide is high (Borries et al. 1999). Clearly, more studies are needed to investigate the infants' affiliative behavior with males, which males they engage with, and whether this has an influence on offspring survival.

The aim of the present study therefore was to investigate male-infant affiliations in wild crested macaques (*Macaca nigra*) using two analytical approaches in order to take the perspective of both males and infants. Crested macaques are endemic to the island of Sulawesi and live in large multi-male multi-female groups with female philopatry (Duboscq et al. 2013). The social system is highly dynamic due to frequent immigration and emigration of males, leading to frequent changes to the males dominance hierarchy (Neumann et al. 2011) and a short average male group tenure (Marty et al. 2015). Furthermore, paternity is highly skewed towards alpha-males due to their successful mate-guarding of fertile females (Engelhardt et al. in revision). As a result, males fight fiercely for dominance, turn-over in alpha males is particularly high in this species and occur exclusively by males coming from outside the group (Marty et al. 2015). In a recent study, we found evidence that a take-over in alpha-male position is the most important determinant of infant mortality in crested macaques (Kerhoas et al. 2014) which suggests that some threat of infanticide may exist even if infanticide has never been directly observed.

In general, infant mortality is high in crested macaques, with 22% of infants dying or disappearing within their first year despite predator pressure from felids being absent on Sulawesi (Kerhoas et al. 2014). Strategies to improve survival should

therefore be particularly important for infant crested macaques. At the same time, males should also be interested in protecting their offspring. So far, it remains unknown for how long fathers stays in the birth group of their offspring, or whether fathers and infants recognize each other. One way for males to assess paternity likelihood may be to use mate-guarding and mating success (Buchan et al. 2003). On the one hand, crested macaque females mate promiscuously throughout the majority of the ovarian cycle, increasing the mating success of many males. On the other hand, females are highly monopolized by the dominant male during the fertile phase of their conceptive cycles (Engelhardt et al. in revision). Mate guarding would allow assessment of paternity likelihood in the case that males are able to recognize this fertile period.

We propose that for infant crested macaques, it is important to receive protection; particularly against infanticidal males, from high ranking males, regardless of whether this male is their father or not. We thus predict that infants would actively initiate affiliations with high ranking males. For males, in contrast, we propose that they should support their own offspring (paternal investment hypothesis) and that high-ranking males would actively provide more care than low-ranking ones based on the reproductive skew observed in this species (Engelhardt et al. in revision). Hence, we predict that fathers will provide more affiliation towards their offspring than non-fathers towards non-offspring. Given that males should aim to increase offspring survival, affiliation with fathers should be independent of the mother's presence in proximity to the infant. At the same time, we test the care-then-mate hypothesis predicting that a male support unrelated infants in order to create or maintain a social bond with the mother or to advertise its fathering quality so that the mother is more likely to mate with the male in the future. This could be an alternative reproductive strategy for low-ranking males in crested macaques. Consequently, we predict that unrelated males, unlike fathers, interact with infants mainly when mothers are present. Finally, we investigated the effect of mother-male affiliation on infant-male affiliation as they have been found to be linked to one another (Palombit et al. 1997; Moscovice et al. 2009). Accordingly, we predicted that the existence of a strong mother-male bond increases affiliations between the infant and the male.

3.3 Methods

I/ Study population

The study took place in the Tangkoko Reserve (8,867-ha) in Sulawesi, Indonesia (1°31'00.1"N, 125°10'59.9"E). The research area consists of primary and secondary lowland rainforest (O'Brien and Kinnaird 1997; Rosenbaum et al. 1998; Whitten et al. 2001). Data were collected on three groups of wild crested macaques (R1, R2 and PB), fully habituated to human observers with adults and infants individually identified and continuously monitored by the Macaca Nigra Project. Group sizes varied between 50 to 80 individuals during the study period, with 13 to 25 reproducing females and 4 to 11 adult males in each group.

II/ Data collection

Behavioral data were collected from October 2008 to September 2010 by DK and four field assistants using a 30-minutes *focal animal sampling* (Altmann 1974) follow (inter-observer reliability: Cohen's kappa = 0.67-0.80, significant correlation coefficients between behavioral variables = 0.74-0.96, all $P < 0.05$, Kaufman and Rosenthal 2009). We followed 35 infants (21 males, 14 females) across all three groups. However, our analysis was restricted to a total of 30 infants, as we were not able to sample four infants that died during the course of study, and we excluded another infant with genetic samples for which paternity could not be resolved (see below). Infants were followed from birth to one year of age (average weaning age; Kerhoas et al. 2014) excepting five infants who were already born when the study started (1 to 6 months old). During the study period, 30 infants survived to one year of age, and five infants died/disappeared during the study. In our study population, we observed that infants spent less than 50% of their time in proximity of their mother after reaching 5 month of age, suggesting that infants were fairly independent after this time. A total of 3,611 hours of focal observations were collected with an average of 100.63 hrs \pm 23.87 (SD) per infant that survived to one year of age. Observations were conducted from dawn to dusk and focal sampling was spread evenly throughout the day, sometimes with several focal follows per day per infant.

Simultaneously, we recorded (i) all social interactions involving the focal animal using continuous *focal animal sampling* of 30 minutes duration (Altmann 1974); (ii) proximity of the mother and adult males within a 2.5 m radius of the focal infant using *scan sampling* with two minute intervals (Altmann 1974); and (iii) all affiliative interactions of the mother and an adult male when both were within a 2.5m

radius of the focal infant as part of *focal animal sampling*. Since male age was unknown, males were classified as adults if their scrota were fully descended and their canines were fully erupted (Kerhoas et al. 2014). We calculated the proportion of affiliations observed between the mother and an adult male out of the total scans when both were in spatial proximity of the focal infant. All observers were blind to the paternal relationships of the study subjects during behavioral data collection.

We recorded the frequency of agonistic (e.g. half open mouth threat, lunge, chase, etc.; behaviors described for this species in Thierry et al. 2000b) and affiliative interactions. The latter included (1) all socio-positive approaches, that is, no immediate agonistic interaction followed an approach, while the dyad would stay in close spatial proximity of at most 2.5 m for a minimum of 5 sec (cf. Langos et al. 2013), (2) social grooming and (3) friendly behaviors (based on the ethogram described in Thierry et al. 2000b) such as lipsmacks, silent bared teeth face (both greetings), follows (i.e., an individual consistently walks after a moving partner, Thierry et al. 2000b), and peaceful interventions (i.e., intervening in a conflict directing affiliative behaviours towards one of the opponent, Thierry et al. 2000b). Data were recorded using PTab software (PTab Spreadsheet v.3.0; Z4Soft) on Hewlett Packard IPAQ Personal Digital Assistants (model 114) and Psion Workabout Pro M handhelds.

In addition, we collected *ad libitum data* (Altmann 1974) on male migrations, displacement or aggressive interactions for the purposes of calculating male and female dominance hierarchies, births and disappearances/deaths of group members, and monthly female sex skin swelling cycles. Female swellings in this species are a fairly reliable indicator of ovulation (Higham et al. 2012), and because females do not present any swelling while gestating, we were able to identify the conceptive cycle without hormone analysis.

III/ Genetic paternity analysis

Paternity was determined non-invasively by collecting fecal samples before and throughout the study period from all focal infants (N=30), their mothers (N=30) and all potential sires (N=41). Potential sires were defined as all adult males encountered in the study group before or during our study period, irrespective of whether a male was present in the group at the time of a specific infant's conception (unpublished data, Macaca Nigra Project). We excluded 11 natal subadult males who only reached adulthood during the study, but emigrated shortly after reaching maturation. To store the samples after collection, we used the two-step method (Nsubuga et al. 2004):

fresh feces was kept in 90% ethanol for 24 hours and then stored in a tube filled with silica until DNA extraction. We collected and genotyped a minimum of two independent fecal samples for all individuals (except for one infant with only one collected sample) to guard against sample mix-up and animal misidentification. Extractions were done using QIAamp DNA Stool Mini Kit (Qiagen) or GEN-IAL All-Tissue DNA Kit (GEN-IAL GmbH). Samples were genotyped on a total of twelve highly variable microsatellite markers (Engelhardt et al. in revision). Products were analyzed with an ABI PRISM3100 automated sequencer and the ABI peak scanner software. We used a combination of the multiple tube approach (Taberlet et al. 1996; Taberlet and Luikart 1999) and the two-step multiplex PCR to increase the accuracy of the results (PCR details in Engelhardt 2004; Arandjelovic et al. 2009). A heterozygous genotype was accepted when both alleles were confirmed at least two times per extract, i.e., a total of four independent PCRs were required for a given individual. A homozygous genotype was assigned when a single allele occurred in six independent PCRs, in order to control for allelic dropout (Taberlet et al. 1996; Taberlet and Luikart 1999; Engelhardt et al. 2006). In case one heterozygous genotype appeared within the six PCRs, we did up to eleven PCR replications to ensure that we reported a true genotype (Taberlet et al. 1996). In our genetic dataset of 176 individuals, the mean observed heterozygosity was 0.77 ± 0.06 (mean \pm SD), the mean number of alleles per locus was 6.08 ± 1.78 (mean \pm SD) and the mean polymorphic information per allele was 0.66 ± 0.08 (mean \pm SD). There was no deviation from the Hardy-Weinberg equilibrium and no evidence of a null allele occurring at these loci (all calculation performed with CERVUS 3.0, Kalinowski et al. 2007). To assess the minimum number of loci required to assign paternity reliably, we calculated the sibling probability of identity (Waits et al. 2001; Schubert et al. 2011). The sibling probability of identity, i.e. the chance of encountering siblings with an identical genotype on a defined number of markers, was found to be reasonably low (0.001) when eight loci were used. Thus, we genotyped each individual at a minimum of eight loci, with an average of 11.92 markers ± 0.31 genotyped per individual. Maternity derived from field observations was genetically tested and confirmed for all mother-infant pairs (N=30) in our study which were subsequently used in the paternity analysis. We only determined father-offspring and mother-offspring dyads.

For paternity assignment, we considered all genotyped males as potential sires for all 30 infants. We used a combination of exclusion and likelihood analyses as follows. For 18 infants, all potential males were excluded on at least two loci, with

the exception of the assigned sire, who matched the mother-offspring pair at all loci. In eight cases, all potential males were excluded on at least one locus, with the exception of the assigned sire, who matched the mother-offspring pair. In three cases, which were all genotyped on 12 loci, there were no male without mismatch to the mother-offspring pair, but only one male with one mismatch and all the other potential sires with at least two mismatches. In one case, all males were excluded on at least two loci, but two males without a mismatch remained. The assigned sire was the male that was present at the time of conception in the group of the offspring, as the other male was not present in any group at the time and immigrated a year later. All paternity assignments were additionally supported at the 95% confidence level by the likelihood method calculated by CERVUS 3.0 (Kalinowski et al. 2007).

IV/ Statistical analysis

a) Specific male-infant dyads

To test whether specific male-infant dyads were affiliating at random or displayed more frequent social interactions than expected at random, we performed permutation tests (Adams and Anthony 1996; Edgington and Onghena 2007; Whitehead 2008) on contingency tables containing the frequency of affiliative interactions initiated by infants towards males and vice versa, separately for each study group. We permuted the identities of the initiator of the interactions across the identities of the interactant, including only adult males that were present during the entire study period into this analysis. As the test statistic, we used a chi-square test (Siegel and Castellan 1988) and applied 10,000 permutations into which we included the original data as one permutation. The two-tailed P-values were determined as the proportion of chi-square values being at least as large as that of the original data. Permutation tests were calculated in R (version 2.14, R Core Team 2012) using a script written by Roger Mundry.

b) Factors influencing adult male-infant interactions

To investigate which factors influence affiliative interactions between males and infants, we ran Generalized Linear Mixed Models (GLMMs) with a binomial error structure and logit link function (Baayen 2008). GLMMs allow to analyze and control various potential confounding variables simultaneously and are suggested as the optimal approach for data including repeated observations of individuals, as they are capable to avoid false positives and erroneous significances and overly narrow standard errors (Schielzeth and Forstmeier 2009; Barr et al. 2013). We ran two models: in the first model the binary response was whether or not an infant initiated

an affiliation towards a male on a given day (hereafter: the infant model) and in the second model the binary response variable was whether or not a male initiated an affiliation towards an infant on a given day (hereafter: the male model). The data comprised all possible male-infant dyads based upon the presence of males and infants per day in a given group. In other words, the response variable was a binary variable: whether the male-infant dyads within a group were observed affiliating or not on a given day. In both models, we included the following predictor variables which were determined on a daily basis.

Mother and male rank: Male dominance rank may have a strong influence on male-infant interactions as observed in other cercopithecine species (e.g., Japanese macaques, Itani 1959; yellow baboons, *Papio cynocephalus*, Stein 1984) and mountain gorillas (*Gorilla beringei beringei*, Rosenbaum et al. 2015), because they may offer greater status benefits. An adult male's interest in an infant may be influenced by the mother's rank as high-ranking females tend to have a higher infant survival than low-ranking females in some species (e.g., Majolo et al. 2012). However, female crested macaques express a tolerant social style, characterized by low intensity, frequently bidirectional, aggressive interactions, and reconciled conflicts (Duboscq et al. 2013). A previous study found that maternal rank predicted fetal, but not infant survival suggesting that being a dominant female may, in fact, not increase infant survival in this population (Kerhoas et al. 2014).

To obtain a continuous measure of adult male and adult female dominance rank, separately (as males usually outrank all females), we used Elo ratings (Albers and de Vries 2001; Neumann et al. 2011) based on displacements and aggressive dyadic interactions observed *ad libitum* (Altmann 1974) between adult group members. For each observational day, we standardized the Elo rating scores of all adults of the same sex to a range from 0 to 1, in order to obtain comparable ratings across the entire study period. As focal infants are expected to occupy a rank based on the rank of their mother when they reach one year of age (Cheney 1977; Datta 1988), we used the mother's rank as a proxy of the expected infant rank in this study.

Mother presence: In the first year of an infant's life, mothers are expected to have a large impact on the presence of conspecifics who they tolerate in close spatial proximity of their infant. In addition, the "mate-then-care" strategy predicts that males would be more likely to affiliate with infants when the mother is present. Hence, we included the daily number of scans when the mother was in spatial proximity (i.e. within 2.5 m) of her infant.

Mother-Male affiliation: Friendship is defined as a close, affiliative relationship (Silk 2002) that entails high rate of spatial proximity and grooming (Smuts 1985). In rhesus macaques, male-female friendship has been observed during the birth season (Chapais 1983; Manson 1994) and in Assamese macaque (*Macaca assamensis*), the relationships were found to last at least 2-3 years (Ostner et al. 2013). To investigate the influence of mother-male affiliation (or mother-male friendship) on the probability of adult male-infant affiliation, we calculated the frequency of friendly behaviors (e.g. mainly social grooming but also lipsmack, silent bared teeth face, etc.; hereafter affiliations) the mother and an adult male exchanged when both were in spatial proximity to her infant (i.e. within 2.5 m) during the infant's focal follows. This predictor was included, as it was found that males both associate and provide care to infants of their female friends (Smuts 1985; Nguyen et al. 2009; Moscovice et al. 2010; Ostner et al. 2013).

Paternity: We identified 30 father-infant dyads out of a total of 224 adult male-infant dyads. Given the high infant mortality in crested macaques, we expected fathers to invest in affiliative relationships to ensure offspring survival. Hence, we investigated if males affiliate more with their own offspring compared to non-offspring although there are more opportunities for interactions between adult males with unrelated infants. In addition, we investigated whether infants affiliate preferentially with their father rather than non-fathers. We omitted focal follows of the infant who did not have its father anymore in the group at the date of the focal (i.e. for the male and infant models).

Male presence at conception: Adult males may establish a relationship with the respective infant based on their presence during the infant's conception. Given that females mate with multiple males during their likely conception, these males are also likely to have fathered the infant (Borries et al. 1999; Moscovice et al. 2010). We considered all adult males that were present in the group during the conceptive cycle of a given mother per focal infant. We included this variable in the male model only, as infants (not yet born) cannot have witnessed which adult males were present or not at conception.

In addition, we expected several variables to interact with the presence of the mother. In fact, the opportunity of infants to interact with an adult male could be highly dependent on the mother presence and behavior who could either restrict or promote infants' affiliations with a given male, depending upon the male's rank or paternity probability (reviewed in Widdig 2007). Thus, we included the three-way

interaction between paternity, male rank and mother presence. To investigate the influence of mother-male friendship on the male-infant affiliation, we also included the three-way interaction between paternity, male rank and mother-male affiliation. We also included the five associated lower level two-way interactions into the infant and male model.

In addition to these test predictor variables, we controlled for the following variables known to have an effect, however they are not interpreted (cf. Mundry 2014). As in other female phylopatric species, infants may develop their relationships with adults differently according to their sex (Bolin 1981; Evans et al. 2012; Langos et al. 2013). Hence, we controlled for *infant sex*. To account for the social development taking place in the first year of life, when infants are not yet weaned, we included also the daily *infant age*. *Number of adult males in the group* may influence male-male competition and therefore the frequency of male-infant interactions. The activity required to fulfill energetic needs such as foraging may also constrain the time males spent affiliating with infant. Therefore, we controlled for the variation of fruit availability by including *seasonality* as the cosine and sine of date (i.e. day within year) into the model (Stolwijk et al. 1999). As rainfall seasonality affects infant survival in this population (Kerhoas et al. 2014) seasonality may also have an influence on the occurrence of male-infant interactions. *Male tenure* (i.e., the number of days an adult male spent in a group) was added as a variable because this should influence the degree of familiarity between adult males and mothers, which might be important for the formation of friendship. In fact, the duration of male residency in a group is very variable in this species (mean \pm SD= 766.5 \pm 396.7 days, range= 1 to 1549 days). Finally, the *observation time* (i.e., number of scans recorded by day) was incorporated in the model as an offset variable, to account for observation efforts (McCullagh and Nelder 1989). Random effects included in the model were the identity of the *adult male*, the *infant*, the *dyad* (i.e., adult male and infant identity combined), the *social group*, and the *day* of data collection (Table S1 in the Online Resource shows all factors included in the infant and male model). Moreover, to account for random variation in the mean response and the strength of the effect of predictors among different individuals or dyads, as well as to keep type I error rate at 5%, we included all possible random slopes (15 in total, see details in Online Resource) for the tested variables and interactions (Barr et al. 2013).

Furthermore, our datasets were likely to show temporal autocorrelation as the response (organized in the succession of observational days) may not be independent (Burnham and Anderson 2002). Thus, we included two autocorrelation terms (AC

terms), one for the infant and one for the adult male, in each models (as in Langos et al. 2013). The AC terms were calculated by first deriving the residuals from the model described above. Then, separately for each data point, we averaged the residuals of all other data points. The contribution of the residuals was weighted by a function of the time lag between them and the specific data point. These weighted functions had the shape of a Gaussian distribution and their standard deviations were determined such that the likelihood of the model with the autocorrelation was maximized. The AC terms were calculated using a function written by Roger Mundry.

All statistical analyses were carried out in R (version 2.14, R Core Team 2012). Prior to running each model, we checked all predictors for their distribution and, as a consequence, log-transformed mothers' presence to achieve a more symmetrical distribution. Then, we z-transformed all continuous predictors to a mean of zero and a standard deviation of one to get comparable estimates and an easier interpretable model with regard to the interactions. The GLMM was fitted using the function “lmer” of the lme4 package (Bates et al. 2011). We used a likelihood ratio test (LRT, R function “anova”, Dobson 2002) to compare the fit of the full model with the fit of the null model (including only the AC terms, offset, control and random factors) to determine whether the predictor variables as a whole influenced the response variable (Forstmeier and Schielzeth 2011). Given the significance of the full model, we tested the significance of interaction also with LRT's comparing the full model with a model reduced by the respective interaction. In the case an interaction was non-significant, we removed it from the model to reliably infer about the respective lower terms it included. To check for the assumptions of our models, we calculated Variance Inflation Factors (VIF, Quinn and Keough 2002) using the function “vif” of the R package “car” (Fox and Weisberg 2011). Given that the largest VIF for both models reached 3.35, we concluded that collinearity was not a severe issue. We assessed model stability by comparing the estimates derived by a model based on all data with those obtained from models with the levels of the random effects excluded one at a time, which indicated that no influential cases existed.

3.4 Results

We observed a total of 24,082 affiliations between infants and males distributed over 449 days out of a total of 465 days of observations (96.5 %). Furthermore, we found that $22.5\% \pm 4.6$ (mean \pm SD) of all interactions of focal infants involved an adult male; $81.5\% \pm 8.4$ of all male-infant interactions were affiliative, the remaining being aggressive interaction. Infants initiated a total of 15,290 (63.5%) male-infant affiliations (mean of 509 ± 158 per infants). The strength of male-infant association varied between dyads with a mean rate of infant affiliations towards males of 0.043 ± 0.054 (mean \pm SD) and a mean rate of male affiliations towards infants of 0.019 ± 0.016 (mean \pm SD). The vast majority of affiliations initiated either by infants or adult males consisted of tolerated approaches (infant $91.6\% \pm 3.1$, male $96.4\% \pm 11.8$ of all their interactions initiated). In addition, infants' second and third most frequently initiated behaviors towards males were following ($3\% \pm 2.1$) and lipsmacks ($2.9\% \pm 2.6$; Thierry et al. 2000b). In contrast, the behaviors that adult males initiated most, after tolerated approaches, was silent bared-teeth faces towards infants ($1.5\% \pm 6.0$) and peaceful interventions ($0.4\% \pm 0.7$). Infants groomed by adult males were rarely observed (0.1%). The majority of fathers (86.7%) were still present when the offspring completed their 1st year of life. Finally, we calculated the average number of scans an infant was in proximity of a male and its mother. When an infant was near a male, the mean number of scans where the mother was also present was 230 ± 96 , while, on average, in $1123 \text{ scans} \pm 427$ the mother was absent. This was a five times higher probability that an infant was near a male without its mother. When an infant was near the mother, the mean number of scans a male was also present was 220 ± 95 , and in $1380 \text{ scans} \pm 463$, on average, no males were present, representing a six times higher probability of infants being only with the mother.

I/ Specific male-infant dyads

The results of the permutation tests showed that adult male-infant dyads did not affiliate at random, regardless of the group considered and whether infants or adult males initiated the interaction (Table 1). Hence, infants and adult males, respectively, had preferred affiliative interaction partners. More than half of the males (53%) had several preferred infant partners (two or three preferred infants). The majority of infants (26 out of 30, 86 %) approached only one preferred male partner. Finally,

29% of males (10 out of 35 males) did not preferentially affiliate with any infants, whereas only 3% of infants (1 out of 30 infants) had no male associates.

Table 3.1 Results of the permutation tests for both infant and male initiated affiliations for each study group. Chi square values are calculated from observed values

Initiator	Recipient	Group	total N	chi square	p value
Male	Infant	PB	2651	250.4	<0.001
Infant	Male	PB	5817	448.2	<0.001
Male	Infant	R1	3113	617.2	<0.001
Infant	Male	R1	4231	1370.2	<0.001
Male	Infant	R2	4382	873.4	<0.001
Infant	Male	R2	6478	1957.9	<0.001

II/ Factors influencing adult male-infant affiliations

a) Infant model

When comparing the fit of the full model with the fit of the null model (i.e. a model including only the control, offset, and random variables and the AC terms), the infant model was significantly different to the null model. Hence the set of predictors tested had a clear influence on the probability of infants' initiated affiliations towards adult males (LRT: $\chi^2=26.15$, $df=13$, $P=0.016$). To achieve the final model, all interactions were tested for their significant contribution to the full model using a LRT. This resulted in the removal of the two three-way interactions male rank*paternity*mother presence ($\chi^2=1.32$, $df=1$, $P=0.25$) and male rank*paternity*mother-male affiliation ($\chi^2=0$, $df=1$, $P=0.97$). We also removed the following two-way interactions from the infant model: paternity*mother presence ($\chi^2>0.17$, $df=1$, $P=0.68$), male rank*mother presence ($\chi^2=0.01$, $df=1$, $P=0.93$), male rank*paternity ($\chi^2=0.63$, $df=1$, $P=0.42$), paternity*mother-male affiliation ($\chi^2=0.12$, $df=1$, $P=0.72$). We kept the two-way interaction between male rank and mother-male affiliation in the final infant model as it had a significant influence on infant affiliations towards males ($\chi^2=4.36$, $df=1$, $P=0.037$). The results of the interaction showed that infants initiated affiliations predominantly towards high-ranking males, but this effect seemed to be modulated by the affiliative bond between the mother and the respective male, whereby if a male had a stronger relationship to the mother, the infant initiated interactions more towards this male even if it was low ranking (Fig. 1). In addition, infants initiated interactions significantly more towards adult males when the mother was not present in proximity (Table 2). Interestingly, infant

affiliation was not influenced by mothers association with the infant's sire as the two-way interaction between paternity and mother-male affiliation was not significant. Finally, neither paternity nor mother's rank had a significant effect on infants initiating affiliations towards males (Table 2).

Table 3.2 Results of GLMM analyses of the infant model: the significant factors influencing the affiliations of infants toward males are marked in bold (values not shown for the variables comprised by a significant higher interaction and for the control variables, which can be found in the Online Resource)

Fixed effects:	Estimate	SE	LRT df	LRT χ^2	P of LRT
Intercept	-5.32	0.20			
Infant AC term	0.40	0.02	1	442.66	<0.001
Male AC term	0.23	0.02	1	140.53	<0.001
Paternity	0.13	0.12	1	1.11	0.292
Mother rank ⁽¹⁾	0.03	0.02	1	1.56	0.212
Mother presence	-0.17	0.05	1	5.27	<0.022
Male rank* Mother-male affiliation	-0.07	0.03	1	4.36	0.037

b) Male model

Again, the set of predictors tested had a clear influence on the probability of adult males' initiation of affiliations towards infants (LRT, comparing the fit of the full model with the fit of the null model: $\chi^2=26.34$, $df=14$, $P=0.023$). To achieve the final model, we tested all interactions and removed the two three-way interactions male rank*paternity*mother presence ($\chi^2=0.17$, $df=1$, $P=0.68$) and male rank*paternity*mother-male affiliation ($\chi^2=0.07$, $df=1$, $P=0.79$). We also removed all the two-way interactions from the male model: paternity*mother presence ($\chi^2=1.98$, $df=1$, $P=0.15$), male rank*mother presence ($\chi^2=0.92$, $df=1$, $P=0.33$), male rank*paternity ($\chi^2=2.15$, $df=1$, $P=0.14$), paternity*mother-male affiliation ($\chi^2=0.80$, $df=1$, $P=0.37$), male rank*mother-male affiliation ($\chi^2=2.12$, $df=1$, $P=0.14$).

With no three- or two-way interactions significant, all factors were solely tested as single effects, whereby each single effect is controlled by the effect of all others. The results of the final male model showed that adult males that were present during the infant's conception period were significantly more likely to initiate affiliation with the infant than males absent at conception (Fig. 2). In addition, high-ranking males tended to be more likely to initiate affiliations with infants than low-ranking males (Table 3). A mother's proximity to her infant significantly increased the probability of an adult male's affiliation with her infant (Fig. 3); in other words,

males interacted more with an infant when the mother was present. Furthermore, mother-male affiliation also increased the probability of male affiliations towards infants. As in the infant model, paternity and mother rank was found to have no significant influence on the probability of adult males initiating affiliation towards infants.

Table 3.3 Results of GLMM analyses of the male model: the significant factors influencing the affiliations of males toward infants are marked in bold (values not shown for the control variables which can be found in the Online Resource)

Fixed effects:	Estimate	SE	LRT df	LRT χ^2	P of LRT
Intercept	-5.47	0.18			
Infant AC term	0.18	0.02	1	89.27	<0.001
Male AC term	0.19	0.02	1	90.01	<0.001
Paternity	-0.08	0.10	1	0.53	0.465
Mother presence	0.10	0.03	1	4.43	0.035
Male presence at conception	0.35	0.14	1	6.02	0.014
Male rank⁽¹⁾	0.14	0.06	1	3.15	0.015
Mother rank ⁽¹⁾	-0.01	0.02	1	0.15	0.696
Mother-male affiliation	0.07	0.03	1	5.01	0.025

3.5 Discussion

The results of our study suggest that, in wild Sulawesi crested macaques, adult male-infant interactions are mainly positive, with specific males and infants forming affiliative bonds. Adult male-infant affiliations were twice as common when compared to rhesus macaques (Langos et al. 2013) and, interestingly, infants initiated two thirds of them. Paternity did not significantly affect interactions initiated by adult males or infants; therefore our data do not provide any support for the paternal investment hypothesis. However, the probability of male-infant affiliation was significantly higher if the male was present at the infant's conception; a cue that males may use to assess their paternity likelihood, unless they use other cues such as mating success (cf. Buchan et al. 2003), which we were unable to include here. Male dominance rank also influenced their likelihood to affiliate with infants, as higher-ranking males interacted more with infants than lower-ranking males. Interestingly, a male's affiliation with the mother and mother's presence respectively were both important factors determining males' affiliations with infants, which may be an indirect indication to crested macaque males possibly using the "care-then-mate"

strategy. At the same time, our results clearly show that male-infant interactions are predominantly instigated by infants and thus obviously in their interest. We found a significant two-way interaction between male rank and mother-male affiliation on the probability of infants associating with adult males suggesting that infants preferred to affiliate with high-ranking males or low-ranking friends of their mother. In most behavioral studies investigating adult male-infant interactions, the data collection focuses on adult males, thus exploring the underlying evolutionary mechanisms for male care. However, our results clearly show that male-infant interactions are predominantly instigated by infants, in accordance with previous studies (Moscovice et al. 2009; Huchard et al. 2013, but see Langos et al. 2013). Infancy is the life stage that holds the highest mortality (Dittus 1979; Blomquist 2013), so it is reasonable that strategies favoring survival would be strongly selected for. In fact, we have observed that infants target one specific male, increasing the chance of developing a bond with a potential protector, which may in turn promote infants' chance of survival. The high initiation rate of infants may be linked to the high infant mortality rate as male-infant interactions are in fact quite common in our population. In chacma baboons, a species suffering a very high infant mortality (Palombit 2000), infants or juveniles have been observed to mainly initiate proximity with males (Moscovice et al. 2009; Huchard et al. 2013). Hence, future studies should investigate whether male-infant interactions are more likely to be initiated by infants, not males, when infant mortality is high, and whether there is an influence on infant fitness and survival.

I/ Infant model

Infants in our study initiated affiliations preferably towards high-ranking males, but this effect depended on the intensity of mother-male affiliation: with increasing mother-male bond, infants showed a preference even for low-ranking males. Affiliating with high-ranking males could increase an infant's chance of survival, as infants may secure better protection or support (Huchard et al. 2013). In our study population, previous findings revealed that infants suffer high mortality rates when alpha male positions were changed, following the take-over by a newcomer male (Kerhoas et al. 2014). Securing support from a strong ally is the best survival strategy an infant has at its disposal in an infanticidal species (van Schaik and Janson 2000) as the crested macaque seems to be (Kerhoas et al. 2014). Thus, infant crested macaques seem to be under selective pressure to develop bonds with adult males that may provide sufficient protection if an infanticidal male attacks them. Alternatively, infants are usually in the centre of the group, and may interact more with high-

ranking males simply because they are also more often in the centre of the group (Janson 1990; Hemelrijk 2000).

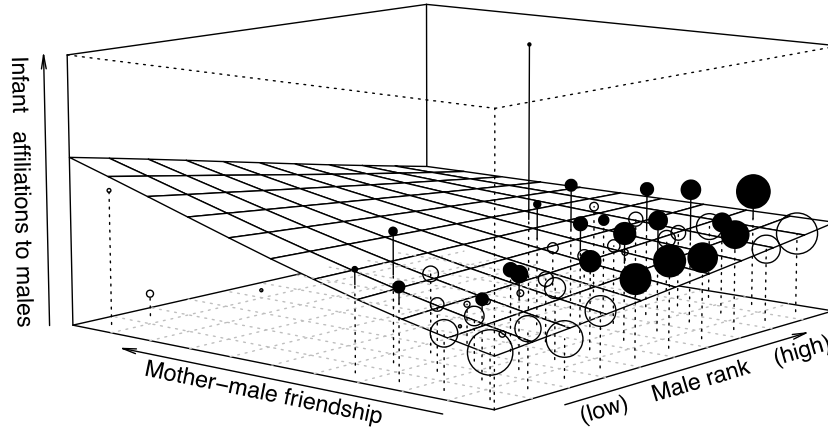


Figure 3.1 Influence of the interaction between male dominance rank and the strength of mother-male friendship on the probability of affiliation of an infant towards a male. The plane depicts the predicted values calculated by the GLMM with each grid representing the mean value per square of the predicted mixed model. Circles represent empirical mean affiliation value per square and the size of the circles is proportional to the number of data points. The filled circles depict the data points that exceed the estimated value and the open circles depict the data point that fall below the estimated values

In addition to male rank, affiliation initiated by infants was also influenced by mother-male bond. Mother-male friendship has been found to promote male-infant bonds in chacma baboons (Moscovice et al. 2009) and Assamese macaques (Ostner et al. 2013). This potentially also influences infants' survival probability as male friends have been found to react more to playback of infanticidal male threats than control males in chacma baboons, a species with high risk of male infanticide (Palombit 2000). In addition, male caretakers also reacted more intensely to the screams of their juvenile associates than to the screams of other juveniles (Moscovice et al. 2009). Mothers and infants may find a male friend, even of low rank, a more reliable protector compared to a high-ranking male who is more likely to invest in future mating and consort. In fact, a consorting male often spends more time in the periphery of the group and far from the proximity of infants (unpublished data). However, these infant-initiated affiliations towards adult males may simply be a by-product of mothers' relationships with these males. In fact, in chacma baboons, mothers are usually responsible for these male-female partnerships (Palombit et al.

1997; Huchard et al. 2010). If this is also the case in crested macaques, infants may merely copy their mother's preference for specific interaction partners.

We also found that infants are more likely to affiliate with males when the mother is absent. This might, in the first place, appear contradictory given that crested macaque mothers are considered to have a high degree of permissiveness when group members interact with their infants (Thierry et al. 2000a). Therefore, the presence of the mother should not impede the infant's affiliations towards males. Several reasons may explain our finding. First, the mother is the primary bonding partner for an infant (Broad et al. 2006), and thus when the mother is absent, the infant will have more occasions to engage with other group members, particularly a close-by male friend of the mother. Second, infants' motor skills increase with age (included here as a control variable), along with the steady decrease of the mother's presence in the infant's proximity. Thus, infants' affiliations with adult males, when the mother is not present, might be a by-product of their increased motor independence. Third, when mothers are absent infants may alternatively seek the proximity of an adult male for potential protection (Borries et al. 1999) or greater access to resources (Huchard et al. 2013).

Surprisingly, and in contrast to our prediction, paternity had no effect on infants' affiliations directed towards adult males. Previous studies discussed several explanations for the absence of kin effects (e.g. *Gorilla beringei beringei*, Rosenbaum et al. 2015): either the infants do not recognize their father, or infants recognize their father but do not benefit from affiliating with him (cf. Mateo 2002). In fact, it has been proposed that the display of a strong father-offspring relationship or phenotypic similarity may prompt infanticide attacks from other males in the group (Johnstone 1997; Pagel 1997; Mateo 2002). However, the fact that infants prefer to affiliate with high-ranking males or mother's low-ranking friends, especially in mother's absence, suggests that infants are under pressure to secure their survival by bonding with a strong or a close-by protector, regardless of whether they are the father or not. As an alternative, but mutually not exclusive, explanation, our finding may indicate that infants try to affiliate with the most likely father or at least with an individual who most likely assumes to be their father (as proposed in Rosenbaum et al. 2015). Nevertheless, the mismatch in paternity by both offspring and fathers remains to be addressed in more detail in future research.

II/ Male model

In contrast to infants, adult males' affiliative behavior towards infants did not decrease but increased in the presence of the mother. In addition, males in a strong affiliative relationship with the mother affiliated more often with her infant than other infants. Both of these results provide support for the assumption that crested macaque males may use the "care-then-mate" strategy (Ménard et al. 2001) to increase their future reproductive success. In fact, if adult males try to increase their future reproductive success through caring for an unrelated infant, we expect to observe an increase in male affiliations towards an infant when its mother is present (Ménard et al. 2001, this study) as well as an increase in affiliations between the male and the mother (Smuts 1985, this study). However, it remains unclear from the available data of this study whether the unrelated care-takers actually had an increase of future mating and reproductive success with the mother. Hence, future studies including data on the consecutive mating and breeding success are needed to confirm this strategy in more detail. As an alternative, male affiliative behaviors towards infants, consisting mainly of socio-positive approaches, may be a by-product of the males approaching and affiliating with the mother, rather than targeting the infant, as mothers may represent a more valuable social partner for males. In fact, given that infants are not often in proximity of their mother, the results that male affiliate with infants more when the mother is present seems to corroborate that males may target mothers rather than their infants. Thus future studies should investigate male affiliations towards lactating mother with either a dependent or independent infant, in order to disentangle whether the males direct their affiliations towards the infant or its mother.

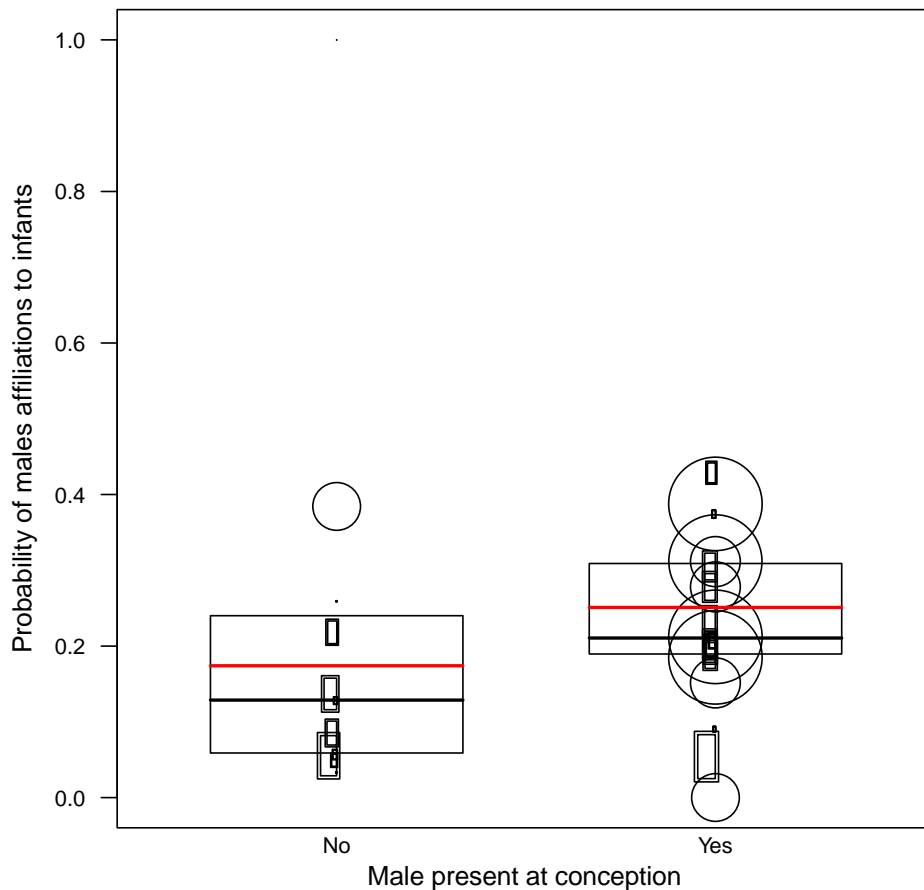


Figure 3.2. Influence of male presence at infant conception on the probability of males to affiliate with an infant. The boxes represent the first to the third quartile of observed values, solid vertical lines in the boxes show the median, and red vertical lines in the boxes show the values fitted by the model. The size of the circles is proportional to the number of male-infant dyads observed

Our results also stress that high-ranking males were more likely to initiate affiliations with infants, regardless of the mother presence. High-ranking males in crested macaques may interact more with infants as they interact in general more with conspecifics and have more group members in close spatial proximity (Reed et al. 1997). In addition, they may interact more with infants due to their higher paternity likelihood. Interestingly, our results show that adult males present at conception interacted more with an infant than males that were not present, suggesting that males may use this cue to assess their paternity probability (cf. “hedging their bets”, Moscovice et al. 2010). However, in contrast to our prediction, sires in this study do not affiliate more with their offspring. This is surprising, given that preliminary data

suggested that paternity certainty might be high in this species, as high-ranking males are potentially able to monopolize females during the fertile phase of their conceptive cycles (Engelhardt, in revision). As all but one fathers (99.7%) were living in the group at the time of birth and as the majority of fathers (86.7%) were still present when the offspring completed their 1st year of life, it is unlikely that mismatches in father-offspring affiliation are due to absence of genetic fathers (cf. Moscovice et al. 2009). Fathers were even of similar dominance rank compared to the time of conception (unpublished data) which should ensure that male access to infants was not reduced. It is more likely that high-ranking fathers may not spend time caring for their own offspring, but rather trying to increase their mating success, thus maximizing the number of future offspring rather than the survival of present offspring. This should be particularly relevant in this reproductively aseasonal species where there is always at least one cycling female and male tenure can be particularly short (Marty et al. 2015). Shorter alpha male tenure in crested macaques may in fact provoke the lack of paternal care and it is likely that males, independent of paternity, display low levels of investment as they may not be present to provide long-term care in this dynamic social system.

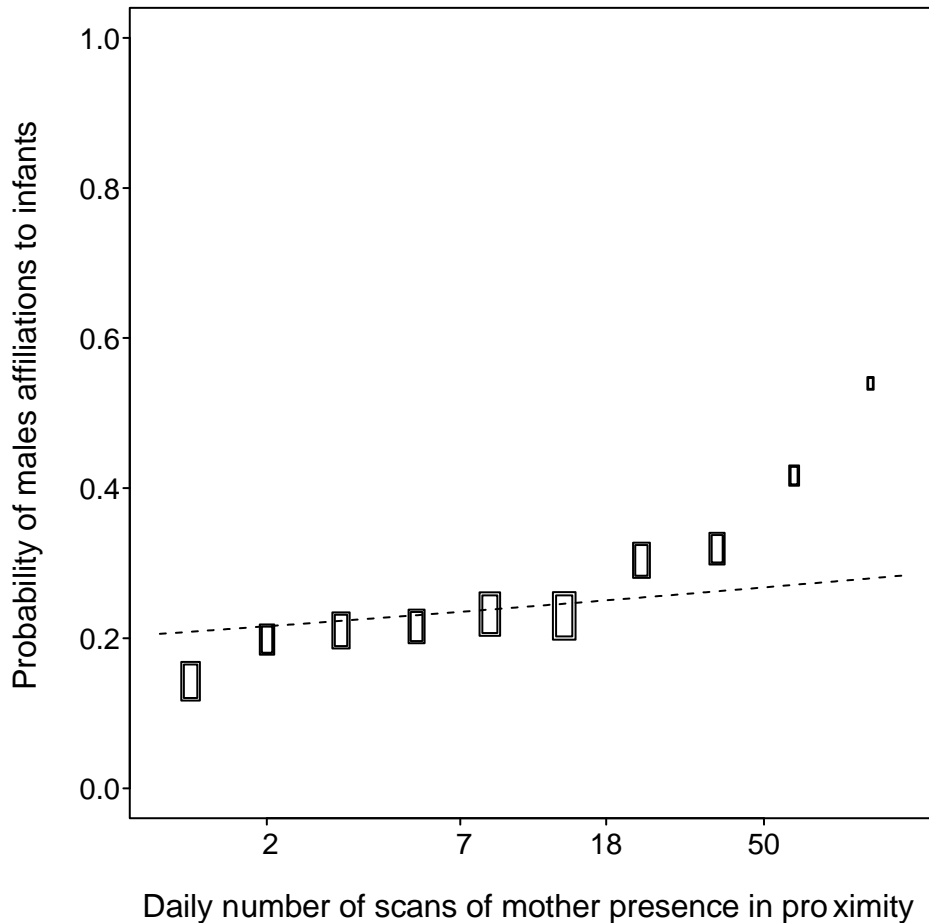


Fig 3.3. Influence of mother spatial presence on the probability of males to affiliate with her infant. The x-axis is a logarithmic scale of mother spatial presence per day per dyad. The dotted line shows the predicted value calculated by the model. The size of the circles is proportional to the number of male-infant dyads observed

Male care in primates has been found to range from low-cost care (e.g., savannah baboons, when fathers side with their own offspring involved in conflicts with another juveniles, Buchan et al. 2003) to high-cost care (e.g., Hanuman langurs, when males protect infants against infanticidal males, Borries et al. 1999). Our results show that, in crested macaques, there may only be low-cost care for infants, generally not provided by the father, but instead by unrelated males. Future studies may investigate the level and strength of investment that males dedicate to infants in primate species. In addition, future studies could specifically investigate the influence of different types of affiliative behavior on males and infants bonds.

Mother rank did not influence male-infant affiliations, since neither infants from high-ranking mothers were more likely to initiate affiliations with adult males, nor did adult males prefer to affiliate with them. This is contrary to other studies that found a positive influence of maternal rank on male-infant affiliations in cercopithecines (Langos et al. 2013; Huchard et al. 2013), but in agreement with a previous study in this population showing no maternal rank effect on infant survival (Kerhoas et al. 2014).

III/ Conclusions

In conclusion, infants affiliate mainly with a male closely bonded with their mothers or a high-ranking male to possibly increase male support during agonistic encounters. Adult male crested macaques did not seem to provide more care to their own offspring than to unrelated infants, however, they probably provided infant care to secure future matings. Females mate promiscuously to confuse paternity, presumably to avoid infanticide, but this may also mean that their infants do not receive protection from the father. This may be the reason why infant mortality is rather high in crested macaques (Kerhoas et al. 2014). Overall, our study revealed for the first time that crested macaques form bonds between adult males and lactating females, which influence the behaviors of infants. Future studies should investigate the strength of the mother-male bond and its influence on infant survival. Furthermore, more data are needed to understand whether the male that develop strong bond with a female is likely to be the father of subsequent infants of this female. Infants have been labeled as “commodities” in social interactions (Henzi and Barrett 2002), however, we observed that infants initiated two thirds of all adult male-infant affiliations, suggesting that infants are the driving force behind adult male-infant relationships and should be the focus of future studies on adult male-infant interactions.

Chapter 4

4 Thesis Conclusion

The results of this thesis provide strong empirical support for the influence of social interactions on direct fitness in crested macaques, a gregarious primate species. In particular, they show that a combination of ecological constraints and social variables, including environmental seasonality, female within-group competition for food sources, and between-group resource defense, has an impact on offspring survival, even at a prenatal stage. In fact, the interplay of resource availability and dominance hierarchy, modulating resource access, is found to directly impact fetal loss, and, to a lesser extent, infant loss. In addition, infant loss was most impaired when a new male took over the top-ranking position in the male hierarchy, revealing that males may be active agents of the high infant mortality in this species. Altogether, these results provide insights on the cost and benefits of sociality in relation to offspring survival.

Furthermore, this thesis shows that male may provide some care to infants. In fact, there are two common social factors that are found to predict affiliations initiated both by infants towards males and by males towards infants: male high rank and mother-male affiliative bond. Infants and males differ mostly in one main aspect: the mother presence in proximity. Infants affiliated more with a male when the mother was not present, while males targeted affiliations towards an infant when the mother was present. In fact, the mother may have been the sole social target of males and affiliations towards infants could be a by-product of males' proximity with the mother. Future studies need to focus on the potential fitness gain of a male close relationship with a mother by measuring, in this species, the following mating success of these males.

Accordingly, these analyses suggest a wide range of male reproductive strategy in crested macaques: infanticide by male, mother-male potential friendship, and care-then-mate strategy. However, we do not observe any paternal care. Thus, in this species, we propose that males' affiliations towards infants may be a male reproductive strategy where males would provide low-cost care to increase future mating opportunities with the mother, rather than high-cost care to increase the infant's survival.

On the other hand, infants have a limited amount of possible survival strategies, but they seem to develop specific relationships with high-ranking males or close/familiar male friends of their mother to secure potential high-cost care. In fact,

it appears clear that infants are the main active agent of male-infant affiliations in this species, as it seems to be the case in several others (Moscovice et al. 2009; Huchard et al. 2013). Infants initiated most of the affiliations, and they targeted a specific male. In addition, infants chose to interact most with a strong male (as high rank males may provide better resource access or protection) or a male in close relationship with their mother. Unfortunately, only few studies focus on infants' behavior when investigating male-infant interactions. This may be due to the general image that infants are not independent or mobile enough to develop social bond on their own before weaning. However, we observed in the field that, after the first few months of life, infants showed a wide behavior repertoire and interacted not at random but with specific individuals. In addition, weaning in this species is a long process, starting at 5 months, and ending at about one year of age. Throughout this time, infants developed rapidly their independence physically and socially. The social relationships they develop during this period may be key to their development and survival. Thus, future studies should concentrate on understanding infants' behavioral choice, as infancy is one of the most critical life stages in regard to survival.

In addition, an important goal of this thesis is to highlight the existence of infant bonds with specific males. It is necessary to further investigate whether those specific bonds are enduring beyond infancy and whether they serve any fitness benefits to the infant and/or the male. Further studies may investigate the reaction of the specific male when the infant is under attack to measure the potential benefits of these bonds for the infant, as observed in other species (Palombit et al. 1997; Moscovice et al. 2009). Finally, additional research could focus on the time budget infants spend on male affiliations in their overall social development.

In conclusion, the results of this thesis highlight the importance of a multivariate analysis, since interplay of social and environmental factors significantly influenced offspring survival and male-infant affiliations. Taken together, the results of this thesis provide us a detailed overview of how sociality could influence individuals' fitness in crested macaques, specifically, adult males' and infants' fitness. It specifically reveals that males in this species use diverse, and non-mutually exclusive, male reproductive strategies. Finally, infants are the main actors of male-infant affiliations, showing a potential survival strategy developed at an early age.

Appendices

Appendix A

Supplementary figure and tables for Chapter 2

Table A1. Demographic composition of the groups studied, social parameters and foetus/infant loss. The average of male hierarchy instability is calculated over all offspring intervals.

	Study groups		
	R1	R2	PB
Study period (in months)	58	58	36
Number of adult males	6-11	3-7	4-8
Number of adult females	18-24	13-21	15-18
Number of study females	23	20	17
Number of conceptions	39	37	23
Number of fetal losses	12	4	2
Number of births	31	38	9
Number of infant losses	5	12	0
Number of male immigrations	23	6	14
Number of intergroup encounters	459	125	142
Number of alpha-male takeovers	4	2	2
Male hierarchy instability index*	0.003	0.009	0.012

* (cf. Neumann et al. 2011)

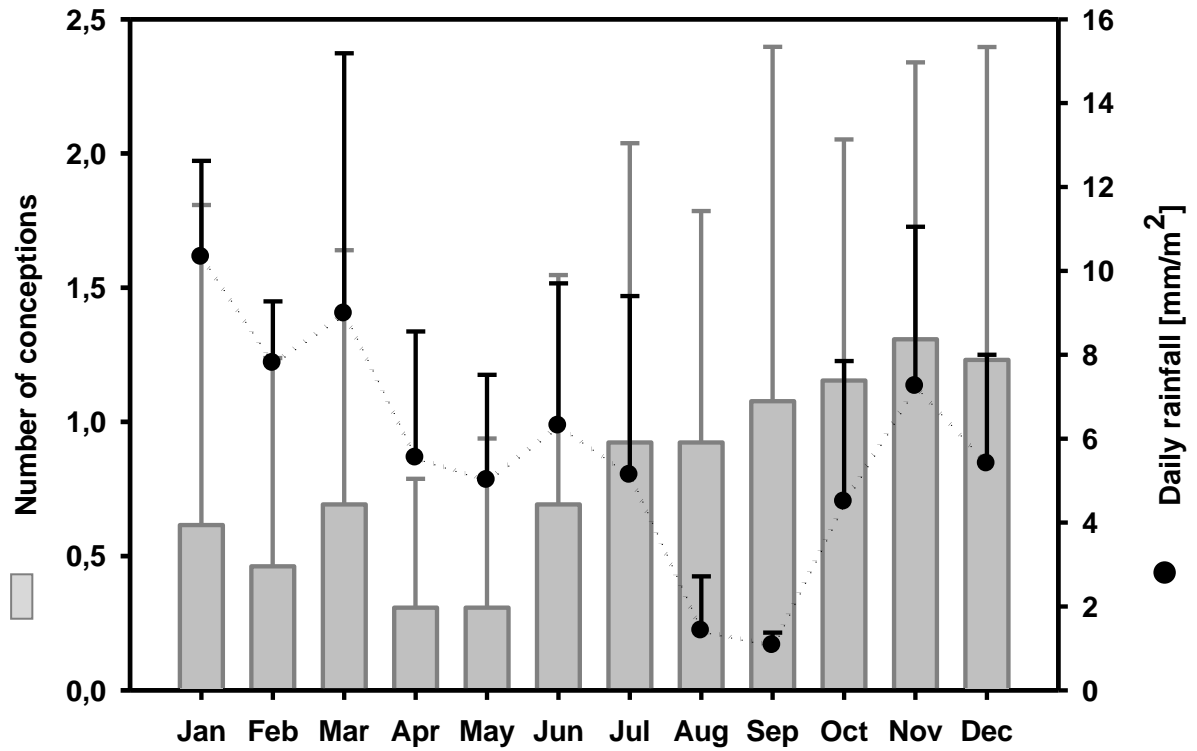


Figure A1. Distribution of conceptions (grey bars; monthly mean across all groups and years) and rainfall (black circles; monthly mean across all years with no offset) over the year. There is a significant negative correlation between monthly mean rainfall and monthly mean number of conceptions (rainfall: $r=-0.769$, $P=0.003$; Pearson's Correlation Coefficient).

Table A2. Group membership, identity of the dead/disappeared infant, year and circumstances of infant death/disappearance. The variable “Wounds” describes whether an open injury was observed on the infant’s dead body (“Yes/No”), while “Unknown” describes cases where the infant’s body was never found, thus presence of wounds is unknown.

Group	Infant	Female	Year	Wounds	Comment
R1	US1	US	2006	Yes	Dead body found with several cuts
R1	GS2	GS	2009	Unknown	
R1	JS2	JS	2009	Unknown	
R1	WS1	WS	2010	Yes	Wounds on forehead and face
R1	ZS1	ZS	2010	Unknown	Mother disappeared as well
R2	LD1	LD	2006	Yes	
R2	MD2	MD	2007	Yes	Injured on hindquarters during an intergroup encounter
R2	SD1	SD	2007	Yes	Injured on head and one leg
R2	UD1	UD	2007	Unknown	
R2	UD2	UD	2008	Unknown	Disappeared after an intergroup encounter
R2	YD2	YD	2008	Yes	Deep injury in the back
R2	GD1	GD	2008	Yes	Injured on head during intergroup encounter
R2	TD2	TD	2009	No	Big bruise on thorax, no open wounds
R2	GD2	GD	2009	Unknown	Disappeared with another infant
R2	LD4	LD	2009	Unknown	Mother disappeared at the same time
R2	TD3	TD	2010	Unknown	
R2	UD4	UD	2010	Unknown	

Appendix B

Supplementary methods and tables for Chapter 3

Table B1. Variables included in the two GLMM analyses on male-infant affiliations.

Variables	Model tested	Variable type:	Description (all parameters were calculated daily)
<u>Response variables:</u>			
Infant affiliations towards a male	Infant	categorical (0/1)	
Male affiliations towards an infant	Male	categorical (0/1)	
<u>Predicting variables:</u>			
Paternity	Infant & Male	categorical (yes/no)	Based on genetic analysis
Male rank	Infant & Male	continuous (0 to 1.0)	Elo ratings of adult males' hierarchy (rating of 1 is the highest)
Male presence at conception	Male	categorical (yes/no)	Male presence in the group during the swelling period of the infant's conception
Mother and male friendship	Infant & Male	continuous (0 to 0.17)	Proportion of affiliations when both the male and the mother were in the infant's proximity
Mother rank	Infant & Male	continuous (0 to 1.0)	Elo ratings of adult females' hierarchy (rating of 1 is the highest)
Mother presence	Infant & Male	discrete (0-96)	Number of scans when the mother is in proximity of her infant
<u>Control variables:</u>			
Number of males	Infant & Male	discrete (3-17)	Number of adult males in the group
Infant gender	Infant & Male	categorical (female/male)	
Infant age	Infant & Male	discrete (0-366)	infant age in days
Seasonality cosine	Infant & Male	continuous (-1.0 to 1.0)	cosine of date to account for food quantity and availability
Seasonality sine	Infant & Male	continuous (-1.0 to 1.0)	sine of date to account for food quantity and availability
Infant autocorrelation terms	Infant & Male	fixed	to account for temporal interdependence of the response
Male autocorrelation terms	Infant & Male	fixed	to account for temporal interdependence of the response
Male tenure ¹	Infant & Male	discrete (1-1549)	number of days since the beginning of the study
<u>Offset variable:</u>			
Observation time	Infant & Male	discrete (1-128)	Number of scans recorded on focal infants by day
<u>Random variables:</u>			
Group identity	Infant & Male	categorical (R1/R2/PB)	name of the group of the focal infant
Male identity	Infant & Male	categorical (total of 27)	name of the males present in the group on a given day
Infant identity	Infant & Male	categorical (total of 30)	name of the infants present in the group on a given day
Dyad identity	Infant & Male	categorical (total of 217)	name of both males and infants
Day	Infant & Male	categorical (total of 452)	name of the days of observation
<u>Interactions:</u>			
Paternity X Mother presence	Infant & Male		
Male rank X Mother presence	Infant & Male		
Mother rank X Mother presence	Infant		
Infant gender X Mother presence	Infant		

¹ Originally male tenure was not in the model, but when plotting we discovered that male tenure was an important component.

Random slopes

We included several random slopes in the model, i.e. for each random effect we considered the following the random slopes term considered: Within group identity, we considered paternity, male rank, mother rank, mother presence, mother-male affiliations, gender, two-way interaction Male rank**Mother presence*, two-way interaction Paternity**Mother presence*, two-way interaction Mother-male affiliation, three-way Male rank**Paternity***Mother presence*. For infant identity, we considered male rank, mother

Appendix B

presence, mother-male affiliations, two-way interaction Male rank*Mother presence. For male identity, we considered only mother presence.

Table B2. Results of GLMM analyses of the infant model: the significant factors influencing the affiliations of infants toward males are marked in bold, including the control variables marked in italics (values not shown for the variables comprised by a significant higher interaction)

Fixed effects:	Estimate	SE	Df	LRT χ^2	P of LRT
(Intercept)	-5.32	0.2			
Infant AC term	0.4	0.02	1	442.66	<0.001
Male AC term	0.23	0.02	1	140.53	<0.001
Paternity	0.13	0.12	1	1.11	0.292
Mother rank ⁽¹⁾	0.03	0.02	1	1.56	0.212
Mother presence	-0.17	0.05	1	5.27	<0.022
Male rank* Mother-male affiliation	-0.07	0.03	1	4.36	0.037
<i>Infant gender</i>	-0.02	0.05	1	0.12	0.734
<i>Number of males</i>	0.01	0.03	1	0.06	0.811
<i>Infant age</i>	0.46	0.03	1	169.72	<0.001
<i>Male tenure</i>	0.34	0.06	1	25.91	<0.001
<i>cosine(day)</i>	0.11	0.03	2	15.31	<0.001
<i>sine(day)</i>	-0.09	0.04			<0.001

⁽¹⁾: larger values indicate larger rank

Table B3. Results of GLMM analyses of the male model: the significant factors influencing the affiliations of males toward infants are marked in bold, including the control variables in italics.

Fixed effects:	Estimate	SE	Df	LRT χ^2	p
(Intercept)	-5.47	0.18			
Infant AC term	0.18	0.02	1	89.27	<0.001
Male AC term	0.19	0.02	1	90.01	<0.001
Paternity	-0.08	0.1	1	0.53	0.465
Mother rank ⁽¹⁾	-0.01	0.02	1	0.15	0.696
Mother presence	0.1	0.03	1	4.43	0.035
Male rank⁽¹⁾	0.14	0.06	1	3.15	0.015
Male presence at conception	0.35	0.14	1	6.02	0.014
Mother-male affiliation	0.07	0.03	1	5.01	0.025
<i>Infant gender</i>	0.03	0.05	1	0.34	0.559
<i>Numbers of males</i>	-0.09	0.03	1	5.90	0.015
<i>Infant age</i>	-0.03	0.03	1	1.44	0.230
<i>Male tenure</i>	0.25	0.05	1	17.58	<0.001
<i>Cosine day</i>	-0.02	0.04	2	0.21	0.899
<i>Sine day</i>	0.00	0.04			

⁽¹⁾: larger values indicate larger rank

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Contributions of co-authors

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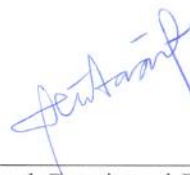
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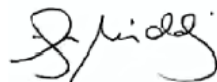


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Male-infant interactions in wild crested black macaques, *Macaca nigra*

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Titel: **Mother-male bond, but not paternity, influences male-infant affiliation in wild crested macaques**

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Anteil Daphne Kerhoas (first author):

- Project idea and conceptualization
- Data collection
- Data processing and analysis
- Programming
- Results interpretation
- Manuscript writing

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- Data processing and analysis
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- Project infrastructure and logistics

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- Project idea and conceptualization
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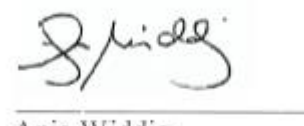
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since 2009 PhD student at the German Primate Center in Goettingen: Male-infant interactions in wild crested black macaques, *Macaca nigra* (Supervisor: Antje Engelhardt)
2005 – 2006 MSc of Ethology at the University of Paris 13, France: “Effect of copulation on pair bonding in monogamous mice, *Mus spicilegus*“ (Supervisor: Bernard Feron & Patrick Gouat)
2000 – 2004 BSc of Biology (Ecology, Zoology & Genetics) at the University of Tours, France
1997 - 2000 High school diploma at Vieljeux Highschool in La Rochelle, France

Work / Field Experience

since 2013 Lecturer in Conservation Science at the Bristol Zoological Society, United Kingdom and supervisor of BSc and MSc thesis

Curriculum vitae

- 2008 - 2010 Field work for PhD thesis, team manager (24 months) and camp manager (6 months) at the Macaca Nigra Project, Indonesia (Supervisor: Anja Widdig & Antje Engelhardt)
- 2006-2007 Research Assistant at the Gashaka Primate Project, Nigeria and Roehampton University, United Kingdom: links between vocalizations and social interactions in Olive baboons (Supervisor: David MacGregor Inglis & Stuart Semple)
- 2004 – 2005 Research assistant at the Monos Projecto, Costa Rica: Social development of wild infant white-headed capuchins (Supervisor: Susan Perry)
- 2004 Undergraduate dissertation project at the Bucknell University, USA: Influence of stress on cognitive capacities of captive squirrel monkeys and lion-tailed macaques (Supervisor: Peter Judge)

Grants

- 2014 Travel grant to the 25th International Primate Society Congress, Hanoi, Vietnam, granted by the “Margot Marsh Foundation“ (2.000\$)
- 2013 Travel grant to the 5th European Federation of Primatology, Antwerp, Belgium, granted by the “Research Academy of Leipzig“ (460€)
- 2013 Travel grant to the 11th International Mammalogical Conference, Belfast, Northern Ireland, granted by the “Research Academy of Leipzig“ (430€)
- 2010 Travel grant to the 23rd International Primate Society Congress, Kyoto, Japan, granted by the “IMPRS School of Human Origins“ (1000€)
- 2005-2006 Merit grant to fund a MSc, granted by the “French Ministry of Education” (5,520€)
- 2003-2004 Scholarship to spend an academic year in an American University, granted by the University of Tours’s Senior Exchange Program (16.000€)

Publications and conference contributions

Journal articles

Daphne Kerhoas, Lars Kulik, Dyah Perwitasari-Farajallah, Muhammad Agil, Antje Engelhardt and Anja Widdig. 2016. "Mother-male bond, but not paternity, influences male-infant affiliation in wild crested macaques." *Behavioral Ecology and Sociobiology* 1-14. doi: [10.1007/s00265-016-2116-0](https://doi.org/10.1007/s00265-016-2116-0)

Daphne Kerhoas, Dyah Perwitasari-Farajallah, Muhammad Agil, Anja Widdig and Antje Engelhardt. 2014. "Social and ecological factors influencing offspring survival in wild macaques." *Behavioral Ecology* 25 (5): 1164-1172. doi: [10.1093/beheco/aru099](https://doi.org/10.1093/beheco/aru099)

Julie Bardet, **Daphne Kerhoas Essens**, Christophe Féron and Patrick Gouat. 2007. "Evaluation of the social bond: a new method tested in *Mus spicilegus*." *Comptes rendus biologies* 330 (11): 837-843. doi: [10.1016/j.crv.2007.08.006](https://doi.org/10.1016/j.crv.2007.08.006)

Conference contributions

Daphne Kerhoas, Alberto Acerbi, Amanda Webber, Christoph Schwitzer. 2015. Enhancing the profile of threatened primates: Impact of 'Top-25' listing on the choice of species for scientific study. Poster at the 27th International Congress of Conservation Biology; Montpellier, France

Daphne Kerhoas, Alberto Acerbi, Amanda Webber, Christoph Schwitzer. 2014. Enhancing the profile of threatened primates: Impact of 'Top 25' listing on the choice of species for scientific study. Talk at the 15th International Primate Society, Hanoi, Vietnam

Publications and conference contributions

Daphne Kerhoas, Antje Engelhardt, Dyah Perwitasari-Farajallah, Anja Widdig. 2013. Male-infant affiliations in wild crested macaques: male and infant perspective. Talk at the 11th International Mammalogical Congress; Belfast, Northern Ireland

Daphne Kerhoas, Dyah Perwitasari-Farajallah, Muhammad Agil, Anja Widdig, Antje Engelhardt. 2013. The interaction of social and ecological parameters on offspring survival in a wild primate. Talk at the 5th European Federation of Primatology; Antwerp, Belgium

Antje Engelhardt, **Daphne Kerhoas**, Dyah Perwitasari-Farajallah, Muhammad Agil, Anja Widdig. 2013 Impact of social and ecological parameters on reproductive success in a wild primate. Talk at the 9th Goettinger Freilandtage; Goettingen, Germany

Daphne Kerhoas, Muhammad Agil, Dyah Perwitasari-Farajallah, Antje Engelhardt, Anja Widdig. 2010. Male-infant social interactions in wild crested macaques (*Macaca nigra*). Talk at the 13th International Primate Society Congress; Kyoto, Japan

Selbstständigkeitserklärung

Hiermit versichere ich, dass ich diese Arbeit selbstständig und nur unter Verwendung der angegebenen Hilfsmittel erstellt habe. Alle wörtlichen und sinngemäßen Zitate aus anderen Werken sind als solche gekennzeichnet. Personen, die an der Erstellung von Teilen der Dissertation beteiligt waren, sind zu Beginn des jeweiligen Kapitels benannt. Der jeweilige Beitrag der beteiligten Personen ist am Ende der Dissertation aufgeführt. Weitere als die jeweils genannten Personen waren an der Erstellung der Arbeit nicht beteiligt. Weiterhin versichere ich, dass die vorgelegte Arbeit in gleicher oder in ähnlicher Form keiner anderen wissenschaftlichen Einrichtung zum Zwecke einer Promotion oder eines anderen Prüfungsverfahrens vorgelegt wurde.

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